Silvics of Whitebark Pine (*Pinus albicaulis*)

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ACKNOWLEDGMENTS

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INTRODUCTION

Whitebark pine (*Pinus* albicaulis Engelm.) is a slow-growing, long-lived tree of the high mountains of southwestern Canada and the Western United States. Whitebark pine is of limited commercial use, but it is valued for watershed protection and esthetics. Its seed crops have become recognized in recent years as an important food source for grizzly bears and other wildlife of the high mountains.

Concern has arisen because in some areas whitebark pine cone crops have diminished as a result of successional replacement and insect and disease epidemics (Amo 1986). Published information on whitebark pine has been sparse. This paper is a review of the literature available in 1981 and has been updated to include some recent ecological findings.

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 drier, inland slope of the Coast and Cascade Ranges. It is entirely 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 90 miles (145 km) east of the nearest stands in the Rocky Mountains across the Great Plains grassland (Thompson and Kuijt 1976).

The coastal and Rocky Mountain distributions lie only 62 miles (100 km) apart at their closest proximily. 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.

Climate

Whitebark pine grows in a cold, windy, snowy, and generally moist climatic zone. In moist mountain ranges, whitebark pine is most abundant on warm, dry exposures. Conversely, in semiarid ranges, it becomes prevalent on
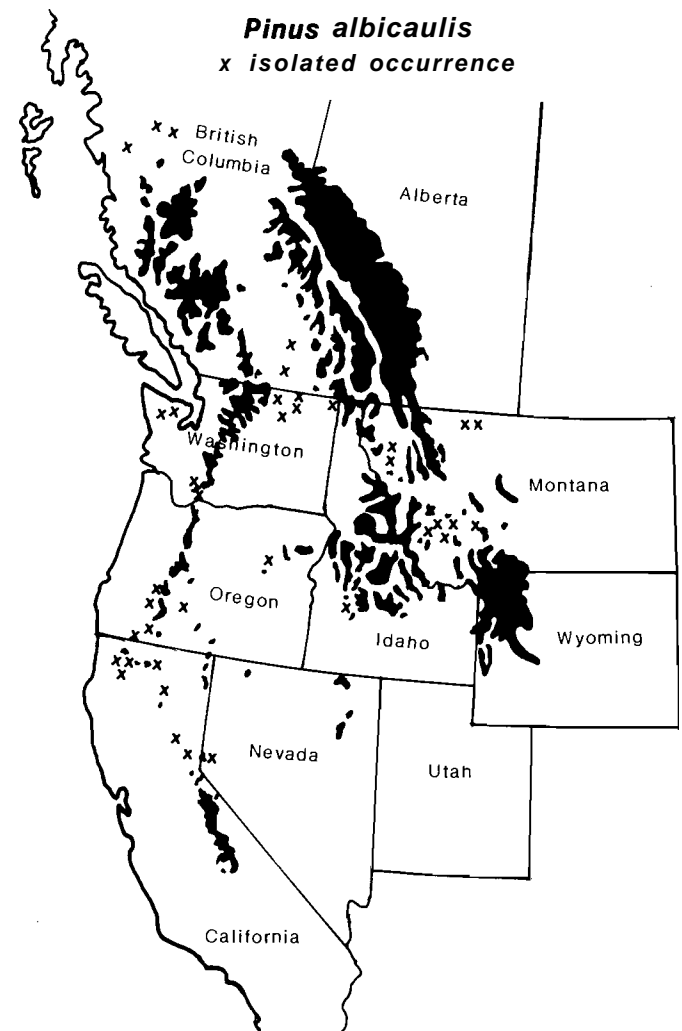

Figure 1 —Natural distribution of whitebark pine.

cool exposures and moist sites. Weather data from several whitebark pine sites in the Inland Northwest suggest the climatic interpretations that follow (Arno 1970; Weaver and Dale 1974). Summers are short and cool with mean July temperatures ranging from 55 to 59 °F (13 to 15 °C) in the whitebark pine forest and from 50 to 54 °F (10 to 12 °C) in the adjacent timberline zone. A cool growing season, as defined by mean temperatures of over 42 °F (5.5 °C) (Baker 1944), lasts about 90 to 110 days in the whitebark pine forest, but light frosts and snowfalls sometimes occur even in midsummer. The hottest summer days reach temperatures of 79 to 86 °F (26 to 30 °C). January mean temperatures range from about 15 °F (–9 °C) in Montana to about 23 °F (–5 °C) in the Cascades and Sierra Nevada. Long-term record low temperatures in Montana and Wyoming stands are probably –40 to –58 °F (–40 to –50 °C).

