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Mountain Pine Beetles: A Century of Knowledge, Control Attempts, and Impacts Central to the Black Hills

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Abstract

This publication chronicles the understanding, controlling, and impacts of mountain pine beetles (MPB) central to the Black Hills of South Dakota and Wyoming from the time they were described by Hopkins in 1902, through the presentation of data from work started by Schmid and Mata in 1985. The plots established by these two men from 1985 through 1994 were subjected to the most intense MPB stress to occur since 1900 in the Black Hills. The differentiation of western bark beetle species is discussed and how the final species designations of MPBs and western pine beetles (WPB) came about. The life cycle of MPBs is described and how it was used to develop direct control strategies. Bark beetles carry from tree to tree with them a suite of mites, fungi, nematodes, bacteria, and other organisms that can be both antagonistic and beneficial to the bark beetle and several of these contribute to the death of the tree. The direct control efforts of peeling, burning, harvesting, and spraying trees with chemicals to kill WPBs and MPBs are described. Both Crater Lake and the Black Hills experiences to directly control MPBs are discussed. The millions of dollars that were spent to directly control both species of bark beetles were futile and indirect methods of tree and stand treatments were tried. In the Black Hills, Schmid and Mata established 46 MPB study plots, of which 39 were useable, beginning in 1985 with tree densities ranging from 44 feet^2 of basal area per acre to 199 feet^2 per acre. MPB-caused tree mortality commenced on some of the plots in 1985 and maximum tree densities occurring on the plots ranged from 75 feet^2 of basal area per acre to 217 feet^2. During this time, MPB populations within the Hills expanded and the fate of the trees on each plot is shown. Plots with densities over 150 feet^2 of basal area per acre experienced major mortality as early as 1987 and all of the plots with densities of 90 feet^2 of basal area per acre or greater experienced major mortality by 2010. Stands and landscapes within the Black Hills with tree densities ranging from 40 to 80 feet^2 of basal area per acre showed considerable resistance to MPBs. Most likely these outcomes were related to the disruption of pheromone plumes facilitated by the open canopy conditions. However, there were exceptions to these findings currently and historically and they are discussed. This publication strives to synthesize a large portion of the information produced in the last 115 years on MPBs and provide this context for informing, planning, and executing forest treatments to produce MPB resilient forests. In addition, it tells an intriguing and fascinating story about bark beetles and the people who tried to understand and control them.

Keywords: western pine beetles, forest structure, ponderosa pine, forest management, weather

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Preface

The story of bark beetles in the western United States had its genesis 35 million years ago, and the narrative of mountain pine beetles here began ≈115 years ago in the Black Hills of South Dakota and Wyoming (Furniss and Carolin 1977; Hopkins 1902). It's a story of ponderosa pine forests, bark beetles, managers, scientists, and the public trying to understand bark beetle dynamics and the major forest destruction they cause (Bentz and others 2009; Fiedler and Arno 2015; Furniss 1997). Scientists can be rather peculiar, as Bryson (2003) described. He offered several examples of scientists holding on to strong views about their findings long after they had been proven false or advocating positions or solutions to problems long proven to be irrelevant. He also chronicled the large egos many scientists have and how competitive and secretive many were about their work. Alt (2001) described the decades (1923 through 1972) it took for Bretz to receive his due credit for describing how a large flood scoured the scablands of eastern Washington. Many of his detractors went to their graves resolutely challenging that floods created the scablands but rather orderly and slow erosion processes created the landscapes. Bretz was confronted in scientific journals and by organizations of his time, while in this information-age, science findings are frequently challenged by the public, policy makers, and managers. Some of the currently disputed science is associated with climate change, evolution, vaccinations, genetically modified foods, and even the moon landings (Achenback 2015). Instead of using science to inform decisions, many science users are looking for knowledge to support their desired decisions while discarding the science that does not. Managers and policy makers have a difficult mission in making decisions as they tend to make the easy ones and often table the hard ones that require more deliberation, involve more analysis, and challenge the status quo. McNamara (1995), reflecting on the Vietnam War, suggested it was easier to make decisions on troop and aircraft numbers and war tactics than asking the tough questions about what was being accomplished and the rationale for U.S. policy. Similar themes of decision-makers struggling to make difficult choices, perceptions of science findings, scientists and their work, and science use permeate the story of understanding and controlling bark beetles in the western United States.

The story of bark beetles could also be made into a film noir. It has sex, murder, fights, incest, parasitism, infidelity, necrophilous (eating the dead), cannibalism, and predation. For example, after mating, if the male mountain pine beetle remains and helps the female construct the egg gallery, the female kills the male when the gallery is finished and adds his body to the packed frass (refuse and excrement of wood boring insects) in the gallery, which discourages other bark beetles and predators from entering. If he leaves and finds another female, he will receive the same fate. Other intriguing parts of the story include: the metropolis of organisms that live with and prey on bark beetles under tree bark; the chemicals, heating, burning, and numerous other things we use to kill them; and the sophisticated way bark beetles communicate with pheromones. As such, the story of western bark beetles, their associated organisms, the people studying them and trying to control them, the damage they caused, and forest treatments aimed at minimizing their damage is 115 years old and ongoing; enjoy.

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Black Hills

The Black Hills are an isolated mountain range surrounded by prairie located on the eastern edge of the Rocky Mountains. They straddle the Wyoming and South Dakota border and are covered by ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests (fig. 1). They were formed by a regional uplift millions of years ago as a volcanic intrusion forced its way through limestone sediments. About two-thirds of this elliptically shaped domal structure lies in South Dakota and the other third, the Bear Lodge Mountains, is located in northeastern Wyoming (fig. 2). The Black Hills has a total land base of about 6,000 mi^2: 125 miles from north to south and about 60 miles from east to west. White spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), lodgepole pine (*P. contorta*), and even limber pine (*P. flexilis*) occur in the Black Hills. Nearly 1.5 million acres of ponderosa pine dominate the forests of the Black Hills with 884,900 acres occurring on the Black Hills National Forest (Boldt and Van Deusen 1974; Walters et al. 2013) (fig. 3).

Figure 1—Ponderosa pine (variety *scopulorum*) forests dominate the Black Hills of western South Dakota and northeastern Wyoming.

