Whitebark Pine

Whitebark pine (*Pinus albicaulis* Engelm. pictured above) is a keystone species of the upper subalpine ecosystem throughout the northern Rocky Mountains, Cascade Range, Sierra Nevada and British Columbia Coastal Ranges (Arno and Hoff 1990). It grows at high elevations and establishes in areas with poor soils, high winds and steep slopes where its competitors are disadvantaged. While whitebark pine is of low commercial value due to its inaccessibility and gnarled growth form, it plays a key role in the ecology of the subalpine forest ecosystem. Frequently noted by outdoor recreationists, it is a prominent visual element of the subalpine zone. It is most widely known as a food source for the threatened grizzly bear and other wildlife species. These and a multitude of other aspects validate the importance of whitebark pine in the GYE and necessitate the long-term monitoring of this valuable icon.

Distribution

Whitebark pine is found in two relatively disjunct north-south transects extending south from British Columbia to California and Nevada. The majority of whitebark pine stands in North America occur in the northern Rocky Mountains (from Alberta to Wyoming), the Cascade Range, the Sierra Nevadas and the Coastal Ranges of British Columbia (Arno and Hoff 1990). While this distribution is largely similar to its historic distribution (going back approximately 10,000 years), whitebark pine is contracting within some of the boundaries of its range due to numerous threats (detailed below). Since whitebark pine generally inhabits high-elevation ecosystems, most stands are isolated by large valleys (Arno and Hoff 1990). Whitebark pine extends to 3,660m (12,000ft) elevation at the southern end of its range in the Sierra Nevada, 3,200m (10,500ft) in Wyoming and 900m (2,950ft) in British Columbia, with its elevational limit dropping with increasing latitude (McCaughey and Schmidt 2001). Whitebark pine is found in association with the following species in the Yellowstone region of the northern Rocky Mountains: lodgepole pine (*Pinus contorta* var. latifolia), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), limber pine (*Pinus flexilis*) and Douglas-fir (*Pseudotsuga menziesii* [McCaughey and Schmidt 2001]).

Ecology

Habitat

Whitebark pine occurs mostly on poorly developed, immature soils that have been recently glaciated (Arno and Hoff 1990). Development of the soils through chemical weathering and microbial activity is retarded by low soil temperature, short summer seasons and highly acidic soils in some areas (Arno and Hoff 1990). Almost all soils on which whitebark pine establishes are cold-climate soils and are classified as cryochrepts (Weaver 2001).

The climatic zone that whitebark pine inhabits is dominated by short, cool summers and long, cold winters with significant snowfall accumulation (Arno and Hoff 1990). In the majority of its range, including the Yellowstone region, whitebark pine is found on warm, south-facing aspects and areas that are exposed to sun and wind (Arno and Hoff 1990). In fact, solar radiation values for whitebark pine forests nearly equal those for the southwestern US during summer (Weaver 2001).

Life History

Whitebark pine is one of five stone pines worldwide. These pines comprise the subsection Cembrae of the section Strobus in the subgenus Strobus and genus Pinus in the family Pinaceae (McCaughey and Schmidt 2001). Other stone pines include Swiss stone pine (*Pinus cembra*), Korean stone pine (*Pinus koraiensis*), Siberian stone pine (*Pinus sibirica*) and Japanese stone pine (*Pinus pumila*). All stone pines share the following characteristics (from McCaughey and Schmidt 2001): five needles per fascicle (or bundle); indehiscent cones, which remain closed even when mature and, therefore, seeds cannot fall to the ground or be wind dispersed; and wingless seeds, which are dispersed by nutcrackers (which are in the family Corvidae and genus *Nucifraga*).