Mean annual precipitation for most stands where whitebark pine is a major component probably is between 24 and 72 inches (600 and 1,800 mm). 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 (Arno 1970). 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 a maximum depth, ranging from about 24 to 50 inches (60 to 125 cm) in stands east of the Continental Divide and in other semiarid areas, to 100 to 120 inches (250 to 300 cm) in the relatively moist whitebark pine-subalpine fir stands of the Cascades and inland-maritime mountains. Most stands probably have mean annual snowfalls between 180 and 500 inches (460 and 1,270 cm). Whitebark pine also grows in stunted or krummholz (shrublike) form on windswept ridgetops where little snow accumulates.

Strong winds, thunderstorms, and severe blizzards are common to whitebark pine habitats. Wind gusts of hurricane velocity in the tree crowns (more than 73 mi/h or 117 km/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 (Mehringer and others 1977). 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 temperatures 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 (USDA SCS 1975). 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 (Nimlos 1963). All of these are young soils, showing less leaching, weathering, and horizon development than Spodosols, although they are quite 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 (Pfister and others 1977). Data on nutrient availability in these soils have been provided (Weaver and Dale 1974).

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). 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 (Pfister and others 1977) and Idaho (Steele and others 1983) stands, but in Alberta average values are 7.8 to 8 (Baig 1972). These soils would evidently be classified as Typic Cryoborolls within the order Mollisols. Also, in some of the same areas soils that have a dark surface but a low level of 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 or in cirque basins, where subalpine fir, Engelmann spruce (Picea engelmannii), mountain hemlock, or subalpine 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 5,200 ft (1,580 m) elevation (McAvoy 1931). 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 5,800 and 7,000 ft (1,170 and 2,130 m). East of the Cascade crest it becomes abundant within both the subalpine forest and the timberline zone. For instance, it is common between 5,300 and 8,000 ft (1,620 and 2,440 m) in central Washington's Stuart Range, generally forming krummholz above 7,000 ft (2,130 m) (Arno and Hammerly 1984). The lowest reported natural stand of whitebark pine throughout its

range is at 3,600 ft (1,100 m) near Government Camp on the southwest slope of Mount Hood in Oregon (Franklin 1966).

Whitebark pine becomes a major component of high-elevation forests in the Cascades of southern Oregon and northern California, growing between 8,000 and 9,500 ft (2,440 and 2,900 m) on Mount Shasta. In the central and southern Sierra Nevada it is found between 10,000 and 11,500 ft (3,050 and 3,510 m), but occasionally reaches 12,000 ft (3,660 m) as krummholz cushions (Arno and Hammerly 1984).

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, 6,500 to 7,500 ft (1,980 to 2,290 m). 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 5,900 and 8,200 ft (1,800 and 2,500 m) in north-western Montana and 7,000 and 9,300 ft (2,130 and 2,830 m) in west-central Montana. In western Wyoming, it is abundant at 8,000 to 10,500 ft (2,440 to 3,200 m).

Associated Forest Cover

Whitebark pine is most frequently found growing with other high mountain conifers, although pure whitebark pine stands are common in relatively dry mountain ranges. The forest cover type Whitebark Pine (Society of American Foresters Type 208) (Society of American Foresters 1980) 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 con*torta var. rnurrayana), western white pine (P. rnonticola), and locally, foxtail (P. balfouriana) and limber (P. *flexilis*) pines.

In the drier 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 (Critchfield and Allenbaugh 1969).

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 lasiocarpa habitat types (Daubenmire and Daubenmire 1968; Pfister and others 1977). Whitebark pine is also a climax species in other habitat types, mostly on dry sites, in Montana, central Idaho, and western Wyoming, and in Alberta (Baig 1972; Steele and others 1983; Steele and others 1981; Weaver and Dale 1974). *Pinus albicaulis*/Vaccinium scopariurn 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 (Forcella 1978; Forcella and Weaver 1977; Weaver and Dale 1974).

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* scopariurn habitat types (Pfister and others 1977). 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 in comparison with competing fir and spruce (Arno 1986).