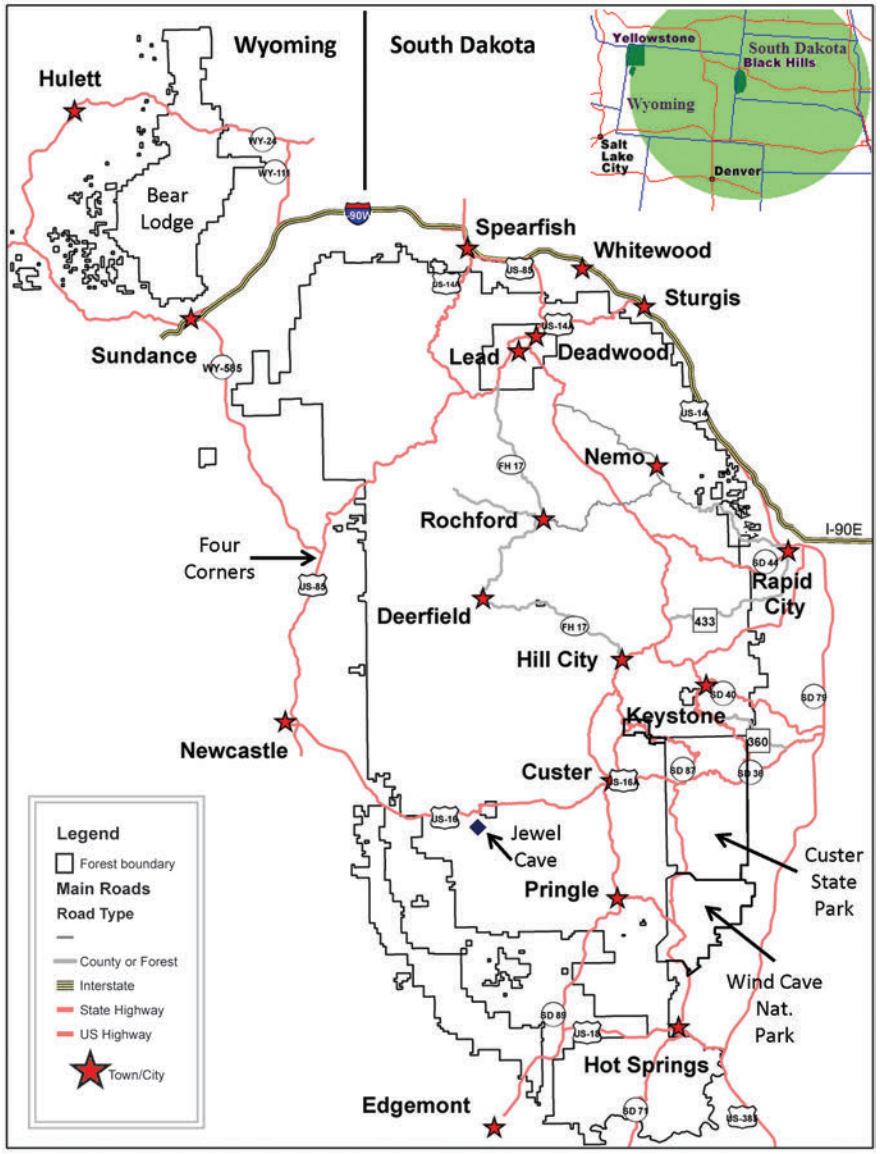

Figure 2—While the majority of the Black Hills National Forest occurs in South Dakota, a portion also occurs in the Bear Lodge Mountains of Wyoming.

This amount of forest is remarkable in that the Black Hills has had over a century of consumptive use (Boldt and Van Deusen 1974). During this period, virtually all of the area's unreserved and operable forest acres have been cut over at least once, and many acres have received multiple partial cuts (fig. 4). Large tracts that were logged free of regulatory restraints prior to establishment of the Forest Reserve in 1897 were commercially clearcut and practically stripped of all trees large enough to yield a mine timber or a railroad tie. Persistent harvesting, coupled with the destructive impacts of wildfire, insects, diseases, and wind have nearly eliminated the original old-growth stands on most of the commercial forest acres in the Black Hills and left only few scattered old-growth remnants on the remaining acreage (Boldt and Van Deusen 1974).