Whitebark pine is monoecious, which means that both male and female cones are found on one tree (Arno and Hoff 1990). Pollen is generally disseminated and flowers are receptive during July of each year with cones ripening in August or September of the following year (Arno and Hoff 1990, Tomback 2001). Once mature, the cone scales open slightly, which allows the seeds to be harvested by the Clark's nutcracker (*Nucifraga columbiana*). Germination of whitebark pine seeds is relatively poor (8-14% [Arno and Hoff 1990]), possibly due to being harvested by nutcrackers before they have fully developed (Tomback 2001). Clark's nutcrackers store groups of seeds (from 28 to 150 seeds) in a sublingual (throat) pouch for transport. The nutcrackers will then cache groups of one to 15 (average of 3-5) seeds a few to several hundred meters from the source tree on steep, rocky slopes or in recently burned areas (Tomback 2001). Once the snow melts, the nutcrackers retrieve the seeds the following June or July. Caches that are not retrieved germinate to form whitebark pine seedlings. Because many caches contain multiple seeds, more than one seedling may germinate at once. As a result, many whitebark pine trees have a multi-stemmed form, which is indicative of numerous genetically related individuals establishing at the same site (Tomback 2001).

Vegetative growth, or layering, is less common in whitebark pine than in subalpine fir and Engelmann spruce. Layering occurs when branches of the tree are pressed into moist growth (often under the weight of snowpack) and develop roots. Rather than being genetic relatives, like trees that have germinated from seed caches, the new tree is genetically identical to the original individual (Arno and Hoff 1990). At its upper elevational limit, whitebark pine forms shrub-like krummholz mats, in which trees grow in a stunted, dwarf form. This is due to the harsh environmental constraints on growth such as wind, damage from ice particles and a short growing season. Lateral growth from a central leader is common in krummholz mats. Some leaders develop roots (Arno and Hoff 1990).

Whitebark pine is moderately shade intolerant and less tolerant of shade than are subalpine fir and Engelmann spruce, its main competitors in the Yellowstone region (Arno and Hoff 1990). On sites that are moist and sheltered from wind, whitebark pine serves as a nurse plant for, and is occasionally out competed by, shade-tolerant spruce and fir; however, it may be a late-seral dominant on such sites after severe disturbances, such as fire, windthrow or avalanches. In general, however, whitebark pine is a climax species on comparably droughty sites where it is longer lived and more durable than its competitors (Arno and Hoff 1990).

Ecological Role

Whitebark pine has very large seeds (average of 175 mg per seed) with a high fat content. This makes them a desirable food source for wildlife. In addition to caching by nutcrackers, a variety of other avian species (woodpeckers, jays, ravens, chickadees, nuthatches and finches), small mammals (chipmunks, ground squirrels, mice and red squirrels) and large mammals (black and grizzly bears) feed on the seeds (Tomback et al. 2001). Red squirrels harvest the seeds and stash them in middens. Thus, red squirrels are the primary vehicle for moving seeds from the trees to a place where grizzly bears can feed on them. Once the seeds are cached in middens, grizzly bears can access them. In some ecosystems such as the Yellowstone, whitebark pine seeds are a primary food source for grizzly bears (Tomback et al. 2001).

The role of whitebark pine seeds in the diet of grizzly bears is one of the major reasons for its conservation status. Because the grizzly bear is listed as threatened, the availability of a major food source is of much interest. In addition, studies have shown that the "availability of whitebark pine seeds has the greatest potential of any food-related factor to impact behavior and demography of the Yellowstone grizzly bear population" (Mattson et al. 1992). When whitebark pine cone crops are large, grizzly bears stay at higher elevations longer in the summer; when cone crops are relatively small, bears search for alternative food sources at lower elevations, leading to increased interactions with humans and increased need for management interference (Mattson et al. 1992).

Status in the Greater Yellowstone Ecosystem

Threats

White Pine Blister Rust: White pine blister rust is an introduced pathogen that first appeared in Vancouver, British Columbia, in 1910. It enters the stomata of the pine needles and then erupts into cankers on the branches. This leads to the cessation of cone production and in some cases, the eventual death of the tree (Tomback et al. 2001). White pine blister rust requires *Ribes* spp (black currants) as an alternate host (Tomback et al. 2001). Recent evidence suggests that the family Orobanchaceae (*Pedicularis racemosa* and *Castilleja miniata*) may also function as alternate hosts (McDonald et al. 2006). Depending on the level of infection, a tree with white pine blister rust can live for several years. Saplings that are infected generally die within three years (Koteen 2002). Infection by blister rust weakens the tree and precipitates in the death of the tree by an accumulation of factors, including mountain pine beetle, other pathogens, root diseases and unfavorable climatic conditions (Koteen 2002).