Principal undergrowth species in Rocky Mountain and northern Cascade stands include grouse whortleberry (Vaccinium scopariurn), mountain arnica (Arnica *latifo*lia), red mountain heath (*Phyllodoce* ernpetriforrnis), rustyleaf menziesia (Menziesia *ferruginea*), smooth woodrush (Luzula hitchcockii), beargrass (Xerophyllurn *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* pensyluanica) and Wheeler bluegrass (*Poa* neruosa) (Hopkins 1979). Undergrowth is sparse in Sierra Nevada stands. Common juniper (Juniperus cornrnunis) is a major undergrowth plant in Alberta stands (Baig 1972).

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. Whitebark pine flowers are receptive, and pollen is shed during the first half of July, but at some midelevation 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 self-pollination, which is less successful in pines than cross-pollination.

The female or seed cones ripen by early September of the second year (USDA FS 1974). Although there are no good exterior signs of cone and seed ripeness, the cones become somewhat loose 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

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produced more frequently in the southern parts of whitebark pine's distribution (Bailey 1975). In a Sierra Nevada study area, whitebark pine cone crops were moderate to heavy in each of 4 years, 1973 to 1976 (Tomback 1978). A study of 29 whitebark pine stands in the Northern Rockies found that cone production averaged about 6,000 per acre (14,000 per hectare) over an 8-year period (Weaver and Forcella 1986). Seeds number from 2,200 to 3,000/lb (4,850 to 6,600/kg) (USDA FS 1974).

The large, heavy, wingless seeds are borne in a dense, fleshy, egg-shaped cone usually 2 to 3 inches (5 to 8 cm) long. This cone is unusual among North American pines in that it evidently remains closed (indehiscent) after ripening rather than spreading its scales to release seeds (Tomback 1981). If the cone falls to the ground, it disintegrates rapidly by decay and depredations by animals. Observations in southwestern Alberta indicate that groups of whitebark pine seedlings often appear around the rotting residue of cones (Day 1967).

In most stands, however, only a small fraction of the cones are allowed to fall in this manner. Instead, Clark's nutcrackers and red squirrels attack the ripening cones in the tree tops during August, September, and October. As a result of cone predation, it is quite 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 (Bailey 1975).

Clark's nutcrackers apparently have an essential role in planting whitebark pine and limber pine seeds (Hutchings and Lanner 1982; Lanner 1980; Lanner and Vander Wall 1980; Tomback 1978). Nutcrackers can carry as many as 150 whitebark pine seeds in their sublingual pouch, and they cache groups of one to five seeds in the soil at a depth of 1 inch (2 to 3 cm), suitable for germination. Nutcrackers cached an estimated 13,600 limber pine seeds per acre (33,600/hectare) in one open burned area during one summer. Whitebark pine seeds sustain these birds much of the year, but a large proportion of the seed caches go unrecovered.

Evidence indicates that seed planting by Clark's nutcrackers facilitates the regeneration and spread of whitebark pine. Despite its heavy wingless seed, this species often regenerates promptly on burned or clearcut areas where the seed source is locally absent. Moreover, whitebark pine seedlings in open areas often arise together in tight clumps of two to five. The species has become established atop a young geologic island — Wizard Island in Crater Lake, OR (Jackson and Faller 1973)—where seed dispersal by birds would have been necessary. Lone whitebark pine trees and saplings grow along alpine ridges often a few miles from the nearest possible seed source (Arno and Hammerly 1984). 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 lower elevation stands in autumn bringing whitebark pine seeds with them (Arno and Hammerly 1984; Tomback 1978).

Various mammals also transport and cache whitebark pine seeds. Red squirrels harvest large quantities of whitebark pine cones and store them in rotten logs and in the ground. Black bears 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 three to 176 seeds per cache have been found (Kendall 1981).

Some seeds probably fall onto favorable seedbeds beneath or near the parent trees. Seeds may occasionally be carried by snow avalanches into lower elevations. Because of periodic disturbances and cold air drainage in avalanche chutes, whitebark pine saplings often occupy sites at relatively low elevations.