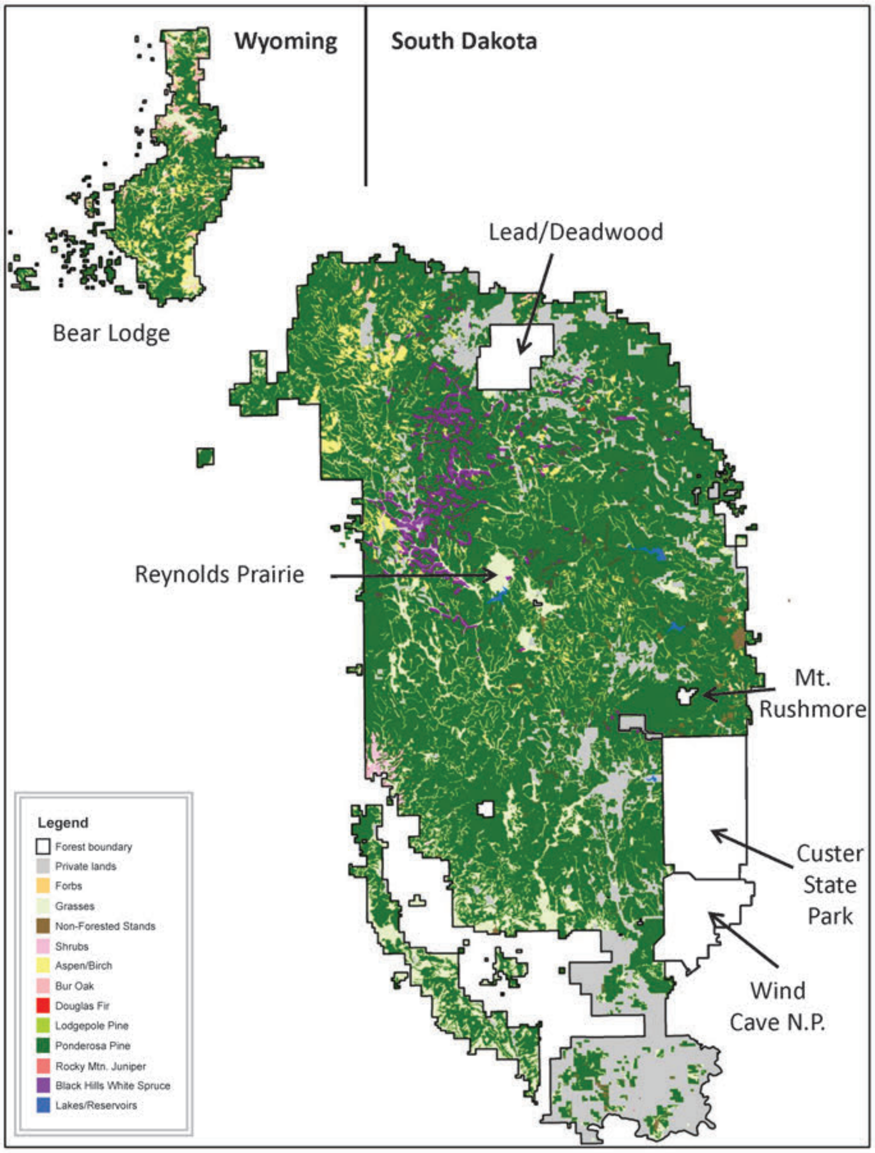

Figure 3—Ponderosa pine forests dominate the Black Hills vegetation, with a considerable amount of white spruce occurring in the north-central Black Hills and a variety of other conifers, hardwoods, meadows, and prairies comprising the remainder.

Figure 4—Timber harvesting began in the Black Hills in 1898 with Case One, the first commercial timber sale on Federal property within the United States. The left photo shows Case 78 cutting in 1910 and the right photo shows tractor yarding near Moskee, Wyoming, in 1938.

The unregulated harvest was controlled by the early 1900s and for 50 years or so, a variety of partial cutting systems was used to manage the forests, resulting in highly heterogeneous forests containing a wide variety of tree sizes arranged in a wide variety of mosaics (Harmon 1955) (fig. 5). In the 1960s, forest management changed to more intensive practices that tended to develop two and three age classes or canopies in many forests (Boldt and Van Deusen 1974) (fig. 6). However, wildfires burned and bark beetles and diseases killed trees during this period, adding complexity to the forests. The majority of the area is forested and, in many areas, densely covered with trees, which can lead to large wildfires. A key feature of these ponderosa pine forests is the intermediate shade tolerance of ponderosa pine that allows regeneration under partial shade as well as full sunlight. Ponderosa pine seed is produced almost every year with abundant crops every 2 to 5 years (Boldt and Van Deusen 1974). Also, *scopulorum* is the variety of ponderosa pine that occurs in the Hills and it has many different traits from those of the *ponderosa* variety that grows on the west side of the Continental Divide (Potter et al. 2013). Frequent rain showers throughout the growing season, which lasts from early March to August, is the major climatic factor contributing to the prolific growth and establishment of ponderosa pine (fig. 7). In response to

Figure 5—A variety of forest structures remained after the Boodleman area of the Black Hills was harvested in 1911.

Figure 6—By the mid to late 1960s, most harvesting in the Black Hills was done using two-step shelterwoods.

Figure 7—In the Black Hills, because of the spring and summer rains and abundant seed crops, ponderosa pine readily regenerates and carpets the forest floor in most locales.

natural disturbances and because of the ease of regeneration that occurs in the Black Hills, the area has had one of the most consistent commercial timber harvest programs in the United States since Case One was sold to the Homestake Mining Company in 1898 (Clow 1998; Freeman 2015).

Black Hills Beetle

Bark beetles[1] are a major forest disturbance impacting all western North American coniferous forests. For centuries they attacked and killed conifer trees at differing levels of intensity (Furniss and Carolin 1977). As Native Americans lived and traveled through the Black Hills prior to European exploration, they undoubtedly encountered areas where bark beetles had killed ponderosa pine trees. Similarly, when General Custer (Brevet Major General Lieutenant Colonel) explored the Black Hills in 1874 he encountered abundant

[1] Bark beetles are so named because most of them live and mine between the bark and wood of trees. Adults bore through the bark and make a tunnel between the bark and the wood in which they lay their eggs. Upon hatching, the larvae mine out from the egg tunnel. The egg tunnels and larval mines together often form a characteristic pattern that will identify the genus and sometimes the species. Bark beetles have evolved to prefer attacking different tree species with the spruce beetle, Douglas fir beetle, western pine beetle, and mountain pine beetle being the most destructive insects of western conifers (Furniss and Carolin 1977). Hopkins (1905, 1909) described both the Black Hills and mountain pine beetles as two separate species, which Wood (1963) combined into one, and called the species mountain pine beetle (*Dendroctonus ponderosae*).

down and dead trees when he descended Harney Peak, likely killed by bark beetles (Ludlow 1875). Hopkins (1905) indicated that the Black Hills beetle had been present and killing trees since the 1850s throughout the Rocky Mountains and he also suggested that much of the dead and dying trees that were attributed to wildfires were actually killed by bark beetles (Hopkins 1909).

Figure 8—Andrew D. Hopkins, having only a rural school education, was awarded an Honorary Doctorate by West Virginia University in 1893 and went on to be one of the most, if not the most, prominent figure in describing and understanding bark beetles in North America.

The first documented epidemic of bark beetles in the Black Hills occurred in 1895, in the northwestern corner, near the Wyoming border where trees were dying in clumps (Blackman 1931). Graves in his reconnaissance of the Black Hills Forest Reserve visited the same area in 1897 and noted that large numbers of trees on several ridges in the vicinity of Crooks Tower and the headwaters of Little Spearfish Creek were dead or dying (Graves 1899). In 1898 Gifford Pinchot was named head of Division of Forestry and he was hearing reports of bark beetle depredations from throughout the country. However, the Division had no expertise in entomology; to fill this inadequacy, Pinchot hired Andrew D. Hopkins in 1901 to conduct special investigations (Furniss 1997) (fig. 8).