White pine blister is less likely to cause mortality when cankers originate in stems or branches that are more than 24 inches from the bole (Koteen 2002). In addition, when blister rust first infects the upper-most portion of the tree, it is more likely to cause cessation of cone and seed production (Koteen 2002). Instead of spreading to other parts of the tree from already-existing infections, pines can only be infected by sporidia. Sporidia, an annual, develop on the host species *Ribes* (Koteen 2002). If these sporidia do not infect pines in a particular year, then the cycle is effectively stopped for that season. The fungus cannot recur in the exact same spot on the *Ribes* the following year (Koteen 2002). However, if the sporidia do infect the pine during a given year, then the infection on the pine produces aeciospores that can reinfect *Ribes* and continue the cycle (Koteen 2002). For an in-depth review of the very complex blister rust cycle, please see Koteen 2002: 354-357.

While white pine blister rust has devastated populations in areas with maritime climates, producing infection rates of 82% in the north Cascades (Kendall and Keane 2001) and 90% in Glacier National Park (Koteen 2002), some researchers have suggested that the drier climate of the Greater Yellowstone Ecosystem (GYE) may be relatively inhospitable to the spread of blister rust (Koteen 2002). Results from previous surveys on infection rates in the GYE have shown average rates of <5% in Yellowstone and <15% in Grand Teton, and a highest single-site incidence of 40-44% in Grand Teton (Kendall and Keane 2001), an increase from the 1.1% average infection rate found in 1967 (with the highest single-site incidence of 2.3% [Koteen 2002]).

Climate Change: Climate change is hypothesized to affect whitebark pine communities through three mechanisms: 1) causing a shift in pathogen ranges, which may lead to new regions of hospitable climate for white pine blister rust and, thus, increase the potential for infection; 2) increasing temperatures, which can lead to decreases in range availability for whitebark pine, due to competitive exclusion by more heat-tolerant species such as lodgepole pine (Mattson et al. 2001); and 3) changes in the frequency of severe fires, which lead to overall decreases in whitebark pine numbers (while they are adapted to small fires, large, stand-replacing fires may be detrimental to their overall distribution and abundance) (Koteen 2002). According to Koteen (2002), climate change can also affect the range of blister rust through the following processes: "1) alter[ing] the dispersal, reproductive or developmental processes of the pathogen directly; 2) increas[ing] pathogen virulence or growth to host populations; or 3) increas[ing] pathogen predation of host species by mediating pathogen competition with symbiotic organisms, such as mycorrhizae, that protect plants against pathogens."

In general, changes in climate can affect the resiliency of tree populations because seed production, germination and establishment are particularly sensitive to variations in the environment (Brubaker 1986). While recruitment may decrease significantly due to climate change, persistence of adult trees (albeit without reproducing) can lead to a deceptively "healthy" looking forest (Brubaker 1986).

Altered Fire Regimes: Fire is an integral part of the ecology of whitebark pine communities. Whitebark pine has adapted to a fire-prone ecosystem using two strategies: 1) large trees (i.e., trees with a diameter larger than a pole) can survive low to moderate severity fires and 2) Clark's nutcracker facilitates the establishment of whitebark pine in newly burned areas that are created by mixed severity and stand-replacement fires by caching whitebark pine seeds (USFS n/a). Larger, stand-replacing fires can, however, kill mature, seed-producing whitebark pine trees, which may increase in frequency with a warmer and drier climate (Koteen 2002). However, a lack of fire, in conjunction with an increase in temperature and decrease in precipitation (as discussed above in "climate change"), may allow later successional species such as subalpine fir and Engelmann spruce to out compete whitebark pine (Tomback et al. 2001).

