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Effects of whitebark pine (Pinus albicaulis) restoration treatments on the distribution of bark beetle attacks

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ABSTRACT

Whitebark pine is an important component of high elevation ecosystems in the western United States and Canada. Many wildlife species, including grizzly and black bears, squirrels, and birds, forage on the large, wingless seed. Whitebark pine relies heavily upon the Clark's nutcracker for seed dispersal and regeneration. Due to fire exclusion, white pine blister rust, and the mountain pine beetle, whitebark pine is declining across most of its range. In western Montana and eastern Idaho, researchers are implementing restoration treatments in an effort to combat the decline and increase natural regeneration. Treatments include silvicultural strategies, prescribed fire, and combinations of the two; the treatment that best restores and preserves whitebark pine may be implemented at a large scale in the future.

This study was conducted to evaluate the effects of the restoration treatments on bark beetle attacks, to monitor flight periods of the mountain pine beetle and the pine engraver, and to survey insects infesting whitebark pine. The main study site was located on Beaver Ridge, Powell Area, Lochsa District, Clearwater National Forest. Silvicultural treatments were implemented in summer 1998 and 1999 at this site. Tenth-acre permanent plots were established throughout the treatment areas to measure tree data. Within plots, tree and site characteristics were measured and a bark beetle survey was conducted.

Although bark beetle population levels were endemic, a significant treatment effect on bark beetle attacks was found using logistic regression. Bark beetles preferentially attacked trees in nutcracker opening and slashing treatments rather than control treatments. However, plots surveyed for two years, 1998 and 1999, showed no increase in bark beetle populations. The mountain pine beetle attacked only whitebark pine at the site, which supports a mixed species forest with a significant lodgepole pine component. Whitebark pine had a smaller mean diameter and height, as well as significantly more bark beetle attacks per tree than lodgepole pine. The reasons underlying mountain pine beetle preference for whitebark pine warrants further examination. The results of this study show that managers must consider the insect component of whitebark pine ecosystems before implementing restoration treatments.

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CHAPTER ONE: BACKGROUND

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is a five-needled pine occurring in high elevations throughout the western United States and Canada (Arno and Hoff 1989). The elevation range of whitebark pine is from about 1800m to 3500m, depending on latitude, but outliers can be found as low as 1100m and as high as 3660m (Arno and Hoff 1989, Weaver and Dale 1974).

Whitebark pine has large, wingless seeds that are an important food source for many wildlife species, including the grizzly bear (*Ursus arctos horribilis* Ord.), black bear (*U. americanus* Pallas), red squirrel (*Tamiasciurus hudsonicus* Erxleben) and Clark's Nutcracker (*Nucifraga columbiana* Wilson), among other small mammals and birds (Arno and Hoff 1989, Kendall and Arno 1990). Grizzly bears in Yellowstone National Park tend to have fewer troublesome encounters with humans in years when large whitebark pine cone crops are produced. During these years, bears stay in high elevation areas longer to forage on whitebark pine seeds (Mattson et al.1992, Pease and Mattson 1999).

Whitebark pine is also important to high elevation ecosystems for snowpack retention, erosion prevention, and aesthetics (Kendall and Arno 1990, Arno 1986, Arno and Hoff 1989). Many people enjoy the scenic qualities of high mountain areas where whitebark pine is found (McCool 1998). Whitebark pine is a valuable and unique component of the upper subalpine ecosystem; understanding its ecology is important in developing effective management strategies, conducting research, and providing low-impact recreational opportunities in these areas.

Whitebark pine ecosystems

In Montana, whitebark pine is a component of most upper subalpine ecosystems occurring over 1800m (6000ft) in elevation. In the Bitterroot Mountains of southwestern Montana and eastern Idaho, whitebark pine occurs with lodgepole pine (*Pinus contorta* Dougl.), subalpine fir (*Abies lasiocarpa* Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and alpine larch (*Larix lyallii* Parl.). Growing conditions in whitebark pine ecosystems can be harsh. The main limiting factor for growth is climate; other factors limiting growth include severe wind, shallow rocky soil, and heavy snow accumulations (Pfister et al. 1977, Arno and Hoff 1989).

Whitebark pine can be either a seral or climax component of a given stand. Usually, climax whitebark pine stands occur at or near timberline, where subalpine fir grows poorly and becomes stunted (Pfister et al. 1977). Climax stands have a diverse understory, usually dominated by grouse whortleberry (*Vaccinium scoparium* Leiberg). Other understory species include heart-leafed arnica (*Arnica latifolia* Bong.), wood's rush (*Luzula hitchcockii* Hamet-Ahti), and several species of mountain heath (Pfister et al. 1977, Weaver and Dale 1974). The trees often grow in rows or clumps, with an average of 13% rock and 6% bare soil in the stands. The soil is acidic with a thin duff layer (< 3 cm.) (Pfister et al. 1977, Weaver and Dale 1974).

Whitebark pine occurs as a seral species in stands dominated by subalpine fir and lodgepole pine, with similar understory species as the climax stands. Although the soil is acidic in both climax and seral stands, the duff layer is somewhat thicker (4 cm.) in seral stands (Pfister et al. 1977). Soils under whitebark pine are generally low in microbial and nitrogen-fixing activity (Arno and Hoff 1989). Weaver and Dale (1974) found that in Montana, whitebark pine soils tended to be lower in potassium, calcium, magnesium and sodium than Montana agricultural soils. Soil orders encountered in whitebark pine forests include Inceptisols, Entisols, and Mollisols (Arno and Hoff 1989). However, Inceptisols are the most frequently encountered, and Typic and Andic Cryochrepts are common types found within this order (Arno and Hoff 1989, Wilson et al. 1983).

Regeneration

Whitebark pine regeneration is, for the most part, dependent upon the Clark's Nutcracker (Tomback 1982, Hutchins and Lanner 1982, Lanner 1982, 1996). Clark's Nutcracker collects seeds from cones, located primarily in the uppermost branches of whitebark pine, and caches them underground for use as a future food source (Tomback 1982). The nutcracker tends to store many more seeds than necessary for food (Lanner 1982, 1996); un-recovered seed caches form the basis for whitebark pine regeneration. Nutcracker seed caches often give rise to multiple stemmed clumps of closely related trees (Lanner 1980).

The nutcracker uses memory and visual cues to relocate seed caches, and prefers open areas to more dense forest stands for caching (Vander Wall 1982). Therefore, whitebark pine has an advantage over wind-dispersed trees when colonizing recently disturbed sites. Soon after a disturbance event, such as a burn or harvest, the nutcracker caches seeds in these open areas. Other tree species, which depend upon the wind to disperse their seeds, are at a disadvantage when openings are large (Lanner

1982, Tomback et al. 1995). Although many other mammals and birds also utilize whitebark pine seeds as forage, they do not play a significant role in regeneration (Hutchins and Lanner 1982).

Whitebark pine has evolved several traits that facilitate and encourage nutcracker foraging. These include cone retention, seed size and seed energy content (Lanner 1982). Whitebark pine cones are retained on the tree when ripe rather than falling to the ground. Displaying the cones in this manner may reduce nutcracker search time and allow the nutcracker to forage in the canopy instead of on the ground, where the nutcracker would be more exposed to predators (Lanner 1982). Whitebark pine seeds are much larger than other pine seeds and subsequently may contain more energy. Selection of larger seeds also improves nutcracker foraging efficiency. The cones are located in the uppermost branches of the tree, where the nutcracker can easily locate them from the air (Lanner 1982). This has resulted a morphological adaptation by the tree: a distinctive, upswept branching pattern, easily recognizable from a distance.

Bark beetles inhabiting whitebark pine

Mountain pine beetle

The mountain pine beetle is an aggressive bark beetle that, in most cases, must kill its host tree to successfully reproduce. Strip attacks are the exception: only the attacked strip dies from the attack. Mountain pine beetle kills a tree through a chemically mediated mass attack beginning with the release of aggregation pheromones by a single pioneer beetle. The pheromone attracts sufficient beetles to the tree to overcome the tree's defense mechanisms (Borden 1982). The density of attacks required for host tree mortality to occur varies considerably among trees and increases with increasing host tree vigor. Anything that stresses a tree, or reduces its vigor, therefore, can increase a tree's susceptibility to beetle attack. Fire scorch is one stress factor that has been found to increase the susceptibility of pines to mountain pine beetle (Rust 1933, Fellin 1980, Geizler et al. 1984).

To a large extent, mountain pine beetle development is affected by tree size and phloem thickness (Cole and Amman 1980). The mountain pine beetle inhabits the phloem, which is the food source for developing beetle larvae. Large trees, which tend to have thicker phloem, facilitate beetle development by providing greater food resources than smaller trees. The mountain pine beetle does not prefer small trees, under 10cm diameter at breast height (DBH), because of their limited phloem resources (Furniss and Carolin 1977, Cole and Amman 1980).

Mountain pine beetle exhibits temperature-dependent development. The beetle emerges and breeds when warm summer temperatures are reached, and, for successful overwintering, development of the new brood must attain mid- to late-instar stages before the freezing temperatures of late fall and winter (Logan and Bentz 2000). Elevation thus plays a significant role in mountain pine beetle development; as elevation increases, the growing season is shorter and temperatures are cooler. The shorter growing and developmental periods at higher elevations can limit tree mortality in lodgepole pine by restricting beetle development (Cole and Amman 1980). Most mountain pine beetle populations exhibit a one-year life cycle, however, at high elevations, development may extend to two years as a result of the shorter developmental period (Furniss and Carolin 1977, Cole and Amman 1980).

Host trees for the mountain pine beetle include many western North American pines, including lodgepole and whitebark pine. Mountain pine beetle outbreaks have been thought to move through lower elevation lodgepole pine stands and "spill over" into whitebark pine (Bartos and Gibson 1990, Ciesla and Furniss 1975). Extensive outbreaks in the early 1900's were observed in both lodgepole and whitebark pine (Gibson 1943). Evidence of such epidemics remained decades later as "ghost" forests: standing whitebark pine snags, remnant from mountain pine beetle outbreaks occurring early in the 1900's (Ciesla and Furniss 1975). Mountain pine beetle outbreaks in whitebark pine can cause extensive mortality of cone-bearing trees. This can have major implications for regeneration because the cone crop is substantially reduced for many years. At endemic population levels, mountain pine beetle sometimes prefers whitebark pine to lodgepole pine, perhaps due to its thicker phloem (Baker et al. 1971).

Limber pine, a white pine closely related to whitebark pine, may exhibit similar characteristics and effects on mountain pine beetle development as whitebark pine. Mountain pine beetle prefers limber pine (*Pinus flexilis* James) to lodgepole pine in some populations (Langor 1989, Langor et al. 1990, Langor and Spence 1991). Limber pine tends to have thicker phloem than lodgepole pine and may also have more nutritious phloem (Langor 1989, Langor et al. 1990, Langor and Spence 1991). Cerezke (1995) found that mountain pine beetle reared in limber pine had larger females with higher fecundity than those reared in lodgepole pine. However, it should be noted that in another study (Amman 1982), a significant host effect was not found when rearing mountain pine beetle in four species of pine (including both lodgepole and whitebark pine).

Pine engraver .

The pine engraver (*Ips pini* Say) commonly infests lodgepole and ponderosa pine (*Pinus ponderosae* Dougl.) as well as most other pine species (Furniss and Carolin 1977). It is most often a problem where large amounts of slash are generated or in extensive areas of blowdown. It can rapidly increase in numbers in slash and then attack and kill surrounding small replacement trees or top-kill larger diameter trees (Furniss and Carolin 1977). Although pine engraver attacks in whitebark pine have not been recorded, whitebark is a likely host, especially when pine engraver populations are high. Pine engraver attacks on whitebark pine may cause mortality or top-kill. Top-kill could be especially destructive in whitebark pine because tree tops are where whitebark cones are produced.

Red turpentine beetle

The red turpentine beetle (*D.* valens LeConte) is a secondary beetle that colonizes pine trees throughout western and central North America (Furniss and Carolin 1977). Secondary beetles rarely cause tree mortality except when the tree is already stressed or weakened. The red turpentine beetle seldom kills the trees it infests except when populations are large and numerous attacks result in the complete girdling of the tree. Attacks typically occur on the lower few meters of the tree bole and proceed downward into the root collar (Coulson and Witter 1984). Red turpentine beetle often occurs in weakened or stressed trees, such as those that may occur after harvesting or in campgrounds (Furniss and Carolin 1977). In scorched trees at burn sites and in fresh stumps at sites where trees have been recently cut, the red turpentine beetle often increases greatly in numbers (Furniss and Carolin 1977, Coulson and Witter 1984). In these situations, large numbers of attacks around the base of living trees may cause mortality or extreme stress. Stressed trees are then susceptible to subsequent attacks by western pine beetle (*D. brevicomis* LeConte) or mountain pine beetle (Miller and Keen 1960, Furniss and Carolin 1977).