Hopkins' education was limited to the county schools of West Virginia and his self-taught knowledge as he started running his grandfather's farm at age 17. In 1890 the newly created Agricultural Experiment Station of West Virginia hired Hopkins on a trial basis to evaluate insect problems throughout the State. Primarily surveying agricultural insects, he discovered vast tracts of pines and spruces damaged or killed by bark beetles. The southern pine beetle (*Dendroctonus frontalis*) was causing the damage and Hopkins did an exhaustive study of the beetle. Because of this work, West Virginia University awarded him an honorary Ph.D. in 1893, just 3 years after he quit farming. Although Hopkins did brilliant work at West Virginia University on many insects important to agriculture, his growing prominence as an expert on bark beetles would soon shape his future and that of American forest entomology (Furniss 1997).

Along with Pinchot and field assistant E. M. Griffith, Hopkins went to the Black Hills to further investigate the beetle activity that Graves described. During September 1–4, 1901, they traversed through the Reserve from Spearfish via Iron Creek, and Bear Gulch, South Dakota, to Rifle Pit and Cement Ridge, Wyoming, and back to Little Spearfish Creek finishing at Lead, South Dakota (Hopkins 1902) (fig. 9). In these 4 days he collected and described 4,363 beetle specimens, described how they attacked trees, described the galleries they left under the bark, and even speculated on using trap trees to control the bark beetle damage (fig. 10). Hopkins wrote up the results of his Black Hills trip, which were published only 3 months later (Hopkins 1902). In that bulletin, he named the beetle *Dendroctonus ponderosa,* later corrected to *D. ponderosae* to conform to nomenclatural rules concerning

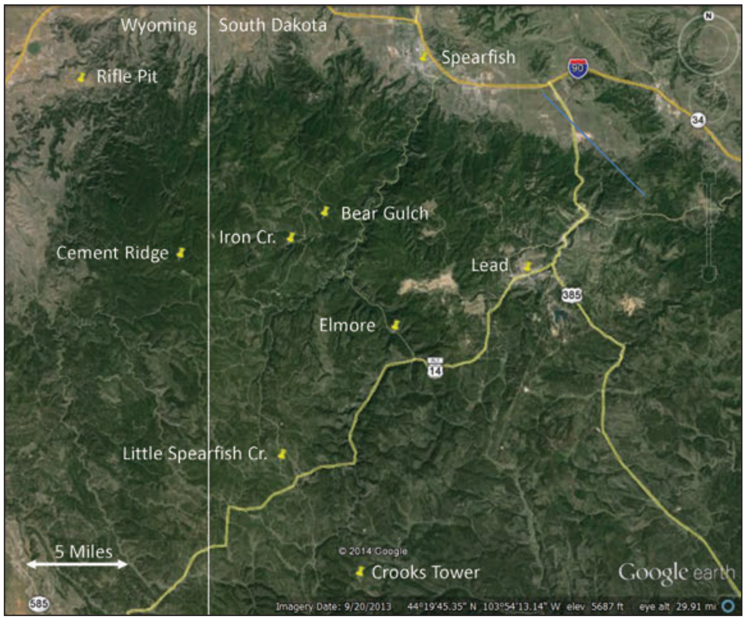

Figure 9—This is the area of the Black Hills that Graves visited in 1897 and noted abundant tree mortality likely caused by insects. Hopkins, Pinchot, and Griffith visited the same area on September 1–4, 1901, and identified and described the Black Hills beetle.

Figure 10—Pinchot took this picture of a bark beetle infested tree when he accompanied Hopkins and Griffith to the Black Hills in 1901. Official caption for the photo reads "Pitch tubes of Bk. Hills Bark beetle. Fire of June 1899. (Ocunpaugh's fire). (*Dendroctonus ponderosa, Pinus ponderosa*). In Lopple and McLaughlin's cutting on Iron Creek."

gender of Latin names. He referred to it as "the pine-destroying beetle of the Black Hills," shortening it later to "the Black Hills beetle" (Hopkins 1905) (fig. 11).

Jesse Webb, after meeting Hopkins in 1899 at Washington State College (now University), went on to study under Hopkins at West Virginia University and received the first forest entomology degree conferred in the United States. He was assigned to Elmore, South Dakota, (no longer a town) located approximately 1.5 miles north of Cheyenne Crossing (junction of Alt. Highway 14 and Highway 85) in Spearfish Canyon and in the vicinity where Hopkins visited in 1901 (fig. 9). Following a detailed study plan written by Hopkins, through the summer, Webb collected and described numerous bark beetles, recorded timing of their flights to attack new trees, and discovered they had one generation per year. He also studied different methods of controlling the bark beetle (Furniss 1997).

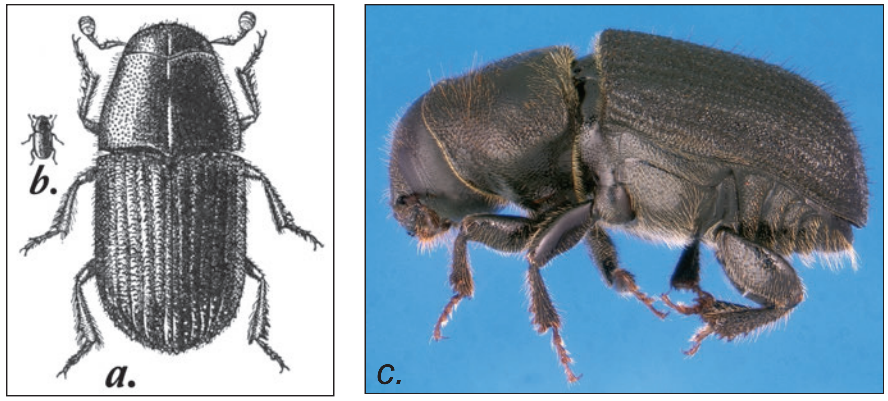

Figure 11—The left two drawings (a, b) were prepared from information Hopkins gathered during his trip to the Black Hills in 1901 with (b) depicting the actual size of the insect (Hopkins 1902). The right photo (c) shows the intricate details of the mountain pine beetle (photo: Erich G. Vallery, USDA Forest Service-SRS-4552, Bugwood.org).