While fire suppression is often identified as a major reason for a decline in the number of whitebark pine communities, the effects of fire suppression are dependent on the severity of the fire and the fire return interval. It is worthwhile to note that it was not until after World War II (1939-1945) that humans possessed sufficient aerial technology to fight fires effectively (Schullery 1997). Therefore, while 1886 marks the first involvement of the federal government in firefighting on federal lands, "effective" fire suppression has occurred for less than 60 years in the park (Schullery 1997). Thus, it is most likely that fire suppression has more greatly influenced the grassland communities than the forests (Schullery 1997). Whitebark pine fire return intervals are extremely variable and have been reported as 30 to 350+ years in some publications (USFS n/a) and changing from 40 to 500 year intervals to 3,000 year intervals in others (Tomback et al. 2001). However, these return interval ranges generally do not specify the severity of the fire, which can be of major importance to the community. In a review, researchers found moderate severity fire return interval means of 25 to 75 years, while the mean interval for stand-replacement fire was 140+ years (USFS n/a). In addition, "whitebark pine and mixed-conifer communities from 6,000 to 11,000 feet (2,000-3,300 m) [in Yellowstone National Park] experienced stand-replacement fire every 350 years or more. Slow fuel accretion and moist fuels restricted fire spread, and large fires occurred only in extreme fire weather years such as 1988" (USFS n/a, Romme 1982).

A shift to longer fire-suppression intervals has been documented in the West Bighole Range in the Bitterroot Mountains, where reduced fire frequencies have caused a decrease of 87% in total area burned (USFS n/a). Based on fires from 1754-1873, the calculated actual fire return interval was 184 years; modeling based on data from 1874-1993 suggests a return interval of 1364 years (USFS n/a, Tomback et al. 2001). Documented evidence of a similar shift in the GYE is difficult to obtain. According to Tomback et al. (2001), residential development in areas bordering on—or within—potential whitebark pine habitat may have lead to an increase in local fire suppression and caused a decrease in the frequency and duration of low-elevation fires. This can lead to a decrease in fires that reach upper-elevation sites where whitebark pine trees occur (Tomback et al. 2001).

Mountain Pine Beetles: The mountain pine beetle (*Dendroctonus ponderosae*) is a native insect that has coevolved with pine forests in the western U.S. (Logan and Powell 2001). Host tree species of mountain pine beetle include: ponderosa pine, lodgepole pine, western white pine and whitebark pine (Kipfmueller and Swetnam 2002). The mountain pine beetle plays a significant role in the continuation of some species such as lodgepole pine on the landscape by providing periodic disturbances that kill trees and create vast tracks of dead needles that serve as fine fuels for fire ignition and spread (Logan and Powell 2001). Without these periodic burns, lodgepole pine would be outcompeted by spruce and fir and lose part of its range (Logan and Powell 2001). However, high-elevation species, such as whitebark pine, may be particularly vulnerable to mountain pine beetle outbreaks, since they invest significant resources in their offspring (Logan and Powell 2001) and can be weakened due to the other threats mentioned in this document.

Mountain pine beetles complete the final stages of their life cycle under the bark of the tree, laying eggs in so-called “galleries”. The larvae then feed on the inner phloem of the tree (Kipfmueller and Swetnam 2002). This process results in tree girdling that slows nutrient and water transport throughout the tree. Release of a blue staining fungus by the beetles entirely stops the transport of water and nutrients and is usually the cause of tree death (Kipfmueller and Swetnam 2002). Outbreaks generally occur for 3–20 years and disproportionately affect large, mature trees (Kipfmueller and Swetnam 2002).

The mountain pine beetle relies on timing and synchrony to complete its life cycle (Logan and Powell 2001). To complete the life cycle in one season, adult emergence must occur after the cessation of lethal spring temperatures, but allow enough time for the completion of oviposition (Logan and Powell 2001). Synchrony of large numbers of insects is required for successful reproduction, as the mountain pine beetle must kill its host tree in order to complete reproduction (Logan and Powell 2001). However, fitness, which at first increases with increasing population size at low densities, decreases when the densities hit high levels, as space in phloem tissue in the tree is limited (Logan and Powell 2001).

Variations in climate are largely responsible for the success of mountain pine beetle outbreaks. Mild summers and winters tend to favor outbreaks, while cold winters and hot summers tend to decrease beetle activity and increase brood mortality (Kipfmueller and Swetnam 2002). While such climatic events directly affect beetle populations, climate also influences the host tree population. For example, moisture stress, induced by high temperatures and low rainfall, leads to a decrease in resin flow in the tree, which decreases the ability of the species to resist attack (Kipfmueller and Swetnam 2002). Evidence has shown that mountain pine beetles tend to attack—and are more successful when attacking—trees that are already weakened by some other process such as moisture stress, pathogens or mistletoe (Kipfmueller and Swetnam 2002). In fact, Kipfmueller and Swetnam (2002) and Logan and Powell (2001) found correlations between beetle-induced tree mortality and July temperatures in the Selway-Bitterroot Wilderness and on Railroad Ridge, White Cloud Mountains, central Idaho, suggesting that above average July temperatures could lead to decreased resistance of whitebark pine trees to mountain pine beetle attacks.