Other beetles

Several secondary bark beetle species have been recorded in whitebark pine but the information available about these species is limited. Bartos and Gibson (1990) describe strip attacks and tree mortality due to secondary beetles, but identification of the beetles was not made. After the 1988 Yellowstone fires, mountain pine beetle and a secondary beetle (possibly *Ips montanus* Eichhoff) were the most common insects killing whitebark pine (Ryan and Amman 1996). Several secondary beetles have been found to attack the boles of whitebark pine including the Monterey pine ips (*Ips mexicanus* Hopkins), two *Pityogenes* spp. (*P. carinulatus* LeConte and *P. fossifrons* LeConte) (Furniss and Carolin 1977) and two species of *Pityophthorus* (*P. aquilonius* and *P. collinus*) (Bright 1968); these insects do not usually kill healthy trees, but rather colonize trees already stressed or killed by aggressive bark beetles, disease, or other factors.

Diseases infecting whitebark pine

White pine blister rust (*Cronartium ribicola* J.C. Fisch), an exotic disease, is the most prevalent disease of whitebark pine (Hoff and Hagle 1990). Whitebark pine is among the most blister rust-susceptible pines (Bingham 1972, Hoff et al. 1980). The rust causes stem and bole cankers that girdle and kill individual branches and, eventually, the tree. Bole cankers often result in top-kill, reducing cone production in the tree. Some whitebark pine stands in western Montana have up to a 90% infection rate of white pine blister rust (Keane and Arno 1996).

Infection of whitebark pine trees by white pine blister rust may increase susceptibility to mountain pine beetle attack. In western white pine, white pine blister rust and root disease has been found to increase susceptibility to mountain pine beetle attack (Kulhavy et al.1984). Endemic populations of mountain pine beetle in lodgepole pine appear to attack trees more heavily infected with pathogens (comandra blister rust, root diseases) than un-infected or lightly infected trees (Bartos and Schmitz 1998, Rasmussen 1987, Tkacz and Schmitz 1986). However, research on endemic populations of mountain pine beetle is limited; more research employing larger sample sizes is necessary to draw solid conclusions regarding beetle / pathogen interactions.

Dwarf mistletoes can pose a serious problem in whitebark pine stands. Whitebark pine is a primary host of limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* Coulter & A. Nels.) and a minor host of lodgepole pine dwarf mistletoe (*A. americanum* Nutt. Ex. Engelm.) (Jackson and Faller 1973, Knutson and Tinnin 1981, Mathiason and Hawksworth 1988, Hoff and Hagle 1990). Whitebark pine has also been reported as a host for hemlock dwarf mistletoe (*A. tsugense*) and larch dwarf mistletoe (*A. laricis*) (Hawksworth and Wiens 1972). Dwarf mistletoe causes brooming of the lower branches first, eventually moving into the upper branches and killing the top. Mistletoe infection also slows growth and reduces tree vigor (Hawksworth and Wiens 1996).

Many other pathogens infect whitebark pine, but do not cause as much damage as white pine blister rust or dwarf mistletoes. These include various root diseases, which have been shown to increase susceptibility to the mountain pine beetle in other tree species (Bartos and Schmitz 1998, Eckberg et al. 1994, Kulhavy et al. 1984). Both annosus (*Heterobasidion annosum Bref.*) and Armillaria (*Armillaria ostoyae* Herink) root diseases are common in whitebark pine (Hoff and Hagle 1990). Needle casts and needle blights also infect whitebark pine, as do several species of stem and branch cankers, including *Lachnellula* spp. (Hoff and Hagle 1990, Hansen and Lewis 1997, Taylor and Walla 1999).

Decline of whitebark pine

Whitebark pine is in a state of serious decline throughout its range (Arno and Hoff 1989, Kendall and Arno 1990, Arno 1986, Keane and Arno 1993). The decline, which has resulted in widespread ecosystem change, was first noted in the late 1970's and early 1980's (Schmidt and McDonald 1990, Arno 1986, Jonkel 1978). The cause of decline has since been attributed to the interaction of three key factors: white pine blister rust, fire exclusion and the mountain pine beetle. The following discussion details fire exclusion, as white pine blister rust and mountain pine beetle were discussed previously.

The fire return interval in whitebark pine ecosystems ranges from 50 to 500 years (Arno 1986, Arno and Peterson 1983, Morgan and Bunting 1990). Fire exclusion, which began in the early 1900's, has created conditions in many areas that are not favorable for whitebark pine. Shade tolerant tree species, such as mountain hemlock (*Tsuga mertensiana* Carr.), subalpine fir, and Engelmann spruce have encroached into once-open whitebark pine stands, due to lack of fire events coupled with white pine blister rust and mountain pine beetle (Keane and Arno 1996). Although this is a natural process, historically, periodic fires would have created a mosaic of different stand structures and age classes across the landscape (Morgan and Bunting 1990).

Without fire, the landscape is more homogenous and open stands are scarce. Whitebark pine is shade intolerant, and thus does not compete well in closed conditions. Closed conditions are not preferable for nutcracker seed caching either, which leads to a decrease in whitebark pine regeneration. Historically, fires in whitebark pine ecosystems included both light intensity understory burns and high intensity stand replacement fires. To diminish whitebark pine decline, restoration efforts have been implemented in parts of Idaho and Montana (Keane and Arno 1996). These efforts include silvicultural treatments and prescribed burning, in attempts to encourage Clark's nutcracker caching and limit competition with whitebark pine in the over- and understory.

Summary

Whitebark pine is considered a keystone species in many high elevation ecosystems, meaning that if whitebark pine were to disappear, many other species would follow (Lanner 1996). As a keystone species, it is invaluable to numerous wildlife species and the integrity of the entire ecosystem. Populations of grizzly and black bears, along with red squirrels, birds and other small mammals may decline greatly if whitebark pine were to disappear from the high elevation ecosystem. Negative effects may also include less snowpack retention, more erosion, and a reduction in aesthetics (valued by recreationists).

Whitebark pine is a host for a variety of insects and diseases. Of these, the mountain pine beetle and white pine blister rust have had, and continue to have, the most lasting effects on whitebark pine. Fire history patterns indicate that whitebark ecosystems have been impacted heavily by fire exclusion as well.

Justification

Decline of whitebark pine is apparent at many sites, and researchers have begun evaluation of restoration treatments. Restoration treatments are aimed at encouraging whitebark pine regeneration, increasing natural resistance to white pine blister rust, and reducing competition. Whitebark pine ecosystems have not been heavily managed in the past, so the effects of management are largely unknown. Research aimed at investigating the effects of restoration treatments is directly applicable to managing these areas. The following research attempts to increase knowledge about whitebark pine while investigating effects of restoration treatments.

Objectives

The main objective of this research was to examine the effects of whitebark pine restoration treatments on bark beetle populations. Although restoration treatments are currently being implemented, there has not been an extensive survey of bark beetles in whitebark pine, especially as related to restoration work. Additionally, it is important to monitor the bark beetle flight periods to more fully understand the biology of the beetles at high elevations. Specific objectives of the project were:

1. To document which bark beetle species infest whitebark pine.
2. To document changes in bark beetle populations, and consequently tree mortality associated with bark beetles, in various silvicultural and prescribed burn treatments used in efforts to restore whitebark pine ecosystems.
3. To monitor flight periods of the pine engraver and mountain pine beetle at whitebark pine restoration sites.

References

Amman, G.D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Env. Ent. 11: 590-593.

Arno, S.F. 1986. Whitebark pine cone crops - A diminishing source of wildlife food? W. J. of App. For. 1: 92-94.

Arno, S.F. and T.D. Peterson. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. USDA For. Serv. Int. For. and Range Exp. Stn. Res. Pap. INT-301, Ogden, UT. 28 pp.

Arno, S.F. and R.J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). USDA For. Serv Gen. Tech. Rep. INT-253. 11 pp.

Baker, B.H., G.D. Amman and G.C. Trostle. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark stands? USDA For. Serv. Int. For. and Range Exp. Stn. Res. Note INT-151, Ogden, UT. 7 pp.

Bartos, D.L. and K.E. Gibson. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. pp. 171-178. *In:* W.C. Schmidt & K.J. McDonald (comp.) Proceed.-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, USDA For. Serv. Gen. Tech. Rep. INT-270, Bozeman, MT.

Bartos, D.L. and R.F. Schmitz. 1998. Characteristics of endemic-level mountain pine beetle populations in south-central Wyoming. USDA For. Serv. Res. Paper RMRS-RP-13, Ogden, UT. 9 pp.

Bingham, R.T. 1972. Taxonomy, crossibility, and relative blister rust resistance of 5-needled white pines. pp. 271-280 *In:* Biology of rust resistance in forest trees: Proceedings of a NATO-IUFRO advanced study institute, USDA Misc. Pub. 1221, Washington, D.C.

Borden, J.H. 1982. Aggregation pheromones. pp. 527 pp. *In:* J.B. Mitton & K.B. Sturgeon (ed.) Bark beetles in North American conifers, Univ. of Texas Press, Austin, TX.

Bright, D.E., Jr. 1968. Three new species of *Pityophthorus* from Canada (Coleoptera: Scolytidae). Can. Ent. 100: 604-608.

Ciesla, W.M. and M.M. Furniss. 1975. Idaho's haunted forests. Am. For. 81: 32-35.

Cerezke, H.F. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) in three pine hosts. Can. Ent. 127: 955-965.

Cole, W.E. and G.D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests Part I: Course of an infestation. USDA For. Serv Int. For. and Range Exp. Stn. Gen. Tech. Rep. INT-89, Ogden, UT. 56 pp.

Coulson, R.N. and J.A. Witter. 1984. Forest entomology: ecology and management. Wiley, New York, N.Y. 669 pp.

Eckberg, T.B., J.M. Schmid, S.A. Mata and J.E. Lundquist. 1994 Primary focus trees for the mountain pine beetle in the Black Hills. USDA For. Serv Rocky Mtn. For. and Range Exp. Stn. Res. Note RM-RP-531, Fort Collins, CO. 11 pp.

Fellin, D.G. 1980. A review of some interactions between harvesting, residue management, fire, and forest insects and diseases. pp. 335-414 *In:* Proceed. Environmental consequences of timber harvesting in Rocky Mountain coniferous forests, USDA For. Serv. Int. For. and Range Exp. Stn. INT-90, Ogden, UT.

Furniss, R.L. and V.M. Carolin. 1977. Western Forest Insects. USDA For. Serv. Misc. Pub. No. 1339, Washington, D.C. 654 pp.

Gibson, A.L. 1943. Penetrating sprays to control the mountain pine beetle. J. Econ. Ent. 36: 396-398.

Giezler, D.F., R.I. Gara and W.R. Littke. 1984. Bark beetle infestations of lodgepole pine following a fire in south central Oregon. Z. Ang. Ent. 98: 389-394.

Hansen, E.M. and K.J. Lewis. 1997. Compendium of conifer diseases. American Phytopathological Soc., St. Paul, MN. 101 pp.

Hawksworth, F.G. and D. Wiens. 1972. Biology and classification of dwarf mistletoe (*Arceuthobium*). USDA For. Serv. Ag. Hdbk 401, Washington, D.C. 34 pp.

Hawksworth, F.G. and D. Wiens. 1996. Dwarf mistletoes: biology, pathology, and systematics. USDA For. Serv. Ag. Hdbk. 709, Washington, DC. 410 pp.

Hoff, R.J., R.T. Bingham and G.I. McDonald. 1980. Relative blister rust resistance of white pines. Eur. J. For. Path. 10: 307-316.

Hoff, R. and S. Hagle. 1990. Disease of whitebark pine with special emphasis on white pine blister rust. pp. 179-190. *In:* W.C. Schmidt & K.J. McDonald (comp.) Proceedings - Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, USDA For. Serv. Int. Res. Stn. Gen. Tech. Rep. INT-270, Ogden, UT.

Hutchins, H.E. and R.M. Lanner. 1982. The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55: 192-201.

Jackson, M.T. and A. Faller. 1973. Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. Ecol. Mon. 43: 441-461.

Jonkel, C. 1978. Grizzly bears and the mountain pine beetle. Univ. Mont. Border Grizzly Project Spec. Rep. 21, Moscow, ID. 3 pp.

Keane, R.E. and S.F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. W. J. App. For. 8: 44-47.

Keane, R.E. and S.F. Arno. 1996. Whitebark pine ecosystem restoration in western Montana. pp. 51-53. *In:* C.C. Hardy & S.F. Arno (ed.) The use of fire in forest restoration. USDA For. Serv. Int. Res. Stn. Gen. Tech. Rep. INT-GTR-341, Ogden, UT.

Kendall, K.C. and S.F. Arno. 1990. Whitebark pine-an important but endangered wildlife resource. pp. 264-272. *In:* W.C. Schmidt & K.J. McDonald (comp.) Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, USDA For. Ser. Int. Res. Stn. INT-270, Ogden, UT.

Knutson, D.N. and R.O. Tinnin. 1981. *Arceuthobium cyanocarpum* in Oregon. Plant Dis. 65: 445.

Kulhavy, D.L., A.D. Partridge and R.W. Stark. 1984. Root diseases and blister rust associated with bark beetles (Coleoptera: Scolytidae) in western white pine in Idaho. Env. Ent. 13: 813-817.

Langor, D.W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Ent. 121: 149-157.

Langor, D.W. and J.R. Spence. 1991. Host effects on allozyme and morphological variation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Ent. 123: 395-410.

Langor, D.W., J.R. Spence and G.R. Pohl. 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Evol. 44: 609-618.

Lanner, R.M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. pp. 14-48. *In:* Proceed. Sixth North American forest biology workshop, Edmonton, AB. Univ. of Alberta.