The Black Hills beetle was not confined to attacking and killing ponderosa pine in the Black Hills, as it occurred in Wyoming, Utah, Colorado, Arizona, New Mexico, and extending well into northern Mexico (Hopkins 1908, 1909). M. W. Blackman, Professor of Forest Entomology, New York State College of Forestry, Syracuse, New York (1931), found that six Black Hills beetle epidemics of varying intensities occurred from 1837 to 1926 on the Kaibab Plateau in northern Arizona. Also, he discovered a 400-year-old ponderosa pine with seven unsuccessful attacks by Black Hills beetles occurring throughout its life in the same area. He reported several small Black Hills beetle epidemics in Colorado from 1905 through 1913, a small epidemic on the Crow Indian Reservation in southeastern Montana from 1911 through 1912, and a moderate epidemic occurring in northern Colorado from 1923 through 1930. In addition to attacking the preferred ponderosa pine, the Black Hills beetle aggressively attacked lodgepole pine and did damage to Rocky Mountain bristlecone (*P. aristata*), limber, white bark (*P. albicaulis*), and pinyon (*P. edulis*) pines throughout the Rocky Mountains and sugar pine (*P. lambertiana*) in California. This beetle attacked Engelmann (*Picea engelmannii*) and blue (*P. pungens*) spruces, but it seldom produced broods in these trees (Beal 1939).

Other Bark Beetles

Although the Black Hills was the center of bark beetle research in 1900, the southern bark beetle had been described by Zimmerman in 1868 and in California the western pine beetle (*D. brevicomis*) was described by Le Conte in 1876 and further described by Hopkins (1909) (Le Conte 1869; Zimmerman and Le Conte 1868). Hopkins also described the southwestern pine beetle (*D. barberi*), the roundheaded pine beetle (*D. convexifrons*), the Arizona pine beetle (*D. arizonicus*), the smaller Mexican pine beetle (*D. mexicanus*), the mountain pine beetle *(D. monticolae*), the Jeffrey pine beetle *(D. jeffreyi*), and the lodgepole pine beetle *(D. murrayanae*). Hopkins also described three spruce beetles and the Douglas fir beetle (*D. pseudotsugae*) (Hopkins 1915; Massey 1961). As a result Hopkins proved to be one of the most influential people in understanding bark beetles in the United States, if not in the world. Hopkin's forte was describing bark beetles; then, upon accomplishing the narrative and refining descriptions of the major bark beetles in the United States, he left the field of entomology in 1923 and focused on bioclimatic research (Furniss 1997; Hopkins 1919).

The mountain pine beetle *(D. monticolae*) was first mentioned by Hopkins in 1905 and further described by Hopkins in 1909 (Hopkins 1905, 1909). It attacked pines in Idaho, Montana, northwestern Wyoming, Oregon, Washington, and California, and in the Canadian Province of British Columbia (fig. 12). Occasionally it was a serious menace to young pole stands of ponderosa pine (variety *ponderosa*), especially on cut-over areas and in places where such stands were suffering from severe competition. Older ponderosa pines (variety *ponderosa*) were not as susceptible to its attacks. Evenden et al. (1943) indicated that lodge-pole, western white pine (*P. monticola*), and sugar pine were favored by the mountain pine beetle if they were given a choice. Also, epidemics of mountain pine beetles killing large expanses of lodgepole pine forests in the northern Rocky Mountains were rather common in the 1930s and 1940s (Evenden et al. 1943).

Nearly having the same range in the Western United States as the mountain pine beetle was the western pine beetle. The western pine beetle prefers Coulter (*P. coulteri)* and the *ponderosa* variety of ponderosa pine that occurs in California, Oregon, Washington, Idaho, and western Montana but does not infest the *scopulorum* variety that grow east of the Continental Divide in Montana, the Black Hills, Wyoming, and most of Colorado. Similar to the Black Hills beetle, work on understanding and controlling the western pine beetle started in 1900 (Miller and Keen 1960).

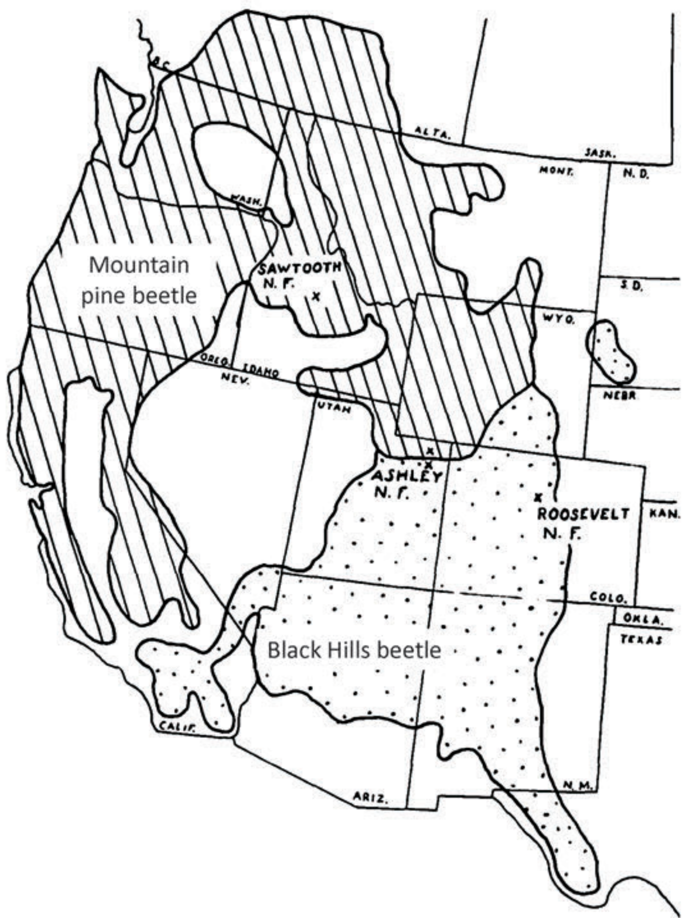

Figure 12—As described by Hopkins, the mountain pine beetle and Black Hills beetle, circa 1950 ranged throughout the western United States (illustration: Hay 1956).