The poor germination rate of whitebark pine seed is apparently related to the development and condition of the embryo and to seedcoat factors. Seeds from three Canadian sources germinated poorly, despite a variety of seedcoat scarification techniques with and without cold stratification (Pitel and Wang 1980). The best results were obtained when a small cut was made in the heavy seedcoat and this was placed adjacent to germination paper to facilitate water uptake. The seedcoat is evidently a major cause of delayed regeneration or seed dormancy. Another factor explaining the relatively 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 seedcoat (Pitel 1981). Stratification for 60 days plus clipping resulted in 91 percent germination. Cold stratification for at least 150 days followed by cracking of the seedcoat has been fairly successful, resulting in 34 percent germination (Hoff 1980).

Seedling Development–Gemination is epigeal (USDA FS 1974). The newly germinated seedlings of whitebark pine are large compared to other mountain conifers. Cotyledons number seven to nine (Hitchcock and others 1969), and while still in the cotyledon stage, the seedlings are 3 to 4 inches (8 to 10 cm) tall, with a 5- to 7-inch (13- to 18-cm) taproot (Day 1967). Whitebark pine germinants and seedlings are often common in burned or other disturbed areas. Germinants can also be found in the midst of alpine tundra vegetation.

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 limit of tree growth, whitebark pine forms islands of shrublike growth (flagged krummholz and cushion krummholz, see fig. 5), similar in general appearance to the layered krummholz of fir and spruce described by Marr (1977). A recent inspection of whitebark pine krummholz in the Montana Bitterroot Range confirmed that layering occurs (Arno 1981). 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 stock plants of either whitebark pine or western white pine. The grafts

grow much faster when the stock plant is western white pine (Johnson 1981).

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 has been of little interest for commercial timber production. Occasionally old-growth whitebark pine makes up a modest proportion of the timber harvested in moist, high-elevation stands.

In Montana. the best sites for whitebark pine timber growth are generally in the *Abies lasiocarpa/Luzula hitchcockii* habitat type, *Menziesia ferruginea* phase (Pfister and others 1977). Although whitebark pines of good form and moderately large size (dominant trees 20 to 30 inches [50 to 75 cm] in d.b.h. and 70 to 100 ft [21 to 30 m] tall at 250 to 300 years of age) sometimes develop on these sites, associated Engelmann spruce grows larger and is the primary object of management. In some commercial forest sites between 5,000 and 6,000 ft (1,520 and 1,830 m) in southwestern Alberta, whitebark pine grows larger than associated lodgepole pine and spruce (Day 1967). In south-central Oregon, annual yields of merchantable timber in a lodgepole pine-whitebark pine type were estimated to be about 29 ft³/acre (2.0 m³/ha) (Hopkins 1979).

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 (Kasper and Szabo 1970) but is graded lower largely because of its slightly darker appearance (Wilson 1981).

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 biomass and productivity in some of the pure, high-elevation whitebark pine stands—*Pinus albicaulis Naccinium scoparium* habitat type—suggests that annual yields of merchantable timber are very low, about 10 to 20 ft³/acre (0.7 to 1.4 m³/ha) (Forcella and Weaver 1977; Pfister and others 1977; Weaver and Dale 1974).

On favorable sites near the forest line this species develops into a large, single-trunk tree commonly 35 to 65 ft (11 to 20 m) tall (fig. 2) and has a life span of 500 years or
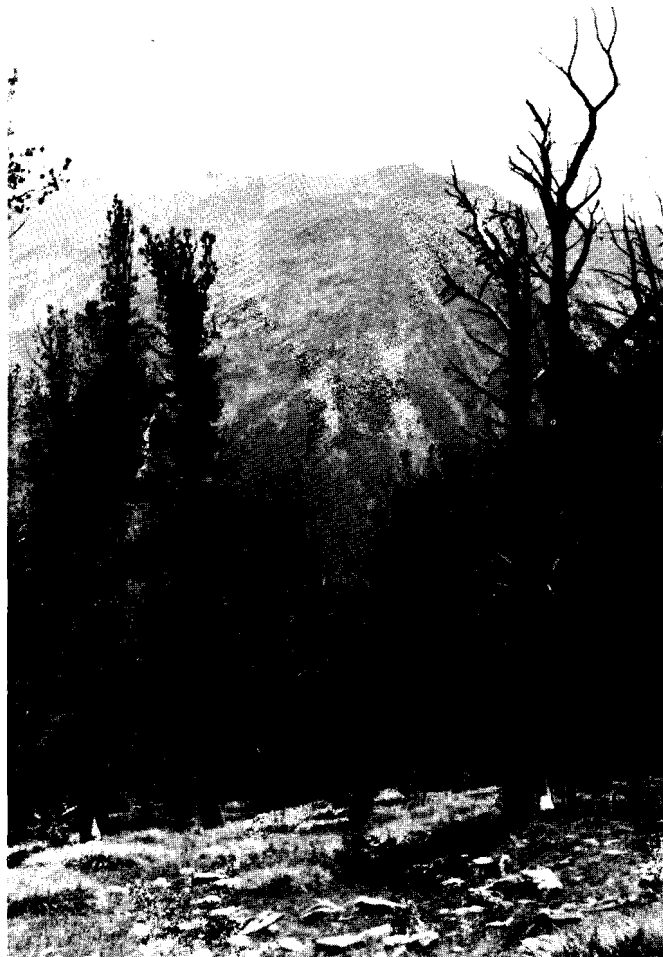