Lanner, R.M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's Nutcracker. Can. J. For. Res. 12: 391-402.

Lanner, R.M. 1996. Made for each other: A symbiosis of birds and pines. Oxford Univ Press, New York, N.Y. 160 pp.

Logan, J.A. and B.J. Bentz. 2000. Model analysis of mountain pine beetle seasonality. Env. Ent. 29.

Mathiasen, R.L. and F.G. Hawksworth. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. For. Sci. 34: 429-440.

Mattson, D.J., B.M. Blanchard and R.R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. J. Wildlife Mgmt. 56: 432-442.

McCool, S.F. 1998. The diminished landscape: Aesthetic and recreational consequences. Present. at: Restoring Whitebark Pine Ecosystems Symposium. Sept. 9-12. Missoula, MT.

Miller, J.M. and F.P. Keen. 1960. Biology and control of the western pine beetle. USDA For. Serv. Misc. Pub. 800, Washington, D.C. 381 pp.

Morgan, P. and S.C. Bunting. 1990. Fire effects in whitebark pine forests. pp. 166-170. *In:* W.C. Schmidt and K.J. McDonald (comp.) Proceedings - Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, USDA For. Serv. Int. Res. Stn. Gen. Tech. Rep. INT-270, Ogden, UT.

Pease, C.M. and D.J. Mattson. 1999. Demography of the Yellowstone grizzly bears. Ecol. 80: 957-975.

Pfister, R.D., B.L. Kovalchik, S.F. Arno and R.C. Presby. 1977. Forest habitat types of Montana. USDA For. Serv. Int. For. and Range Exp. Stn. Gen. Tech. Rep. INT-34, Ogden, UT. 174 pp.

Rasmussen, L.A. 1987. Mountain pine beetle selection of dwarf mistletoe and comandra blister rust infected lodgepole pine, USDA For. Ser. Int. Res. Stn. Res. Note INT-367, Ogden, UT.4 pp. pp.

Ryan, K.C. and G.D. Amman. 1996. Bark beetle activity and delayed tree mortality in the Greater Yellowstone Area following the 1988 fires Ecological implications of fire in Greater Yellowstone, IAWF. 151-158 pp.

Rust, H.J. 1933. Final report on the study of the relation of fire activity to bark beetle attack in ponderosa pine (Tubb's Hill Burn). USDA Bur. Ent. For. Insect Field Stn., Coeur d'Alene, ID. 22 pp.

Schmidt, W.C. and K.J. McDonald (comp.). 1990. Proceedings - Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource. USDA For Serv. Int. Res. Stn. Gen. Tech. Rep. 270, Ogden, UT. 386 pp.

Taylor, J.E. and J.A. Walla. 1999. First report of *Dothistroma septospora*on native limber and whitebark pine in Montana. Plant Dis. 83: 590.

Tkacz, B.M. and R.F. Schmitz. 1986. Association of an endemic mountain pine beetle population with lodgepole pine infected by Armillaria rood disease in Utah, USDA For. Serv. Res. Note INT-353, Ogden, UT. 7 pp.

Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: A mutualism hypothesis. J. Anim. Eco. 51: 451-467.

Tomback, D.F., J.K. Clary, J. Koehler, R.J. Hoff and S.F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: The Sundance Burn of Northern Idaho (U.S.A.). Cons. Bio. 9: 654-664.

Vander Wall, S.B. 1982. An experimental analysis of cache recovery in Clark's Nutcracker. Anim. Beh. 30: 84-94.

Weaver, T. and D. Dale. 1974. *Pinus albicaulis* in Central Montana: environment, vegetation and production. Am. Mid. Nat. 92: 222-230.

Wilson, D., Coyner, J., and T. Deckert. 1983. Land System Inventory of the Clearwater National Forest, First Draft Review. USDA For. Serv. 398 pp.

CHAPTER TWO: EFFECTS OF WHITEBARK PINE RESTORATION TREATMENTS ON THE DISTRIBUTION OF BARK BEETLE ATTACKS

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is a five-needled white pine that grows in high elevation ecosystems in the western United States and Canada. In central Idaho, it often grows with lodgepole pine (*Pinus contorta* Dougl. ex Loud.), subalpine fir (*Abies lasiocarpa* Nutt.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Pfister et al. 1977). However, at or near timberline, whitebark pine may be the only tree species present due to harsh, windy conditions. Whitebark pine is usually not considered a commercial timber species, due in part to the inaccessibility of the high elevations (Keane and Arno 1993). Therefore, management efforts have usually not focused on whitebark pine.

Wildlife species, especially birds, squirrels, and bears, find an excellent food source in the whitebark pine's large, wingless seeds (Arno and Hoff 1989). Whitebark pine and the Clark's Nutcracker (*Nucifraga columbiana* Wilson) have evolved a mutualistic relationship. The tree provides a food source, and in return, the bird disperses the whitebark seeds by caching seeds for later use. Un-recovered seed caches generally form the basis for most whitebark pine regeneration (Tomback 1982). Other contributions to the high elevation ecosystem by whitebark pine include snowpack retention, aesthetics, erosion prevention, summer game range, higher water yields, and the intrinsic value of the species (Arno 1986, Arno and Hoff 1989, Kendall and Arno 1990, McCool 1998, Pfister et al. 1977).

Whitebark pine is in serious decline because of three factors: fire exclusion, white pine blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.), and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Kendall and Arno1990). The exclusion of fires from the high mountain landscape has allowed shade tolerant subalpine fir to out-compete the more shade intolerant whitebark, thereby effectively reducing whitebark pine regeneration. White pine blister rust is an exotic disease that is devastating whitebark pine across its range. With reduced regeneration due to fire exclusion, little natural selection for resistance to white pine blister rust can occur. The mountain pine beetle impacts whitebark pine stands by killing individuals or small groups of large trees, or spreading into whitebark pine stands from outbreaks that develop in adjacent and lower elevation stands of lodgepole pine. Epidemics of mountain pine beetle in lower elevation stands of lodgepole pine have been documented moving into whitebark pine and causing extensive mortality (Ciesla and Furniss 1975, Arno and Hoff 1989). Evidence of past epidemics of mountain pine beetle in whitebark pine can still be seen today as "ghost forests" (Ciesla and Furniss 1975).

Restoration treatments

As a result of this serious decline, projects aimed at restoration of whitebark pine ecosystems have recently been designed and implemented. Current efforts focus upon the use of prescribed fire, silvicultural techniques, and natural and artificial regeneration methods (Keane 1996). The following discussion details restoration treatments that are commonly utilized in western Montana and Eastern Idaho, and may affect the distribution of bark beetle attacks.

Slashing. Slashing involves removal of overstory trees that are shading whitebark pine. Species removed may include the more shade tolerant subalpine fir and Engelmann spruce. Lodgepole pine may also be removed from the overstory, even though it is not considered highly shade tolerant. Slashing improves the growing conditions for whitebark pine by removing competition and creating conditions more conducive to nutcracker caching. Trees removed from the overstory and left on the forest floor provide a more continuous fuel bed if prescribed burning is planned.

Nutcracker openings. Nutcracker openings are small clearcuts (with live whitebark pine left uncut) designed to encourage seed caching by the Clark's nutcracker, which prefers to cache seeds in open areas (Tomback et al. 1995). Open areas are not as prevalent today as they were historically due to fire exclusion. These openings are sometimes implemented in conjunction with slashing treatments between openings.

Prescribed understory burn. Prescribed burning is commonly utilized to open stands and reduce competition (Keane and Arno 1996). It removes much of the understory, as well as some overstory trees, which reduces shading in the stand. Prescribed understory burning at high elevations tends to be patchy due to the lack of fuel continuity and is often used in combination with silvicultural treatments.

Prescribed stand replacement burn. Stand replacement fires are high intensity fires designed to remove both overstory and understory vegetation. Such fires create large openings that encourage seed caching by the Clark's nutcracker. Whitebark pine is often the first tree species to establish following such fires (Tomback et al. 1995), giving whitebark pine an advantage over wind-dispersed and shade tolerant species.

Insects

Whitebark pine ecosystems are characterized by extreme environmental conditions, including cold winter temperatures and short growing seasons (Pfister et al. 1977). However, even under these harsh conditions, many insects have found whitebark pine to be a suitable host.

Both primary and secondary bark beetles (Coleoptera: Scolytidae) colonize whitebark pine. Primary beetles are aggressive and capable of killing trees. Secondary beetles range from non-aggressive to moderately aggressive, colonizing already dead trees or killing weakened or stressed trees. The most damaging bark beetle occurring in whitebark pine is the mountain pine beetle (Amman 1982, Baker et al. 1971, Bartos and Gibson 1990, Gibson 1943). The mountain pine beetle is capable of developing outbreaks and has caused widespread mortality in whitebark pine (Ciesla and Furniss 1975). Other bark beetles that have been recorded in whitebark pine are considered secondary. These beetles usually infest small branches or twigs, and the occasional seedling or sapling. These include: *Ips mexicanus* Hopkins, *I. latidens* LeConte, *Pityogenes fossifrons* LeConte, *P. carinulatus* LeConte and two *Pityopthorus* species, *P aquilonius* and *P. collinus* (Bright 1968, Furniss and Carolin 1977, Bartos and Gibson 1990). *P. fossifrons* is usually considered a secondary beetle, however, it has been recorded as a primary beetle in western white pine reproduction (Furniss and Carolin

1977). *Pityopthorus* are considered twig beetles, aiding in self-pruning rather than causing economic damage (Furniss and Carolin 1977).

Several species of bark beetles, including the mountain pine beetle, can pose serious threats to stands after cutting or burning (Furniss and Carolin 1977). Populations of the pine engraver (*Ips pini* Say) and the red turpentine beetle (*Dendroctonus valens* LeConte) may increase in slash, such as downed logs and stumps, following harvesting (Furniss and Carolin 1977). These larger populations have the potential to move into live trees nearby. Large amounts of downed woody debris are generated in whitebark pine restoration efforts; some is eventually burned in prescribed fire. However, slash that is not burned or is burned after beetles have had an opportunity to breed and develop, may serve as ideal centers for increasing beetle populations (Furniss and Carolin 1977). Cutting can stress residual trees by changing the microclimate and increasing wind speed and solar insolation. Cutting operations and fire treatments may result in additional stress when open wounds on residual tree boles result from falling trees or fire scars (Aho et al. 1983). Stressed trees are more susceptible to successful attack by aggressive bark beetles such as the mountain pine beetle and secondary bark beetles such as pine engraver and red turpentine beetles (Mitchell et al. 1983, Larsson et al. 1983, Miller and Keen 1960).

In addition to bark beetles, an aphid (*Essigella gillettei* Hottes), mealybugs (*Puto spp.*) and the lodgepole pine needletier (*Argyrotaenia tabulana* Freeman) have also been recorded from whitebark pine (Furniss and Carolin 1977). Several cone and seed insects have been recorded in whitebark pine, including: cone beetles (*Conopthorus* *ponderosae*), coneworms (*Dioryctria abietivorella*), seedbugs (*Leptglossus occidentalis*), adelgids (*Pineus spp.*), and seedworms (*Cydia spp.*) (Kegley and Campbell 1997). Although investigations into insects that infest white pine blister rust cankers in whitebark pine have not been conducted, similar work has been done in western white pine (*Pinus monticola* Dougl. ex D. Don). Furniss et al. (1972) found weevils (Coleoptera: *Curculionidae*), bark beetles (*Pityopthorus spp., Procryphalus spp.*), *Drosophilidae* larvae, mites (Acarina), and parasitoids (Hymenoptera: *Ichneumonidae*) in blister rust cankers. They found a Lepidopteran, *Dioryctria abietivorella*, to be the most abundant insect in white pine blister rust cankers on western white pine.

Whitebark pine is a non-commercial tree species that, with few exceptions, has not been subjected to regular management activities or research until the last several years (Gibson 1943, Keane and Arno 1993). The effects of restoration treatments cannot be accurately predicted, given the current state of knowledge about whitebark pine ecosystems. Changes in bark beetle population levels and assessments of possible preventative measures have not been included in research studies assessing the efficacy of whitebark pine restoration efforts. The objective of this study was to assess the effect of whitebark pine restoration treatments on bark beetle attacks, as well as document which insects infest whitebark pine and which tree characteristics each insect prefers. Research results are directly applicable to managers aiming to restore this ecologically important species.

Materials and methods

Study location

The main study was conducted at the Beaver Ridge whitebark pine restoration treatment area. Beaver Ridge is located approximately 65 miles southwest of Missoula, MT, on the Powell Area, Lochsa District, Clearwater National Forest, ID. The restoration area encompasses about 240 hectares (600ac), ranging in elevation from 1966m (6450ft) to 2246m (7370ft). Average slope is 17° on primarily south aspects. Restoration treatments implemented at Beaver Ridge before or during the summer of 1999 included three control treatments, two slashing treatments, and two nutcracker opening treatments (Figure 1). Prescribed burning was conducted in portions of the treatments in October 1999, after sampling for this study was completed.

Soil types present at Beaver Ridge include both Typic and Andic Cryochrepts (Wilson et al. 1983). These soils typically have an ash cap, which helps maintain site productivity. The potential for soil surface erosion is high, and the area is designated as non-commercial forest land (Wilson et al. 1983).