Mountain Pine Beetle Revised

Hopkins described the Black Hills beetle (*D. ponderosae*) and the mountain pine beetle *(D. monticolae*) by using morphological characteristics (Hopkins 1905; 1909). For both bark beetles, he provided precise descriptions and drawings of the beetles. The beetles combined had the potential to attack all of the pines and several other conifer species in the western United States. However, when they attacked the spruces (*Picea* spp.), true firs (*Abies* spp.), and incense cedar (*Calocedrus decurrens*), no brood was produced and attacks were considered overflow from the preferred pine species located nearby (Beal 1939; Evenden et al. 1943; Hopkins 1909; Negrón and Fettig 2014). The two species were so similar in morphological characters, habits, and life history that they could not be distinguished with certainty. As such, the two species were separated by geographical location, hosts, and size of adults rather than other characteristics (Hay 1956) (fig. 12).

Blackman (1938) noted that it was difficult to distinguish the two species within infestations where their distributions overlapped. The host tree offered little or no aid in identification since either species of bark beetle may attack any species of pine found in an area. Blackman went on to examine 2,888 bark beetles from the localities having typical Black Hills beetles (*D. ponderosae*), such as the Black Hills of South Dakota and Uncompahgre National Forests of Colorado, and typical mountain pine beetles (*D. monticolae*) from the Beaverhead of Montana and Coeur d'Alene National Forests of Idaho, and intermingling specimens from the Medicine Bow of Wyoming and Ashley National Forests of Utah. Blackman found that many specimens did not have the typical characteristics of either species. Thus, in any number of specimens of either species, individuals will be found that show more or less strongly the characteristics of the other species. It was Blackman's (1938) opinion that, since the species intermix so widely and differentiation is so difficult, in all probability they were one species that varies according to host, condition of food supply, and region. Blackman's contention was supported by experimental mating of *D. monticolae* and *D. ponderosae* that produced fertile offspring (Amman and Cole 1983; Hay 1956).

The *D. monticolae* and *D. ponderosae* bark beetles and their synonymy (i.e., a list of the scientific names with explanatory matter and location of type or types for a particular taxonomic group) were used by Wood (1963) to combine them into one species. Similarly, Thomas (1965) indicated they were one species after studying the larvae and pupae of the two species. Thus *D. ponderosae* and mountain pine beetle (MPB) were the names given to one of the, if not the most destructive, bark beetles of western North America (Furniss and Carolin 1977) (fig. 13). Also, Wood (1963) combined and revised other species in the genus. Throughout Hopkins' rather short entomological career and passion for describing bark beetles, he had designated 12 species of *Dendroctonus*. After Wood's (1963) revision, Hopkins remained the authority for mountain, Jeffrey, Douglas fir, and lodgepole pine bark beetles.

Western Pine Beetle Revised

Wood (1963) also combined the western pine beetle (*D. brevicomis*) and the southwestern pine beetle (*D. barberi*) into the western pine beetle (*D. brevicomis*). This bark beetle occurs in Washington, Idaho, western Montana, Oregon, California, Arizona, Utah, southwestern Colorado, and New Mexico (DeMars and Roettgering 1982; Hopkins 1909)

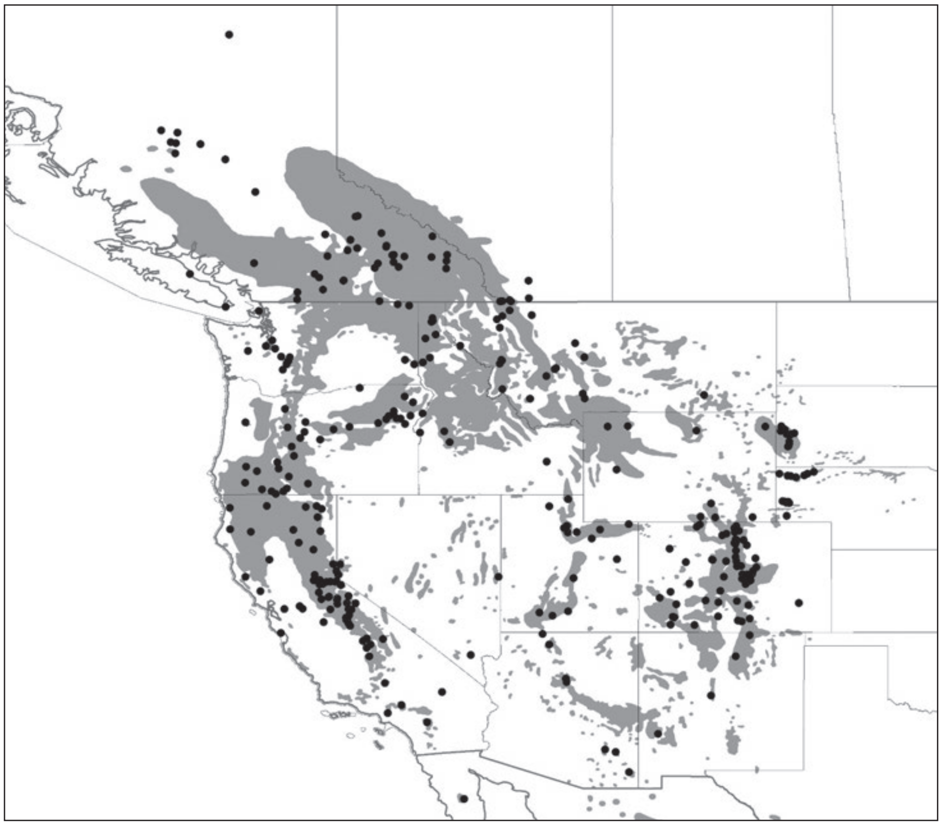

Figure 13—North American distribution of the mountain pine beetle (MPB) (black dots) recorded over potential distribution area suggested by six common hosts: limber, ponderosa, sugar, lodgepole, western white, and whitebark pines (records in northern British Columbia, Canada, are from lodgepole pine data provided by Thomas H. Atkinson; figure by Javier E. Mercado).

Figure 14—The range of the western pine beetle (WPB) in North America overlaps with a large portion of where MPBs range (illustration: DeMars and Roettgering 1982).