It has been suggested that mountain pine beetles move from neighboring lodgepole pine forests to whitebark pine stands (Tomback et al. 2001). These infestations can spread throughout entire forests and demolish whitebark pine populations during outbreak years, such as the 1924–1934 outbreak in the Selway-Bitterroot Wilderness (Kipfmueller and Swetnam 2002, Tomback et al. 2001, Perkins and Roberts 2003). Because some evidence suggests that older trees that have been weakened due to other pathogens are more susceptible to mountain pine beetle infestations, it has been suggested that fire suppression can increase the spread of infestations because it fosters mature, late-successional stands of trees (Perkins and Roberts 2003, Tomback et al. 2001).

Dwarf Mistletoe: Whitebark pine is a primary host of limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*) (Mathiasen and Hawksworth 1988). According to Mathiasen and Hawksworth (1988), mistletoe can “reduce the growth of heavily infected hosts, cause increased mortality, reduce seed and cone production and predispose [host trees] to other diseases and insects.” Surveys have found infection rates of up to 96% for whitebark pine communities in northern California and southern Oregon, with mortality rates of 58% of trees sampled, leading dwarf mistletoe to be labeled one of the “most damaging disease agents in the Pacific Northwest” (Mathiasen and Hawksworth 1988). In Crater Lake National Park, mistletoe infections are mostly limited to Wizard Island.

“Tree size, stand structure, species composition of stands, tree spacing and infection position within tree crowns” influence the spread of dwarf mistletoe among trees (Taylor and Mathiasen 1999). Lateral spread rates of mistletoe are generally 1.5-2 feet per year in single storied stands, with faster rates occurring in stands with multiple stories seeds from mistletoe on overstory trees can "rain down" onto understory trees (Taylor and Mathiasen 1999). Dense tree canopies can slow the rate of spread because fewer mistletoe seeds are produced in the limited light conditions and the occurrence of non-host species can buffer host trees (Taylor and Mathiasen 1999). While birds and other animals can spread seeds long distances, most seeds are spread through local, explosive seed discharge (Taylor and Mathiasen 1999).

Mistletoe directly impacts tree volume and can lead to decreases of up to 50% in severely infected trees (Taylor and Mathiasen 1999). In addition, decreases in cone and seed production cause immediate impacts on the reproductive capabilities of the host tree (Taylor and Mathiasen 1999). The accumulation of these dead trees and witches brooms can lead to increases in fuels available for fires (Taylor and Mathiasen 1999). Some researchers have suggested that alterations of fire regimes that lead to longer fire return intervals may enable widespread dispersal of mistletoe throughout whitebark pine communities (Tomback et al. 2001). However, others have suggested that mistletoe increases the suitability of habitats for wildlife species such as birds, and thus may actually benefit some coniferous ecosystems.

Management Activities

Efforts to eradicate the *Ribes* host plant for white blister rust began in 1945 in Yellowstone National Park, with 1,785,000 plants removed by 1952 (Newcomb 2003). A study conducted in 1966 by the US Forest Service (and a similar study conducted in 1975 in Yellowstone) concluded that removing *Ribes* did not decrease the incidence of blister rust infection in whitebark and limber pines in the region and the eradication effort was therefore discontinued (Newcomb 2003).

More recent monitoring efforts for the occurrence of blister rust have been undertaken by federal agencies on federal lands in the GYE. A monitoring program that began in 1995 on the Gallatin National Forest is ongoing. Surveys on the Targhee, Bridger-Teton and Shoshone national forests and Yellowstone and Grand Teton national parks were also conducted in the late 1990s. In 2001 the Interagency Grizzly Bear Study Team (part of the US Geological Survey) conducted a survey in the grizzly bear recovery zone.

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