Insects were collected from whitebark pine at an additional study site, the Bear Overlook whitebark pine restoration area. Bear Overlook is located west of Victor, MT on the edge of the Selway – Bitterroot Wilderness Area. The site encompasses approximately 80 hectares (200ac). Site characteristics at Bear Overlook are similar to those at Beaver Ridge. The aspect is mostly south facing, and the elevation ranges from about 2134m (7000ft) to about 2287m (7500ft).

Flight period monitoring

Monitoring of the flight period for pine engraver and mountain pine beetle took place during summer 1999 at Beaver Ridge. Standard Lindgren funnel traps were baited with aggregation pheromones appropriate for each beetle. For the pine engraver, traps were baited with racemic ipsdienol and lanierone. The mountain pine beetle bait consisted of trans-verbenol, exo-brevicomin and myrcene.

Traps were located approximately 0.8 km from the western-most treatment boundary. Trap collections began July 27th and continued weekly until August 9th, when collections were made every 2 days until September 4th. A final collection was made October 1st, when the traps were removed from the area.

Permanent plots

Beaver Ridge

Permanent 400m^2 (1/10th acre) circular plots, hereafter referred to as "study plots", were established in summer 1999 to assess the effects of treatments and various stand, site and tree characteristics on bark beetle attacks. Fifteen plots were established in each treatment, for a total of 105 plots. The total number of individual trees measured was: 436 (slashing treatments), 136 (nutcracker opening treatments), and 778 (control treatments). To locate the plot centers, transects were drawn on a topographic map of the area and plots located evenly along each transect. Plot centers were marked with 3-foot rebar stakes and metal tags for future monitoring. All plots were located at least 78m (198ft) apart, except when the plots landed near USFS fixed plots (described below). Plots landing near USFS fixed plots were relocated to avoid overlap. The Beaver Ridge road, (Forest Service road 369), runs east to west through the restoration area (Figure 1). A buffer zone of 52m (132ft) was established along either side of the road to avoid possible road effects such as dust.

Plot level measurements included GPS location, slope, aspect, percent canopy cover and habitat type. GPS position was recorded using a Trimble™ Navigation GeoExplorer hand-held GPS unit. The slope was measured in degrees using the average of up- and downhill readings. Aspect was measured as the azimuth in degrees, closest to the water flow direction, and transformed using the following formula (Beers et al. 1966):

$$A' = \sin(A + 45) + 1$$

where: A' is transformed aspect
A is original azimuth reading

Occular estimates of percent overstory canopy cover were made at plot center. Habitat type was recorded using the habitat type key for Montana (Pfister et al. 1977). Northness index, a measure of solar insolation, was obtained from the slope and aspect data through the following transformation (Borchert et al. 1989):

$$\text{Northness Index (NI)} = \cos(\text{aspect}) * \sin(\text{slope})$$

Breakpoint diameters, the diameter below which no smaller trees were measured, were defined separately for each tree species, based upon research objectives (Table 1). Trees below the breakpoint diameter were not included because they were considered too small to host bark beetles. All trees at or above the breakpoint diameters were included in the plot measurements. In each plot, the following tree characteristics were recorded for each tree: species, diameter at breast height (1.37m), total height and incidence of disease or physical damage. Physical damage included dead/broken tops, forks, animal browsing, recent death, or other defining features.

Bark beetles were surveyed in the plots during late August and early September 1999. At each plot, trees at or above that tree species' break diameter were examined for signs of bark beetle attack. Attacks were confirmed as successful and beetle species determined by peeling the bark at the entrance hole and observing the galleries. Insects present in the galleries were collected for identification in the lab. Attacks were recorded for each tree as presence (successful beetle attack) or absence (unsuccessful or no beetle attack). To investigate the relationship between bark beetle attacks and severity of white pine blister rust infection, whitebark pine was also rated for blister rust using an experimental rating system (Figure 2) (Six, Austin and Baker, Unpub.).

Population levels of the pine engraver and the red turpentine beetle were estimated in downed logs and stumps in the Nutcracker opening and slashing treatment areas. Red turpentine beetles were present only in the stumps. A 20% sub-sample, using a nested plot design, was employed in each study plot. Total area of each nested plot was 135.6 m^2. Only lodgepole pine was surveyed, as subalpine fir and Engelmann spruce are not hosts for these beetles. Number of *Ips* attacks in a 10cm wide circle around logs falling within the nested subplot was counted and midpoint diameter recorded for each log in the small plot. Stumps were assessed for *Ips* in the same manner, except diameter and beetle counts were taken at a height of one foot. All attacks by *D. valens* were recorded regardless of position on the stump.

Bear Overlook

Ten permanent plots were established at Bear Overlook during July 1999 in the same manner as the Beaver Ridge permanent plots. An insect survey was conducted on the plots in September 1999.

Forest Service plots

The USDA Forest Service established permanent plots at Beaver Ridge in 1998 (data on file at the Rocky Mountain Fire Sciences Lab in Missoula, MT). Bark beetle surveys were conducted on these plots, in a manner similar to the study plot surveys, in October 1998 and late summer 1999. All trees larger than 7.60cm were included in these surveys.

Data analysis

Data from the Forest Service plots was analyzed using a Chi-square test for independence to test for differences in number of attacks per plot between years. Logistic regression was used to examine plot data for a treatment effect on bark beetle attacks because of its specific application for binary response variables (such as presence/absence of bark beetles). The logistic regression procedure utilizes variances associated with binary response variables, resulting in a more appropriate regression equation (Gumpertz et al. 2000). Tests for homogeneity of variance precluded the use of standard parametric tests for other comparisons in the study plot data. Therefore, non-parametric tests, including the Mann-Whitney, Kruskal-Wallis, Wilcoxon rank, and the Chi-square test for independence, were used. Except for the Forest Service plots, data was analyzed on an individual tree basis. Analysis was performed using SPSS version 9.0.0 (SPSS Inc. 1998).

Results

Flight periods

Flight period results were incomplete due to lack of access to the study site until early July. Pine engravers were not trapped because beetle emergence and flight probably occurred before monitoring had begun. A second flight, which sometimes occurs with the pine engraver, was not observed, and may not take place at high elevations. However, the endemic mountain pine beetle population at Beaver Ridge was large enough to obtain trap catches and observe the flight period. The flight was already underway when monitoring began, and continued, although dwindling, until early October. The flight period had two peaks, one in early August and one in late August (Figure 3). Very few beetles were collected after the end of August. Weather patterns at Beaver Ridge may account for the decrease in trap catches in mid-August, when a week of cool, wet weather occurred.

Stand composition / habitat types

Lodgepole pine was the most abundant tree at the study site, followed by subalpine fir, whitebark pine, and Engelmann spruce (Table 2). Engelmann spruce, while few in number, tended to be the tallest and largest trees (Table 2). Whitebark pine was the shortest and smallest in diameter (Table 2). The most common habitat type was *Abies lasiocarpa / Luzula hitcockii / Vaccinium scoparium*. The only other habitat type encountered was *Abies lasiocarpa / Luzula hitchockii / Menziesia ferruginea*, and was found on wetter sites near drainages. Moister sites were also more likely to support Engelmann spruce.

Insects

Lodgepole pine, subalpine fir and Engelmann spruce

Several secondary beetles were collected from lodgepole pine. These included *Pityogenes knechteli*, *P. carinulatus*, two *Pityopthorus* species, *Ips mexicanus*, *I. pini*, and *I. latidens.* As well, a weevil (*Pissodes spp.*) was collected out of a stump in a Nutcracker opening. No mountain pine beetle attacks were observed on lodgepole pine.

Beetles collected from subalpine fir included western balsam beetle (*Dryocetes confuses* Swaine), *Scolytus ventralis* LeConte, two *Pityopthorus* species, and a bark beetle predator (*Tenebrionidae spp.*). The only insect occurring in Engelmann spruce was the spruce beetle (*D. rufipennis* Kirby).

Whitebark pine

The two bark beetle species collected most frequently from whitebark pine were the mountain pine beetle and *P. fossifrons.* Both beetles were observed aggressively attacking and killing trees at Beaver Ridge. *P. fossifrons* preferred small sapling-sized trees in Nutcracker openings and was rarely observed elsewhere (Tables 3 and 10). Mountain pine beetle preferred larger, mature trees in more closed conditions, frequently with little to no apparent white pine blister rust infection (Table 3).

Several insects were collected from white pine blister rust cankers on the whitebark pine. These included pitch moth and wood borer larvae and adult *P. fossifrons*. Secondary bark beetles collected included a *Pityopthorus spp.*, *I. latidens*, and *I. mexicanus.* The *Pityopthorus* observed in this study were feeding in saplings. Groups of aphids were frequently seen feeding on apparently healthy seedlings. The only predator collected (Colydiidae*: Lasconotus*) was in a small tree infested by *P. fossifrons.*

Two beetles typically associated with timber harvesting, the pine engraver and the red turpentine beetle, were observed in whitebark pine at Beaver Ridge. Populations of both beetles were present in neighboring slash (stumps and downed logs) created by implementation of restoration treatments. Average number of pine engraver entrance holes found in lodgepole pine logs and stumps was 0.169 attacks per $10cm^2$. Red turpentine beetle attacks in lodgepole stumps averaged 0.012 attacks per $10cm^2$. Neither beetle was observed at Bear Overlook, where little slash was created in restoration efforts.

Tree diseases and damages

Diseases observed in whitebark pine included white pine blister rust and dwarf mistletoe (*Arceuthobium spp.*). Overall infection rate of white pine blister rust on the study plots was 78%. However, it does not appear that bark beetles are selecting whitebark pine with more severe white pine blister rust infections (Figure 4). Comparing all whitebark pine, no significant difference was found between levels of blister rust infection in beetle-attacked and non-attacked trees (Wilcoxon-rank comparison: χ^2 = 0.344, p-value =

0.588, df = 1, n = 192). Similarly, beetle attacks were not dependent on white pine blister rust presence (Table 4).

Dwarf mistletoe infection (probably *A. cyanocarpum*) was estimated at 49% in whitebark, and was the most common disease found in lodgepole pine. Western gall rust (*Endocronartium harknessii*) and comandra blister rust (*Cronartium comandrae*) were also present in lodgepole. The only disease found in subalpine fir appeared to be Armillaria root disease (*Armillaria ostoyae*) and no diseases were found in Engelmann spruce at the site. Broken tops occurred in every species, sometimes as a result of white pine blister rust or dwarf mistletoe infection. Snow damage was observed on many lodgepole pine saplings.

Treatment effects

Bark beetles preferentially chose trees according to treatment type and tree height (logistic regression: $\chi^2 = 18.337$, p = .0004, Table 5). Beetles were found more often in the slashing treatment and Nutcracker openings than in the control treatment (Table 5). A mild correlation was found between tree height and treatment type, resulting in a masking effect in the model (Table 6). Broken tops were abundant among all tree species at Beaver Ridge. A comparison of the data set with and without broken trees was warranted, given the significance of tree height in the logistic regression. A comparison of mean tree height by species shows that exclusion of the broken trees had no effect on the overall pattern of tree height between the species (Figure 5).

Treatments were significantly different from each other with respect to slope, aspect, percent canopy cover and tree species (p-values <0.001, Table 7). The Nutcracker opening treatment tended to have steeper slopes, and hence a different aspect, than the other treatments (Figures 6 and 7). Percent canopy cover was also significantly different (Figure 8) but northness index was not (Figure 9).

Comparisons of whitebark and lodgepole pine

Some bark beetles will infest both whitebark and lodgepole pine, including the mountain pine beetle. Therefore, whitebark and lodgepole pine were separated from the overall data set to allow for comparisons between these two species. All whitebark pine trees with a diameter less than 7.60cm were dropped for this comparison because lodgepole pine trees smaller than 7.60cm were not measured in this study Nonparametric tests were used due to heterogeneous variances in some variables (Levene's test, Table 8). Significant differences were found between all measured variables except proportion individual tree damage (Table 9, Figures 10, 11, and 12). Proportion disease is the proportion of trees infected by pathogens, including, but not limited to, white pine blister rust.

Forest Service plots

Little bark beetle activity was found in either year during surveys on the Forest Service plots (Figure 13). A Chi-square test for independence showed no difference between number of attacked plots in 1998 and 1999 ($\chi^2 = 0.15606$, $p = >0.10$).

Discussion

The distribution of trees at Beaver Ridge is suggestive of the fire history of the area. Much of the area burned in 1910 in a stand replacement event (R.E. Keane, pers. comm.). However, the presence of large spruce indicate that perhaps the wettest sites did not burn in the fire, leaving a somewhat patchy distribution of remnant trees in and around the moist drainages. Stand replacement fires are conducive to both lodgepole and whitebark pine regeneration: serrotinous lodgepole cones open and release seeds upon exposure to heat and whitebark pine seeds are cached in recently burned areas by the Clark's Nutcracker.

Treatment type had a significant effect on the distribution of bark beetle attacks at Beaver Ridge. Bark beetles attacked more trees in the slashing and Nutcracker opening treatments than the control treatments. This suggests that management activities, namely cutting, may be stressing the trees and predisposing them to attack. However, due to the significant differences between environmental variables (slope and aspect) among treatments, treatment effects may have been due to confounding factors and not treatment type. Confounding factors may also exist that were not accounted for in this study, such as microclimate or elevation. Treatment location and lack of true replication and randomization limit the inference that can be made from this study; however, the results are suggestive and warrant further investigation.