(fig. 14). It is important to note that MPBs usually have one generation per year and sometimes a generation every other year at high elevations, but the western pine beetle (WPB) usually has two to three generations per year (Smith 1990). Much like the MPB, the WPB caused immense damage to ponderosa pine. Until large amounts of timber were being used in the western United States as the area was being settled, the WPB was not considered a major forest management issue (Miller and Keen 1960). Miller and Keen (1960) estimated that from 1910 to 1960 WPB killed about 50 billion board feet of timber. As a result, considerable research was undertaken in understanding and developing control strategies for the WPB, paralleling and complementing those aimed at understanding and controlling the MPB.

Bark Beetle Behavior

MPBs can emerge as early as June but typically attack trees in late July and early August, usually flying with the wind, but attractant pheromones influence flight direction (Amman and Cole 1983; Gray et al. 1972) (fig. 15). Several factors interact to cause the dispersal flight distance to vary among individuals. In addition to finding a suitable tree to attack, the amount of fat reserves the beetle can mobilize for flight may determine how far away a tree is attacked. A beetle that flies rather far from the brood tree will likely have higher reproductive fitness as it can avoid inbreeding with siblings and escape predators and parasites that are locally denser near the brood tree. As such, bark beetle flight may have evolved as a balance between flying farther to increase reproductive fitness and becoming exhausted without finding a suitable host (Byers 2000). The fat level required for lengthy dispersal will depend on the conditions in the brood tree during larval development. Site quality and climatic factors will affect the quantity and nutritional quality of the phloem consumed by the larvae and competition among the larvae can reduce the size of adults as well as their fat content (Amman and Cole 1983; Byers 2000).

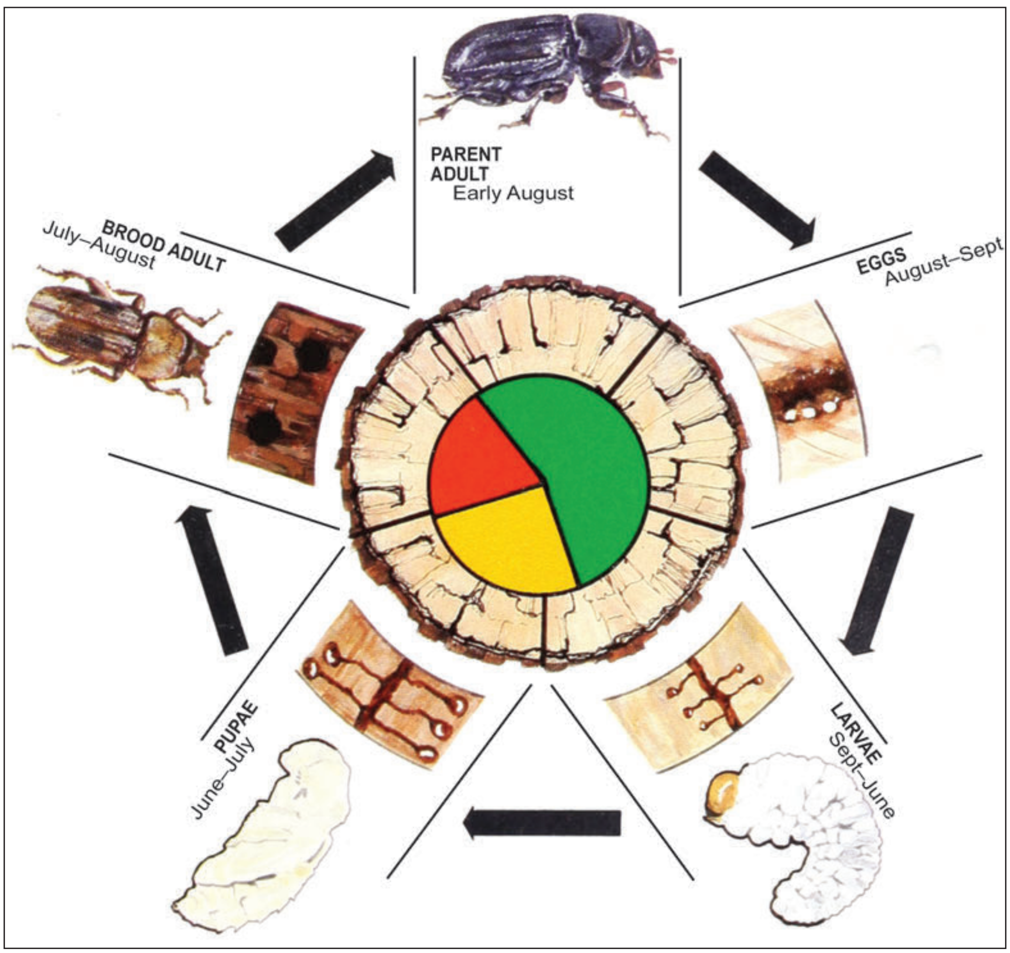

Figure 15—Life cycle of the MPB. Illustration shows the different developmental stages of the MPB and the dates at which they occur. The interior cross section of a typical tree infested shows the color of the needles that would commonly occur on a tree as the MPBs developed (illustration: Amman and Cole 1983).

Nevertheless, most bark beetles find suitable trees for attacking within 100 yards or so of the brood tree (Miller and Keen 1960). Using 8,000 reared and marked WPBs, Miller and Keen (1960) in 1918 showed that WPBs often flew over 440 yards to infest trees. They found 1,460 beetles in an infested tree and only 181 were marked and the remaining 1,279 WPBs came from other sources. Using trap trees in 1920, Miller and Keen (1960) showed that WPBs would fly 1.5 to 2.0 miles to attack trees and under some conditions WPBs were known to fly 6 to 8 miles to attack trees. Also there is anecdotal evidence that winds may disperse MPBs 50 miles or more (Schmid 2015, personal communication).