Figure 2—Pure stand of mature whitebark pine on a south-facing slope at 8,400 ft (2,560 m) elevation in western Montana.

Figure 3—Upswept branch-trunks of an ancient whitebark pine in the timberline zone.

Figure 4—Multistemmed growth form of whitebark pine at tree line in the northeastern part of the Olympic Mountains, **WA.**

more. The oldest individuals in 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 105 inches (267 cm) in **d.b.h.** and 69 ft (21 m) tall (**AFA** 1986). Upwards through the timberline zone, whitebark pine becomes progressively shorter and assumes multistemmed growth forms (fig. 4) evidently arising from the germination of nutcracker seed caches (**Furnier** and others 1987; Linhart and **Tomback** 1985).

At **its** upper limits, whitebark pine is reduced to **shrub-**like growth forms (fig. 5) (Clausen 1965). Such **krumm-**holz 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 (**Tranquillini** 1979). As a result, shoots are easily killed by **frost** or by heating and desiccation on 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. Wind-thrown whitebark pines growing on moraines in Wyoming show pancake-like root systems only 16 inches (40 cm) deep (Lanner 1981). Such 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 (Baker **1949),** recent observers (Day 1967; **Pfister** and others 1977; Steele and others 1983) 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 subalpine larch. Whitebark pine should, therefore, be classed as intermediate in tolerance to shade.

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Figure 5—Krummholz whitebark pine at 10,600-ft (3,230-m)Granite Pass, Sequoia-Kings Canyon National Park in the California Sierra Nevada. The krummholz 'cushion" is protected by winter snowpack; the wind-battered upper branches are called "flags."

Whitebark pine cannot become a climax forest dominant in moist, wind-sheltered sites where its tolerant associates are capable of forming a closed stand. But it can become a long-lived **seral** dominant on these sites as a result of stand replacement by fire, snow avalanche, and other major **disturbances.**

On a broad range of dry, **wind-exposed** sites, whitebark pine is a climax or near-climax species that persists in**definitely** 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 (**Franklin** and **Dyrness** 1973). In dry areas of Wyoming's Wind River and in south-central Oregon, whitebark pine forms a coclimax **with** lodgepole pine in dense subalpine forest stands (**Hopkins** 1979; Steele and others 1983).

Whitebark pine often regenerates following wildfire and after **clearcutting (with** or without site preparation) on southern exposures or ridgetops. **Observations** of **white**bark pine regeneration in natural stands suggest that this species could be perpetuated on relatively dry sites under a **variety** of even-aged or uneven-aged silvicultural systems. To establish whitebark pine regeneration on moist sites, appreciable stand opening and light, localized site preparation would probably be necessary. Watershed values (and often esthetic values) are very high on these sites, however, and use of heavy equipment could be very **damaging.** Wind throw and wind breakage is a danger to residual trees, especially **spruce** and fir, in **partial** cuttings. Whitebark pine can be regenerated by outplanting seedlings or seeds in **mineral** soil or at the soil-litter interface (**McCaughey** 1988). Such artificial **regeneration** might allow the establishment of whitebark pine on sites where it has been scarce because of lack of seed caching by the Clark's nutcracker.

Damaging Agents — Mountain pine beetle (*Dendroc-*tonus *ponderosae*) is by far the most damaging insect in mature stands of whitebark pine. A large proportion of the mature whitebark pine in the Northern Rockies was **killed** by this insect between 1909 and 1940 (**Arno** 1970; Ciesla and **Furniss** 1975; **Furniss** and **Carolin** 1977). 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

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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* tabulanu), 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 (Furniss and Carolin 1977). Two species of Pityophthorus (*P. aquilonius* and P. collinus) have been collected from whitebark pine (Bright 1968). The ponderosa pine cone beetle (*Conophthorus* ponderosae) infests cones of whitebark pine (Wood 1981).