P. fossifrons, found mostly in small whitebark pine in the Nutcracker opening treatments, exhibited aggressive behavior not previously recorded in whitebark pine. This beetle is usually considered a secondary beetle, attacking only stressed or weakened trees. However, most sapling-sized trees infested by this beetle at Beaver Ridge were rated as uninfected or very low for white pine blister rust and had no other visible damage (Table 10). It is probable that removal of the overstory canopy altered the microclimate, resulting in higher temperatures, increased wind flow, and changes in soil moisture. These factors may have stressed the remaining understory trees. It is also possible that *P. fossifrons* prefers open, sunny sites; however, little is known about the behavior of this beetle.

Pine engraver and red turpentine beetles have not been previously recorded in whitebark pine, perhaps due to two reasons: 1. Slash build-up during harvesting operations was not a problem historically due to lack of management in high elevation ecosystems. Such build-up can support large populations of these beetles, and may lead to subsequent attacks on whitebark pine. 2. These beetles have always infested whitebark pine but were not observed due to the lack of research on whitebark pine insects. It should be noted that while attacks by these beetles were observed in whitebark pine, they did not attack any live trees occurring on study plots or Forest Service plots. This indicates that these two beetles were not responsible for the significant treatment effect.

Mountain pine beetle prefers larger diameter trees (>10-12cm) due to their thicker phloem layer (Cole and Amman 1980). Whitebark pine has been found to have thicker phloem than lodgepole pine of similar diameters (Baker et al. 1971, Austin and Six unpub. data), which should create better reproductive conditions for the mountain pine beetle (Cole and Amman 1980). Comparison studies of limber pine (*Pinus flexilis* James), a close relative of whitebark pine, and lodgepole pine have shown that limber pine is a better host for the mountain pine beetle, possibly due to thicker and more nutritious phloem (Langor 1989, Langor and Spence1990, Langor et al. 1991, Cerezke 1995). However, Amman (1982) found no host effects when rearing mountain pine beetle in lodgepole and whitebark pine.

At Beaver Ridge, lodgepole pine has a significantly larger mean diameter than whitebark pine, however, mountain pine beetle was found attacking only whitebark pine. The phloem thickness of the mean diameter tree of each species may be similar, since whitebark pine tends to have thicker phloem. Hence, the larger lodgepole pine may be equivalent to smaller diameter whitebark pine as a host in regard to phloem thickness. Factors affecting mountain pine beetle host tree preference may include differences between the two tree species with regard to host vigor or suitability (Mitchell et al. 1983, Larsson et al.1983). Studies have found that localized endemic mountain pine beetle populations often prefer a particular host tree species even when other suitable host tree species are also present (Kulhavy 1984, Bartos and Schmitz 1998). The mountain pine beetle population at Beaver Ridge, ID, was endemic at the time of this study. Since white pine blister rust does not appear to be affecting the selection of a host tree, mountain pine beetle appears to prefer whitebark pine to lodgepole pine at this site.

The relatively small sample size of bark beetle-attacked whitebark pine made the examination of the relationship between white pine blister rust and bark beetle attacks difficult to assess. Previous research has linked mountain pine beetle host selection with incidence of root disease, comandra blister rust, and possibly white pine blister rust (Bartos and Schmitz 1998, Kulhavy et al. 1984, Rasmussen 1987, Eckberg et al. 1994); however, these findings are not indicative of the pattern seen at Beaver Ridge, where bark beetles appeared to be selecting trees with little to no rust. A study of endemic mountain pine beetle populations in whitebark pine in Canada found that only nine of seventeen beetle-infested trees had white pine blister rust (Campbell 1998). White pine blister rust may cause changes in the phloem of infected trees, creating conditions that are not conducive to successful bark beetle reproduction and survival.

Microclimate cannot be discounted as a possible factor affecting mountain pine beetle host selection. Lodgepole and whitebark pine are growing in significantly different environments. Changes in stand structure across the restoration area are apparent: the lowest elevations are dominated by lodgepole pine, with other tree species occurring as widely scattered individuals. With increasing elevation, the density of whitebark and subalpine fir also increases, while lodgepole pine density decreases. In addition to the elevation gradient, there are significant differences in mean slope and aspect, resulting in dissimilar growing conditions. Research into microclimate affects on mountain pine beetle host selection has been inconclusive (Amman and Logan 1998, Bartos and Amman 1989). However, microclimate may play a role in host selection behavior and beetle distribution at Beaver Ridge.

Significant treatment effects on the distribution of bark beetle attacks were observed, even under the low endemic population levels present at Beaver Ridge during the study. If restoration treatments were responsible for the increase in beetle attacks seen in the slashing and nutcracker opening treatments, then threats to whitebark pine may be considerable in areas with moderate to high bark beetle populations. In such situations, when restoration treatments are implemented, mitigating techniques could be developed to prevent loss of high value whitebark pine from bark beetles. High value trees may include large, cone-bearing trees with little to no white pine blister rust infection. Such trees may be genetically resistant to white pine blister rust and can provide seed for regeneration. Possible preventative techniques include the use of anti-aggregant pheromones and prophylactic treatments with pesticides. Verbenone is the anti-aggregant pheromone of the mountain pine beetle, and has been shown, in some studies, to protect stands of lodgepole pine from the mountain pine beetle (Lindgren et al. 1989, Gibson et al. 1991, Amman et al. 1991, Amman and Lindgren 1993, Amman and Ryan 1994), however, results have been variable. Anti-aggregant pheromones are probably not an option for the pine engraver, as access to whitebark pine sites is usually restricted until after the flight has occurred. Carbaryl is an effective pesticide useful in protecting lodgepole pine from the mountain pine beetle for up to two seasons, which includes success in high elevation areas (Haverty et al. 1998, Page et al. 1985, Gibson and Bennett 1985). These techniques could be tested for effectiveness in protecting whitebark pine at the same time restoration treatments are implemented.

The research presented indicates that we should be aware of the consequences of trying to re-establish historic conditions in whitebark pine ecosystems. Managers need to monitor bark beetle populations and consider mitigating measures if necessary. Future research is needed in many aspects of whitebark pine ecosystems and their interactions with insects, especially bark beetles. Research focusing on mountain pine beetle host effects and preference is needed, especially between whitebark and lodgepole pine. Further research into white pine blister rust effects on tree physiology and phloem conditions in whitebark pine would quantitatively demonstrate the quality of infected whitebark pine as a host for mountain pine beetle.

While most of the insects described in this study do not cause economic damage, they may be cause for concern in regeneration. Several insects, especially *P. fossifrons*, warrant further research, perhaps combined with an investigation of tree physiology. Research on white pine blister rust, such as the possible beneficial effects of white pine blister rust on the success of various insects utilizing the cankers, would expand current knowledge of this disease and its relationship to insects. Little is known about the ecology and behavior of *P. fossifrons,* such as host selection and detailed life history. Additionally, the role of *P. fossifrons* as an aggressive bark beetle should be examined further, along with an investigation of the effect of Nutcracker openings and slashing treatments on understory whitebark pine vigor and physiology.

References

Aho, P.E., G. Fiddler and G.M. Filip. 1983. How to reduce injuries to residual trees during stand management activities, USDA For. Serv. Pac. NW For. and Range Exp. Stn., Portland, OR. 17 pp.

Amman, G.D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Env. Ent. 11: 590-593.

Amman, G.D., R.W. Thier, J.C. Weatherby, L.A. Rasmussen and A.S. Munson. 1991. Optimum dosage of verbenone to reduce infestation of mountain pine beetle in lodgepole pine stands of central Idaho, USDA For. Serv. Int. Res. Stn., Ogden, UT. 4 pp.

Amman, G.D. and B.S. Lindgren. 1993. Semiochemicals for management of mountain pine beetle: status of research and application. *In:* S.M. Salom and K.R. Hobson (ed.) Application of semiochemicals for management of bark beetle infestations., USDA For. Serv. Int. Res. Stn., Ogden, UT, Indianapolis, IN.

Amman, G.D. and K.C. Ryan. 1994. Using pheromones to protect heat-injured lodgepole pine from mountain pine beetle infestation, USDA For. Serv. Res. Note INT-419, Ogden, UT. 7 pp.

Amman, G.D. and J.A. Logan. 1998. Silvicultural control of mountain pine beetle: Prescriptions and the influence of microclimate. Am. Ent. 44: 166-177.

Arno, S.F. 1986. Whitebark pine cone crops - A diminishing source of wildlife food? W. J. of App. For. 1: 92-94.

Arno, S. F. and R. J. Hoff. 1989. Silvics of whitebark pine. US For. Serv. Gen. Tech. Rep. INT-253. 11 pp.

Baker, B. H., G. D. Amman and G. C. Trostle. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands? U.S. For. Serv. Res. Note INT-151. 7 pp.

Bartos, D.L. and G.D. Amman. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations, USDA For. Ser. Int. Res. Stn. Res. Paper INT-400, Ogden, UT. 10 pp.

Bartos, D.L. and K.E. Gibson. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. pp. 171-178. *In:* W.C. Schmidt & K.J. McDonald (comp.) Proceed.- Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource, USDA For. Serv. Gen. Tech. Rep. INT-270, Bozeman, MT.

Bartos, D.L. and R.F. Schmitz. 1998. Characteristics of endemic-level mountain pine beetle populations in south-central Wyoming, USDA For. Serv. Res. Paper RMRS-RP-13, Ogden, UT. 9 pp.

Beers, T.W., P.E. Dress and L.C. Wensel. 1966. Aspect transformation in site productivity research. J. of For. 64: 691-692.

Bright, D.E., Jr. 1968. Three new species of *Pityophthorus* from Canada (Coleoptera: Scolytidae). Can. Ent. 100: 604-608.

Borchert, M.I., Davis, F.W., Michaelson, J., and L.D. Oyler. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology 70(2): 389-404.

Campbell, E.M. 1998. Whitebark pine forests in British Columbia: Composition, dynamics and the effects of blister rust. Master's Thesis. Univ. Victoria. 136 pp.

Ciesla, W.M. and M.M. Furniss. 1975. Idaho's haunted forests. Am. For. 81: 32-35.

Cerezke, H.F. 1995. Egg gallery, brood production, and adult characteristics of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) in three pine hosts. Can. Ent. 127: 955-965.

Cole, W.E. and G.D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests Part I: Course of an infestation, USDA For. Serv. Int. For. and Range Exp. Stn. Gen. Tech. Rep. INT-89, Ogden, UT. 56 pp.

Eckberg, T.B., J.M. Schmid, S.A. Mata and J.E. Lundquist. 1994. Primary focus trees for the mountain pine beetle in the Black Hills, USDA For. Serv. Rocky Mtn. Forest and Range Exp. Stn. Res. Note RM-RP-531, Fort Collins, CO. 11 pp.

Furniss, M.M., R.D. Hungerford and E.F. Wicker. 1972. Insects and mites associated with western white pine blister rust in Idaho. Can. Ent. 104: 1713-1715.

Furniss, R.L. and V.M. Carolin. 1977. Western Forest Insects. USDA For. Serv. Misc. Pub. No. 1339, Washington, D.C. 654 pp.

Gibson, A.L. 1943. Penetrating sprays to control the mountain pine beetle. J. Econ. Ent. 36: 396-398.

Gibson, K.E. and D.D. Bennett. 1985. Effectiveness of carbaryl in preventing attacks on lodgepole pine by the mountain pine beetle. J. For. 83: 109-112.

Gibson, K.E., R.F. Schmitz, G.D. Amman and R.D. Oakes. 1991. Mountain pine beetle response to different verbenone dosages in pine stands of western Montana. USDA For. Serv. Int. Res. Stn. Res. Paper INT-444, Ogden, UT. 11 pp.

Gumpertz, M.L., C. Wu and J.M. Pye. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. For. Sci. 46: 95-107.

Haverty, M.I., P.J. Shea, J.T. Hoffman, J.M. Wenz and K.E. Gibson. 1998. Effectiveness of Esfenvalerate, Cyfluthrin, and Carbaryl in protecting individual lodgepole pines and ponderosa pines from attack by *Dendroctonus* spp., USDA For. Serv. Pac. SW Res. Stn. Res. Paper PSW-RP-237, Albany, CA. 12 pp.

Keane, R.E. and S.F. Arno. 1993. Rapid decline of whitebark pine in western Montana: evidence from 20-year remeasurements. W. J. of App. For. 8: 44-47.

Keane, R. E. and S. F. Arno. 1996. Whitebark pine ecosystem restoration in western Montana. pp. 51-54. In: The Use of Fire in Forest Restoration. Proceed. Society for Ecological Restoration, Seattle, WA. Sept. 14-16, 1995. U.S. For. Serv. Gen. Tech. Rep. INT-GTR-341.

Kegley, S. and N. Campbell. 1997. Cone and seed insects affecting whitebark pine. Nut. Notes No. 8.

Kendall, K.C. and S.F. Arno. 1990. Whitebark pine-an important but endangered wildlife resource. pp. 264-272. *In:* W.C. Schmidt & K.J. McDonald (ed.) Proceedings-Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource, USDA For. Ser. Int. Res. Stn. INT-270, Ogden, UT.

Kulhavy, D. L., A. D. Partridge and R. W. Stark. 1984. Root diseases and blister rust associated with bark beetles (Coleoptera: Scolytidae) in western white pine in Idaho. Env. Ent. 13: 813-817.

Langor, D.W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Ent. 121: 149-157.

Langor, D.W. and J.R. Spence. 1991. Host effects on allozyme and morphological variation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Ent. 123: 395-410.

Langor, D.W., J.R. Spence and G.R. Pohl. 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Evol. 44: 609-618.

Larsson, S., R. Oren, R.H. Waring and J.W. Barrett. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. For. Sci. 29: 395-402.

Lindgren, B.S., J.H. Borden, G.H. Cushon, L.J. Chong and C.J. Higgins. 1989. Reduction of mountain pine beetle (Coleoptera: Scolytidae) attacks by verbenone in lodgepole pine stands in British Columbia. Can. J. of For. Res. 19: 65-68.

Mattson, D.J., B.M. Blanchard and R.R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. J. Wildlife Man. 56: 432-442.

McCool, S.F. 1998. The diminished landscape: Aesthetic and recreational consequences. Speech at: Restoring Whitebark Pine Ecosystems Symposium. Sept. 9-12. Missoula, MT.

Miller, J.M. and F.P. Keen. 1960. Biology and control of the western pine beetle, USDA For. Serv. Misc. Pub. 800, Washington, D.C. 381 pp.

Mitchell, R.G., R.H. Waring and G.B. Pitman. 1983. Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. For. Sci. 29: 204-211.

Page, M., M.I. Haverty and C.E. Richmond. 1985. Residual activity of carbaryl protected lodgepole pine against mountain pine beetle, Dillon, Colorado, 1982 and 1983, USDA For. Serv. Pac. SW For. and Range Res. Stn. Res. Note PSW-375, Berkeley, CA. 4 pp.

Pfister, R.D., Kovalchik, B.L., Arno, S.F., and R.C. Presby. 1977. Forest Habitat Types of Montana. U.S. For. Serv. Gen. Tech. Rep. INT-34. 174 pp.

Rasmussen, L.A. 1987. Mountain pine beetle selection of dwarf mistletoe and comandra blister rust infected lodgepole pine. USDA For. Ser. Int. Res. Stn. Res. Note INT-367, Ogden, UT. 4 pp.

Tomback, D.F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: A mutualism hypothesis. J. Anim. Ecol. 51: 451-467.

Tomback, D.F., Clary, J.K., Koehler, J., Hoff, R.J., and S.F. Arno. 1990. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance Burn of Northern Idaho (U.S.A.). Cons. Bio. 9(3): 654-664.

Wilson, D., Coyner, J., and T. Deckert. 1983. Land System Inventory of the Clearwater National Forest, First Draft Review. USDA For. Serv. 398 pp.

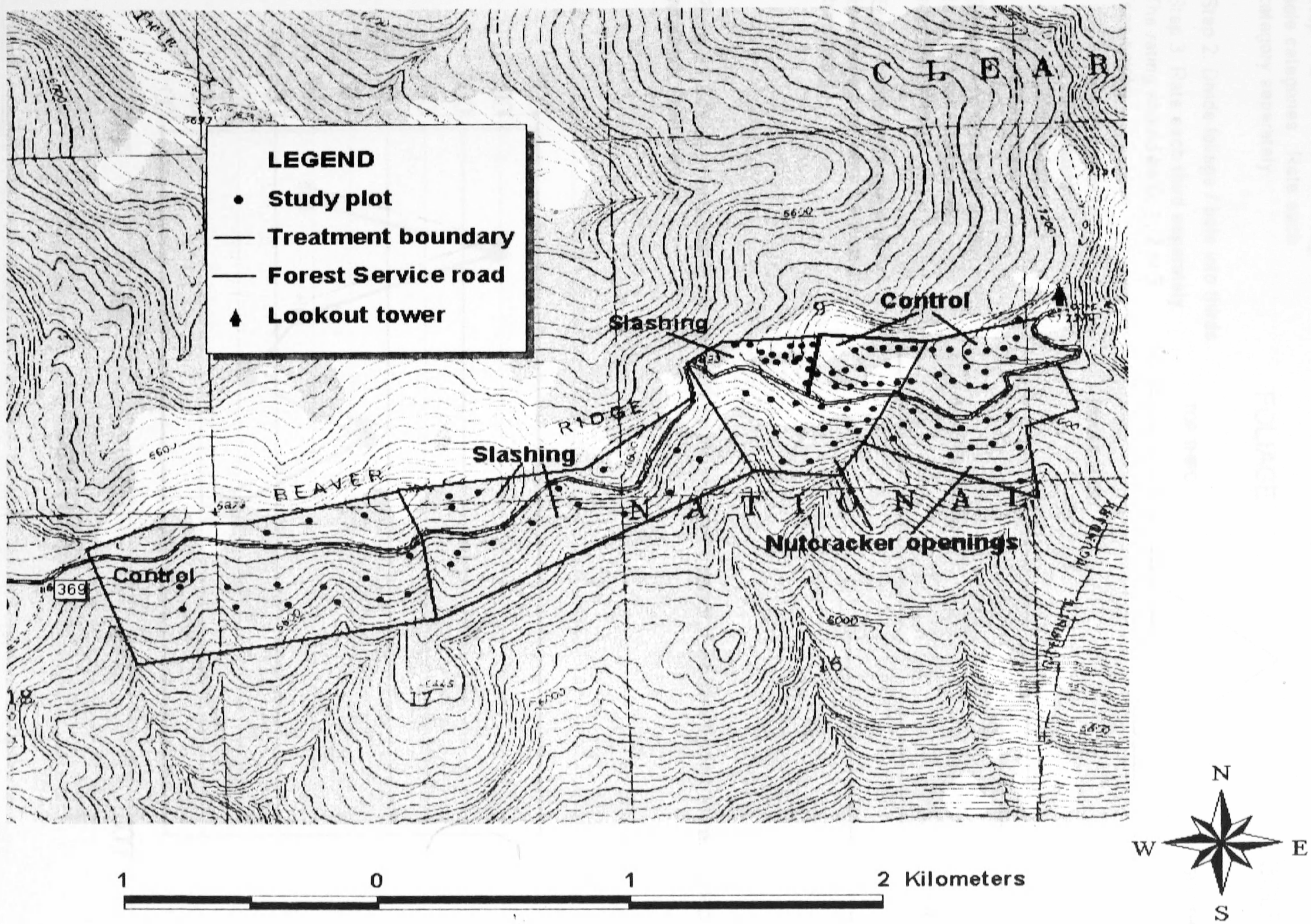

Figure 1. Plot and treatment layout at Beaver Ridge, showing treatment boundaries and plot center locations.

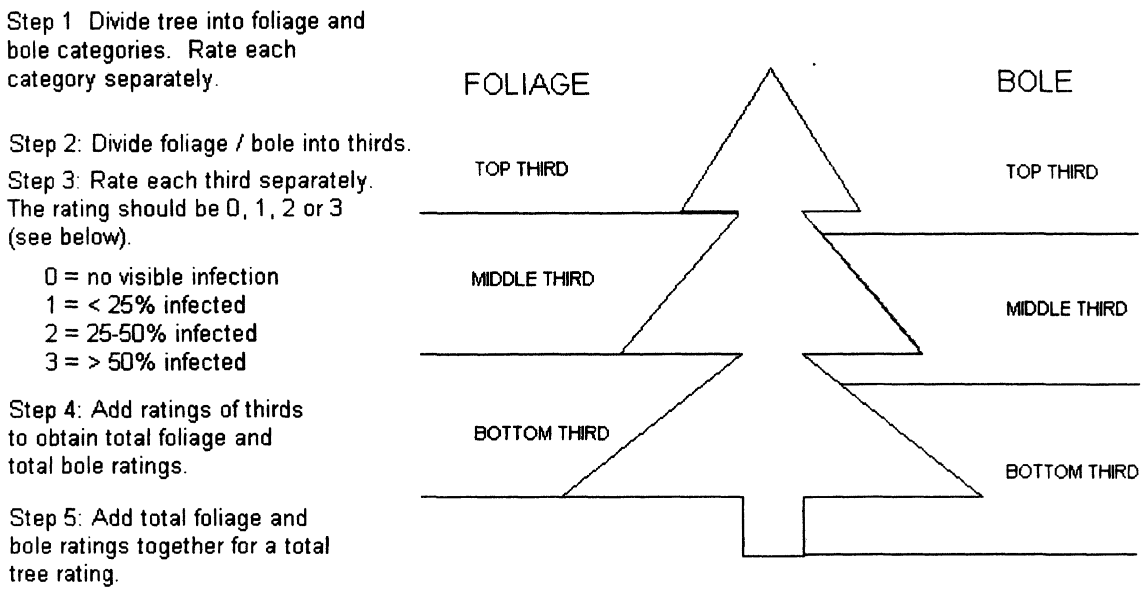

Figure 2. White pine blister rust severity rating system used at Beaver Ridge to rate individual whitebark pine trees.

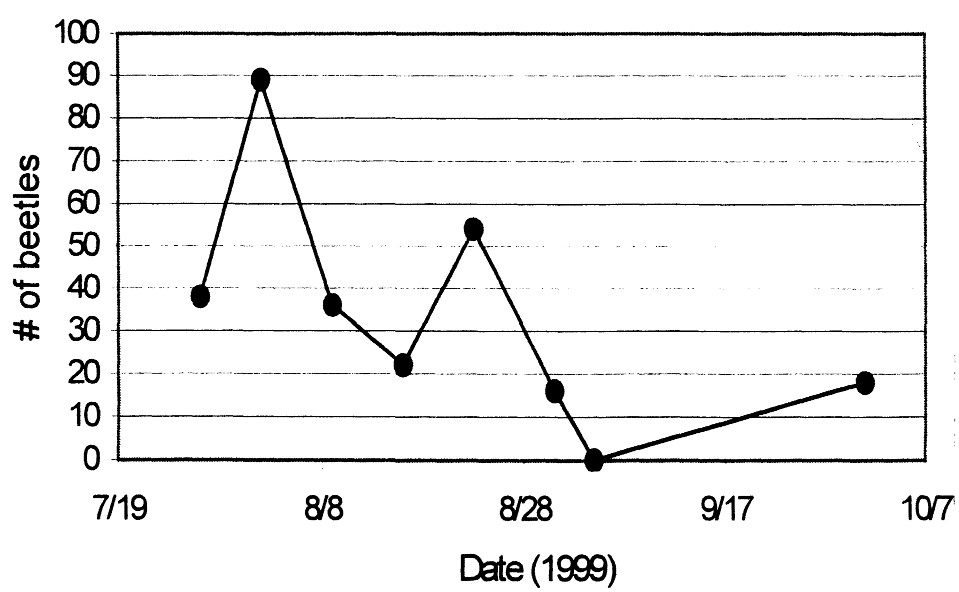

Figure 3. 1999 flight period for the mountain pine beetle at Beaver Ridge. Numbers are the total number of beetles in the trap on collection dates.

Figure 4. Relationship of whitebark pine attacked by bark beetles and white pine blister rust severity. All diameters are represented. Two off-plot trees are included that were not included in the main study. See Figure 2 for white pine blister rust severity rating system.

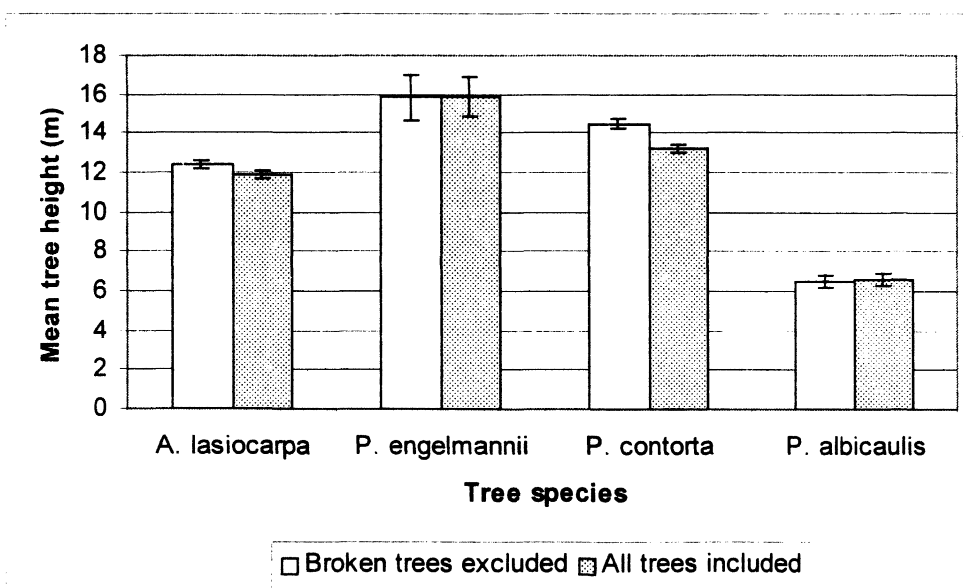

Figure 5. Mean total tree height comparison of all measured trees at Beaver Ridge.