The principal disease is the introduced white pine blister rust (caused by Cronartium *ribicola*). 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, which are the rust's alternate host) 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 of the pine host (Bedwell and Childs 1943). 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. Resistance of whitebark pine is discussed under "genetics" in this paper.

Several other diseases infect whitebark pine, generally with minor consequences (Hepting 1971; Hiratsuka and Funk 1976; Smith 1956). These diseases are stem infections that produce cankers (some very similar to blister rust), such as *Atropellis* pinicola, A. piniphila, Dasyscypha pini, and Gremmeniella abietina; a wood rot organism, Phellinus pini; several root and butt rots caused by Heterobasidion *annosum,* Phaeolus *schwein-*itzii, and *Poria subacida;* and several needle cast fungi including *Lophodermium nitens,* L. pinastri, Bifusella saccata, and B. linearis. When foliage is covered by snow for long periods, a snow mold, Neopeckia coulteri, appears (Hepting 1971; Hiratsuka and Funk 1976; Smith 1956).

The dwarf mistletoes (*Arceuthobium* spp.) cause severe local mortality in whitebark pine. The most widespread species is the limber pine dwarf mistletoe (A. *cyanocar-*pum). 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 (Hawksworth and Wiens 1972).

In addition to these parasitic organisms, several harmless saprophytes grow on whitebark pine: Dasyscypha agassizii on dead bark and cankers of blister rust, D. arida, Tympanis pinastri, and Phoma harknessii on twigs (Hepting 1971). *Cenococcum* graniforme has been identified as an ectotrophic mycorrhizal fungus of whitebark pine (Trappe 1962).

Wildfire is an important vegetation recycling force in whitebark pine stands, although long intervals (mean intervals from 50 to 300 years or more depending on the site) usually occur between fires in a given grove (Arno 1980). 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 forest zones. 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 sizable stands (Arno 1980). 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, windexposed sites, regeneration of whitebark pine (often the pioneer species) may require several decades.

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. Potential use for timber on a sustained yield basis is very limited in most areas.

Whitebark pine seeds are a principal year-round food for the Clark's nutcracker and red squirrels. Seeds are an important, highly nutritious food source for many other seed-eating birds and small mammals, as well as for black bears and grizzly bears (Kendall 1981; Mealey 1980).

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 have occasionally been used as a secondary food source by Native Americans (Malouf 1969).

Whitebark pine helps to stabilize snow, soil, and rocks on steep terrain and has potential for use in land reclamation projects at high elevation (Pitel and Wang 1980). It also provides shelter and fuel for hikers and campers and is a very picturesque mountain tree.

GENETICS

Most of the wide phenotypic variation in whitebark pine is apparently the result of differences in site and climate. Nevertheless, at least two distinct forms are recognized—the alpine and subalpine forms, one a prostrate shrub and the other a fairly typical upright tree (Clausen 1965).

Determination of whether or not these are genetic races will have to await genetic tests. Enzyme studies suggested that high-elevation forms of Engelmann spruce and subalpine fir do have a genetic basis (Grant and Mitton 1977), 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 (Holzer 1975).

Resistance to white pine blister rust is the most notable phenotypic variation observed in whitebark pine. The species is 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 (Bingham 1972). In stands where mortality has been as high as 80 to 90 percent, however, many individuals have survived and some are free of rust symptoms. Testing, using artificial inoculation methods to expose seedlings from uninfected wild parents, has demonstrated resistance to be genetic (Hoff and others 1980). 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, ID, in 1979 (Hoff 1980). Results of this trial may ultimately help reestablish the species in areas where mortality is high and where the impact of birds and rodents on the remaining seed supply is therefore greater.

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 (Bingham and others 1972). Only the cross with limber pine, from subsection Strobi, offers slight hope (Critchfield 1981). No putative hybrids of whitebark pine have been identified in natural stands.

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Whitebark pine (*Pinus albicaulis*) is a long-lived tree inhabiting the upper subalpine forest and timberline zone on high mountains of Western North America. The species' habitat, life history, growth and yield, mortality factors, special uses, and genetics are described.