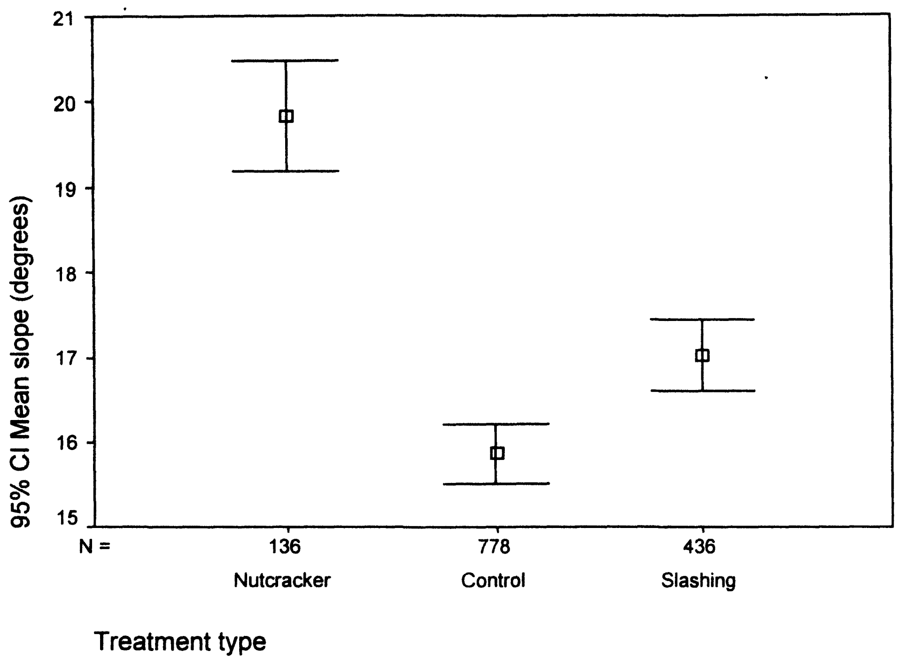

Figure 6. Comparison of mean slope for individual trees on plots located in the three treatment types present at Beaver Ridge during summer 1999.

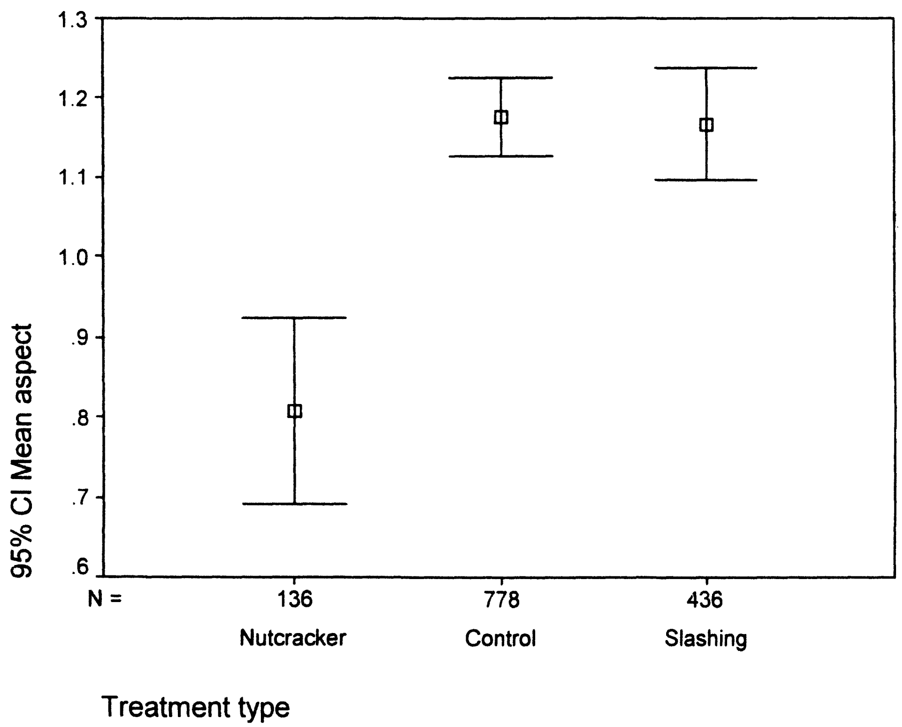

Figure 7. Comparison of mean aspect for individual trees on plots located in the three treatment types present at Beaver Ridge during summer 1999.

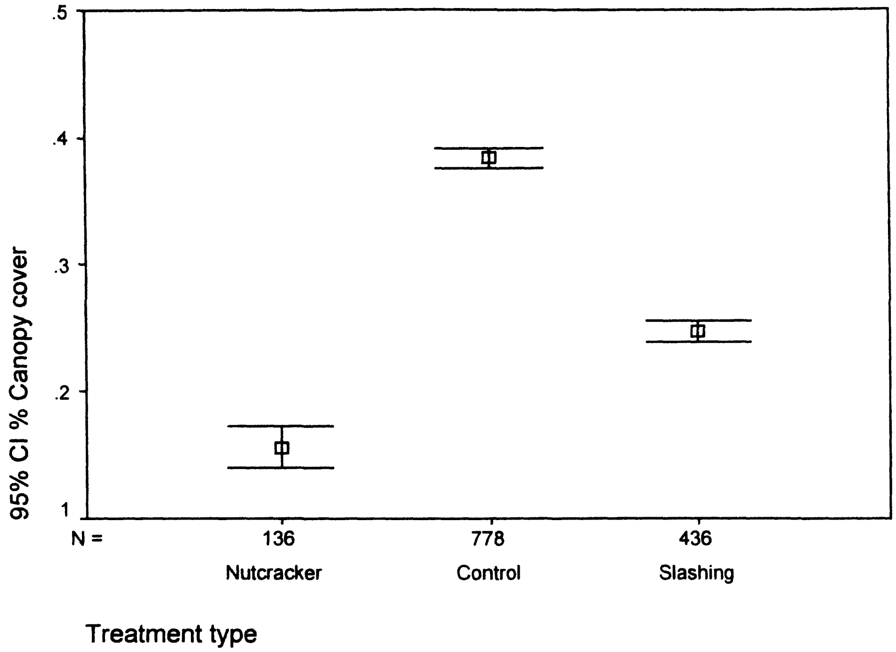

Figure 8. Comparison of mean percent canopy cover for individual trees on plots located in the three treatment types present at Beaver Ridge during summer 1999.

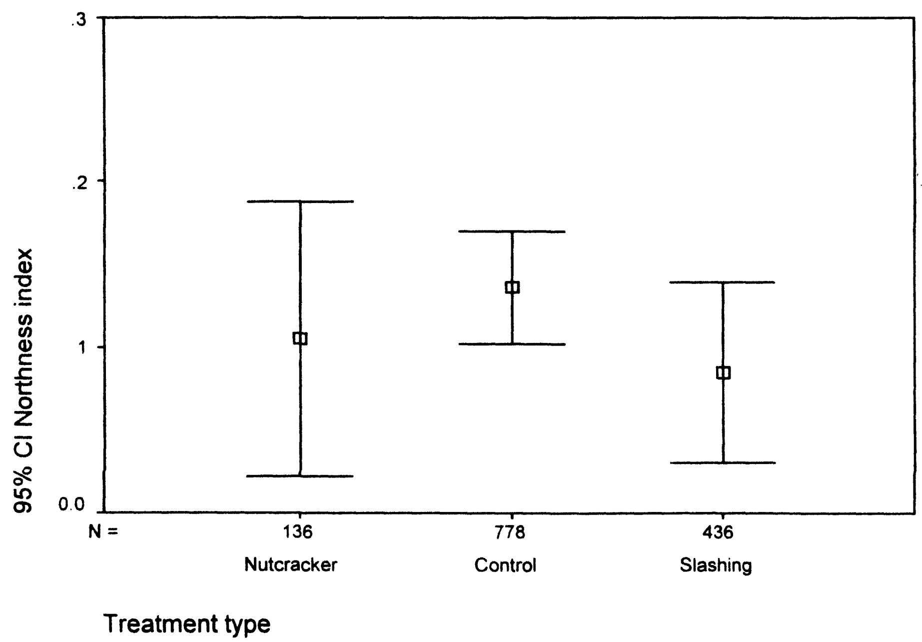

Figure 9. Comparison of mean northness index for individual trees on plots located in the three treatment types present at Beaver Ridge during summer 1999.

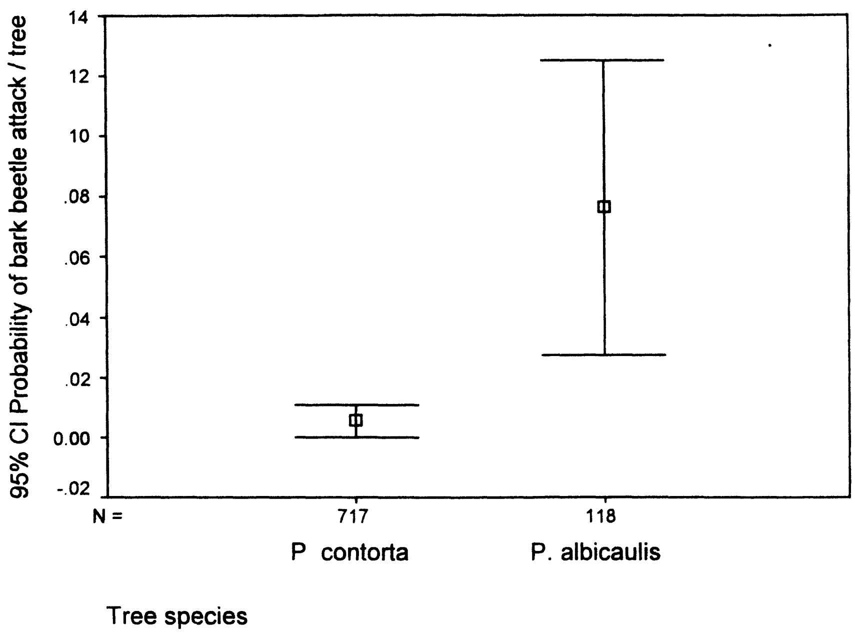

Figure 10. Comparison of mean probability of bark beetle attack per tree for all measured (>7.60cm) lodgepole pine and whitebark pine at Beaver Ridge.

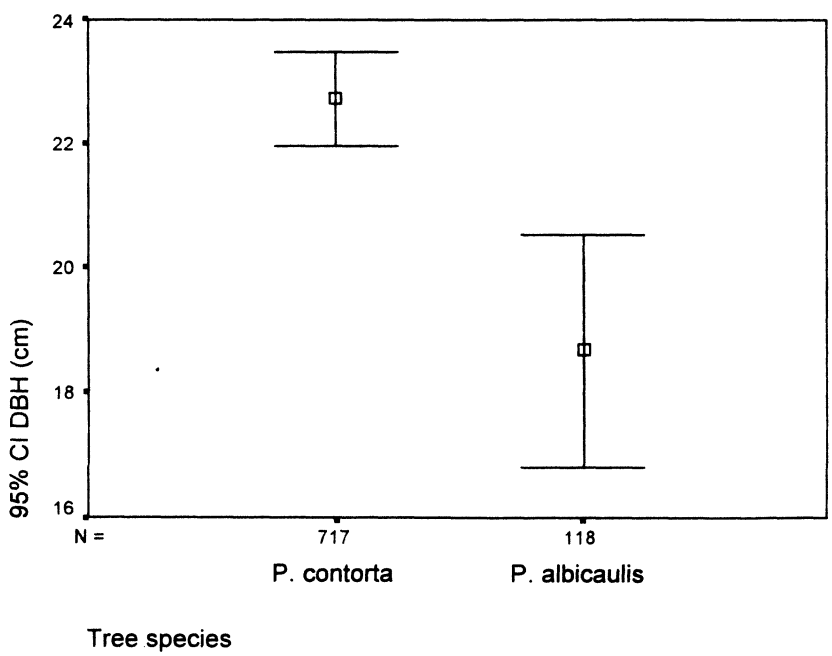

Figure 11. Comparison of mean diameter at breast height for all measured (>7.60cm) lodgepole pine and whitebark pine at Beaver Ridge.

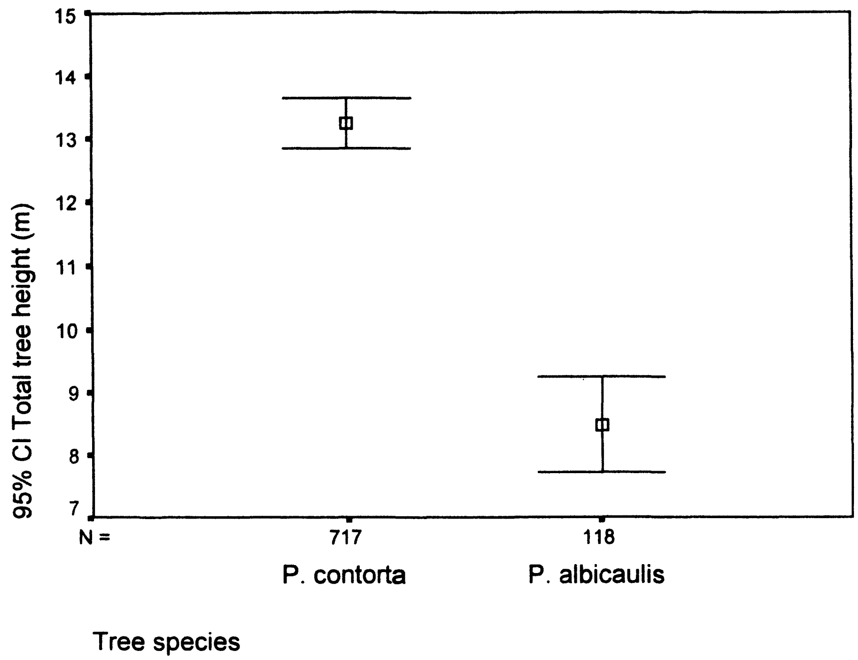

Figure 12. Comparison of mean total tree height for all measured (>7 60cm) lodgepole pine and whitebark pine, Beaver Ridge.

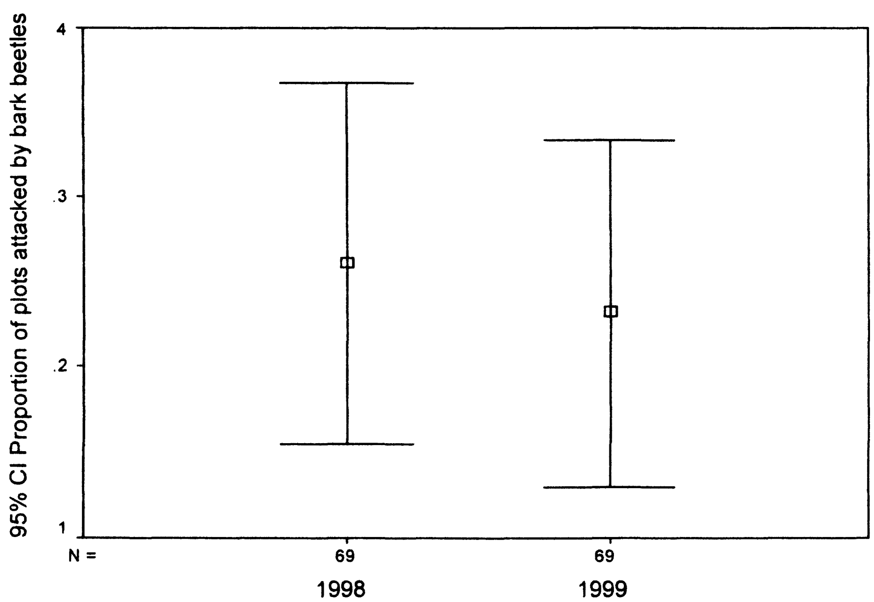

Figure 13. Mean proportion Forest Service plots attacked by bark beetles in 1998 and 1999, Beaver Ridge.

Table 1. Breakpoint diameter at breast height (1.37m) by species used in establishing permanent study plots, Beaver Ridge.

Tree species	Breakpoint DBH
Pinus albicaulis	5.08cm (2in)
Pinus contorta	7.60cm (3in)
Abies lasiocarpa	12.70cm (5in)
Picea engelmanii	12.70cm (5in)

Table 2. Summary of measured tree and site variables by tree species, Beaver Ridge.
Habitat type coding: 1 = ABLA / LUHI-VASC 2 = ABLA / LUHI-MEFE

Tree species	DBH (cm)	Height (m)	Prop. Beetle attacks	% Canopy Cover	Prop. Disease	Prop. Damage	Slope (°)	Aspect	Northness Index	Habitat type
Pinus albicaulis (N=193)										
Mean	13.71	6.61	0.06	0.24	0.87	0.47	16.96	1.13	0.04	1.03
Minimum	4.90	1.83	0.00	0.03	0.00	0.00	7.00	0.00	-0.92	1.00
Maximum	44.02	21.34	1.00	0.60	1.00	1.00	26.00	2.00	0.99	2.00
Std. Dev.	10.14	4.02	0.24	0.13	0.34	0.50	5.04	0.72	0.50	0.11
Pinus contorta (N=718)										
Mean	22.71	13.24	0.01	0.33	0.12	0.51	18.12	1.17	0.16	1.01
Minimum	7.14	1.52	0.00	0.05	0.00	0.00	7.00	0.00	-0.92	1.00
Maximum	61.28	28.19	1 00	0.60	1.00	1.00	28.00	2.00	0.99	2.00
Std. Dev	10.37	5.63	0.07	0.14	0.33	0.50	4.25	0.75	0.53	0.11
Abies lasiocarpa (N=396)										
Mean	20.72	11.91	0.02	0.32	0.10	0.27	14.00	1.08	0.08	1.06
Minimum	10.50	1.37	0.00	0.07	0.00	0.00	7.00	0.00	-0.92	1.00
Maximum	44.38	29.26	1 00	0.55	1.00	1.00	25.00	2.00	0.97	2.00
Std. Dev	6.39	3.83	0.13	0.11	0.29	0.44	4.53	0.68	0.49	0.24
Picea engelmannii (N=43)										
Mean	33.30	15.85	0.00	0.32	0.02	0.37	15.47	1.06	0.12	1.16
Minimum	11.87	6.71	0.00	0.10	0.00	0.00	7.50	0.00	-0.61	1.00
Maximum	79.48	35.66	0.00	0.55	1.00	1.00	25.00	2.00	0.97	2.00
Std. Dev	16.34	6.44	0.00	0.11	0.15	0.49	4.49	0.67	0.41	0.37
GRAND TOTAL (N=1350)										
Mean	21 18	11.98	0.02	0.32	0.22	0.43	16.63	1.14	0.12	1.03
Minimum	4.90	1.37	0.00	0.03	0.00	0.00	7.00	0.00	-0.92	1.00
Maximum	79.48	35.66	1.00	0.60	1.00	1.00	28.00	2.00	0.99	2.00
Std. Dev	10.30	5.49	0.13	0.13	0.41	0.49	4.80	0.72	0.51	0.18

Table 3. Summary characteristics of trees attacked by *P. fossifrons* and *D. ponderosae,* Beaver Ridge.

Beetle species	DBH (cm)	Height (m)	Canopy Cover (%)
Pityogenes fossifrons (N = 4)			
Mean	7.84	4.11	9
Std. Dev.	2.28	1.66	8
Min.	5.43	1.83	5
Max.	10.90	5.79	20
Dendroctonus ponderosae (N = 6)			
Mean	31.29	11.80	29
Std. Dev.	9.75	3.50	7
Min.	18.26	5.70	20
Max.	44.02	15.39	40

Table 4. Chi-square contingency table on the relationship between bark beetle attacks and white pine blister rust infection in whitebark pine at Beaver Ridge.
WPBR = white pine blister rust.
Chi square test for independence: χ^2 = 1.8173, p-value > .10, df =1

Beetles	WPBR present	WPBR absent	Total
Attacked	7	5	12
Not attacked	144	36	180
Total	151	41	192

Table 5. Logistic regression of bark beetle attacks by treatment type and tree height, Beaver Ridge. The Wald statistic and corresponding p-value determine significance of the variables.

Variable	ß	S.E.	Wald statistic	df	p-value
Constant	-2.9934	0.6162	23.5951	1	<0.001
Slashing			6.3476	2	0.0418
Nutcracker openings	1.3035	0.6065	4.6186	1	0.0316
Control	0.1600	0.0472	0.0864	1	0.7688
Tree Height	-0.1382	0.0472	8.5839	1	0.0034

Table 6. Pearson's correlations: Correlations between measured tree / site variables and bark beetle presence / absence.
NI = Northness Index

		Tree spp.	Slope	Aspect	NI	Habitat type	% Canopy cover	Trtmt type	DBH (cm)	Height (m)	Prop. beetle attacks	Prop. disease incidence	Prop. damage incidence
Tree spp.	Pearson Correlation	1.000	.314**	.044	.024	- 119**	-.090**	- 127**	-.109**	- 145**	.048	.389**	192**
	p-value. (2-tailed)		.000	.104	.378	.000	.001	.000	.000	.000	.076	.000	.000
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Slope	Pearson Correlation	.314**	1.000	.110**	-.045	159**	-.121**	-.068*	.020	130**	.029	-.018	174**
	p-value. (2-tailed)	.000		.000	100	.000	.000	.012	.455	.000	.285	.501	.000
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Aspect	Pearson Correlation	.044	110**	1.000	191**	- 125**	.029	.097**	-.031	.002	-.014	-.021	.037
	p-value. (2-tailed)	104	.000		.000	.000	.284	.000	.253	.937	.609	.445	.179
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
NI	Pearson Correlation	.024	-.045	191**	1.000	-.047	181**	-.029	-.025	.014	.004	-.056*	-.018
	p-value. (2-tailed)	.378	100	.000		.086	.000	.288	.360	.610	.886	.039	.514
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Habitat type	Pearson Correlation	-.119**	.159**	-.125**	-.047	1.000	-.024	-.061*	.088**	.098**	-.024	-.038	-.035
	p-value. (2-tailed)	.000	.000	.000	.086		.372	.026	.001	.000	.369	166	.202
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
% Canopy cover	Pearson Correlation	-.090**	- 121**	.029	.181**	-.024	1.000	-.077**	-.062*	.080**	-.052	-.278**	-.060*
	p-value. (2-tailed)	.001	.000	.284	.000	.372		.005	.022	.003	.058	.000	.027
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Trtmt type	Pearson Correlation	-.127**	-.068*	.097**	-.029	-.061*	-.077**	1.000	.007	.063*	-.067*	- 185**	-.053
	p-value. (2-tailed)	.000	.012	.000	.288	.026	.005		.805	.020	.014	.000	.050
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
DBH (cm)	Pearson Correlation	- 109**	.020	-.031	-.025	.088**	-.062*	.007	1.000	.800**	-.014	-.056*	.024
	p-value. (2-tailed)	.000	.455	.253	.360	.001	.022	.805		.000	.613	.039	.374
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Height (m)	Pearson Correlation	- 145**	130**	.002	.014	.098**	.080**	.063*	.800**	1.000	-.092**	- 168**	-.159**
	p-value. (2-tailed)	.000	.000	.937	.610	.000	.003	.020	.000		.001	.000	.000
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Prop. beetle attacks	Pearson Correlation	.048	.029	-.014	.004	-.024	-.052	-.067*	-.014	-.092**	1.000	.056*	118**
	p-value. (2-tailed)	.076	.285	.609	.886	.369	.058	.014	.613	.001		.041	.000
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Prop. disease incidence	Pearson Correlation	.389**	-.018	-.021	-.056*	-.038	-.278**	- 185**	-.056*	- 168**	.056*	1.000	.063*
	p-value. (2-tailed)	.000	.501	.445	.039	166	.000	.000	.039	.000	.041		.022
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350
Prop. damage incidence	Pearson Correlation	192**	174**	.037	-.018	-.035	-.060*	-.053	.024	- 159**	118**	.063*	1.000
	p-value. (2-tailed)	.000	.000	179	.514	.202	.027	.050	.374	.000	.000	.022	
	N	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350	1350

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 7 Kruskal-Wallis test for significant differences of measured tree / site variables between the three treatment types present at Beaver Ridge during summer 1999.
N (individual trees) = 136 (Nutcracker openings), 436 (Slashing) and 778 (Control).

	Slope	Aspect	% canopy cover	Tree species	Northness Index
Chi-Square	69.693	31.634	504.162	117.794	4 190
df	2	2	2	2	2
Asymp. sign. (p-value)	< 0.001	< 0.001	< 0.001	< 0.001	0.123

Table 8. Test for homogeneity of variance in the measured tree / site variables.
Data was grouped by tree species (lodgepole pine and whitebark pine only).

	Levene's statistic	p-value
Slope	2.810	0.094
Aspect	6.228	0.013
Northness index	2.092	0.148
Habitat type	25.465	<0.001
% canopy cover	3.110	0.078
Treatment type	0.552	0.458
DBH (cm)	0.746	0.388
Height (m)	23.605	<.001
Prop. Disease	0.028	0.868
Prop. Damage	2.811	0.094
Prop. Beetle attacks	144.249	<.001

Table 9. Mann-Whitney U test for significant differences of measured tree / site variables between lodgepole pine and whitebark pine, Beaver Ridge.

	Mann-Whitney U	Wilcoxon W	Z	Asymp. Sign. (p-value)
Slope	32650.5	39671.5	-3.988	<.001
Aspect	37421.0	44442.0	-2.013	.044
Northness Index	36270.0	43291.0	-2.486	.013
Habitat type	40982.5	298385.5	-2.537	.011
% Canopy cover	29555.5	36576.5	-5.299	<.001
Treatment type	34135.5	41156.5	-3.752	<.001
DBH (cm)	31772.0	38793.0	-4.338	<.001
Height (m)	21288.0	28309.0	-8.656	<.001
Prop. Disease	10152.0	267555.0	-18.203	<.001
Prop. Damage	40662.5	47683.5	-.780	.333
Prop. Beetle attacks	39312.5	296715.5	-5.744	<.001

Table 10. Whitebark pine location and white pine blister rust infection level of trees infested with *P fossifrons* at Beaver Ridge.
WPBR = white pine blister rust.

Tree #	WPBR rating, whole tree	Treatment type
1	1	Nutcracker opening
2	0	Nutcracker opening
3	0	Nutcracker opening
4	16	Slashing