Female MPBs most likely colonize trees at random but tree condition (e.g., diseased, damaged, previous unsuccessful MPB attack), bark beetle fitness, and flight conditions also influence host tree selection (Amman and Logan 1998; Negrón and Fettig 2014; Progar et al. 2014). Random landing, however, does not necessarily mean attack, but possibly only a necessary resting or shelter spot for the night when temperatures or light conditions fall below the threshold for flight. Also, large dark objects, especially those set against light background, were more attractive in a laboratory setting to MPB landings than small dark objects, which indicates that MPBs use some visual cues when locating trees (Amman and Cole 1983; Progar et al. 2014). Even when small trees were treated with an attractant (i.e., *trans*-verbenol and alpha-pinene), MPBs would be attracted to the area of the baited tree, but usually selected a nearby host tree of larger diameter (Amman and Cole 1983). Byers (2000) suggested that bark beetles such as the MPB have a strong aggregation pheromone and do not utilize tree volatiles as much in selecting a susceptible host as those with weak aggregation pheromones. Also, he postulated for these species that there could be two types of beetles (based on behavior), one that behaves as a pioneer and tests trees for susceptibility and another type that only searches for aggregation pheromone and trees undergoing colonization. Such colonization strategies are most likely related to the level of fat reserves a beetle has when it emerges as an adult. Those with high fat reserves likely disperse readily and ignore tree and pheromone cues and those with low fat reserves depend on pheromones and nearby acceptable trees for attacking (Byers 1999, 2000).

MPBs can strike the bark of a tree with such force that an audible tap can be heard several feet from the tree (Blackman 1931). Upon establishing a foothold on a tree, the female slowly progresses up the tree examining each crevice carefully as they prefer rough over smooth areas of bark (Amman and Cole 1983). The MPB soon finds a place of its liking most frequently located on the northern aspect of the tree where bark surface temperatures tend to be cooler (Progar et al. 2014; Rasmussen 1974; Reid 1963). There she begins burrowing in a direction diagonally upward making “ticking” sounds (Blackman 1931). After gallery initiation, aggregation pheromones are released by the female to attract additional MPBs. Occasionally two males will be at the entrance of a gallery containing a female and commence fighting until one succeeds in pushing the other out of the gallery and sometimes off the tree. Numerous males have been observed ascending a tree—most likely those that have lost battles over females (Blackman 1931). From burrows, occasionally a rubbing sound or stridulation can be heard indicating that a male is in the gallery. Both pre-entry and stress stridulations have been identified and these sounds may be part of territorial behavior discouraging other males from entering the gallery. Also, these “chirps” notify the female that a male bark beetle is in the gallery and not a predacious beetle (Fleming et al. 2013).

Males also release pheromones further augmenting the attraction of high numbers (hundreds to thousands) of MPBs that "mass attack" the host tree (Amman and Cole 1983; Progar et al. 2014). Recruiting a critical minimum number of beetles to "mass attack" a tree enables MPBs and their symbionts (e.g., fungi, mites, nematodes, mites) to overcome tree defenses (Krokene 2015; Progar et al. 2014). Conifers have several defenses to bark beetle attacks including tree structure (e.g, bark surface, resin ducts, rays, tracheids), chemical (e.g., terpenes, phenolics), and induced (e.g., resinosis, traumatic resin ducts, wound response). Also critical for bark beetle reproductive success is that the tree's induced defenses do not kill the developing brood. Tree stress and ultimate tree death are not a requirement for brood development, but rather an outcome of the mining and tunneling by bark beetles and the detrimental effects of associated symbionts that contribute to overcoming tree defenses (Krokene 2015).

When the tree is fully involved (colonized) with MPBs, antiaggregation pheromones are released by females encouraging other bark beetles to attack adjacent trees. As a result, the number of MPBs infesting a tree is limited to a density that increases the likelihood of brood survival (Negrón and Fettig 2014; Progar et al. 2014). If trees are not mass attacked within 48 hours of the initial attack, the tree will not likely be colonized. Lack of beetles (e.g., end of flight season) or insufficient attractant pheromones are likely causes of mass attack failures. In some cases, trees are only strip attacked (i.e., attacks concentrated on one side of the bole) on the tree side facing other mass attacked trees. The females that initiated the attack, in non-colonized trees, will abandon their galleries if they have constructed 2 inches or less (Amman and Cole 1983).

After mating, the male may leave the gallery and seek another female to mate, or he may stay in the gallery with the female. Should the male stay, he pushes boring dust (that the female chews away in the process of making the gallery) and resin out of or into the bottom of the gallery. The boring dust packed in the entrance of the gallery dissuades other MPBs and enemies from entering. If a male gets in the way of the female, she kills him and packs him along with the boring dust into the bottom of the gallery (Blackman 1931; Amman and Cole 1983).

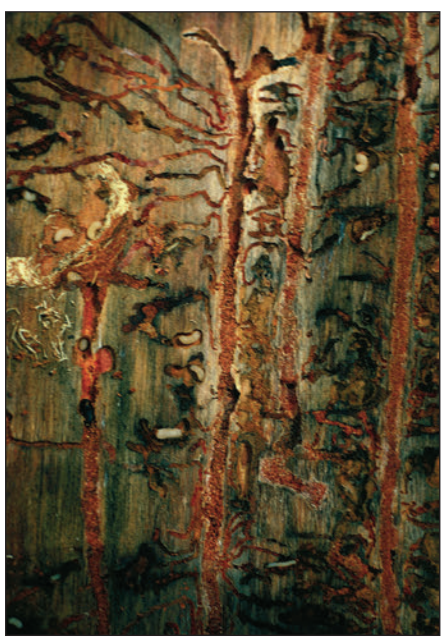

Figure 16—Galleries excavated by MPBs under the bark of a ponderosa pine on the Helena National Forest in Montana (photo: William M. Ciesla, Forest Health Management International, Bugwood.org).

The female MPB constructs egg galleries that are long, vertical, nearly straight, and located in the inner bark (Amman and Cole 1983) (fig. 16). The female usually lays single eggs in niches located on both sides of the gallery (Amman and Cole 1983; Blackman 1931) (fig. 17). The total number of eggs from one female likely exceeds 200 and may even surpass 300 with a mean of 8.4 eggs per inch of gallery. With the typical gallery being 22 inches in length it would produce about 184 beetles and, if no larval, pupae, or adult mortality occurred, 92 beetle

Figure 17—Single eggs are laid by the female in niches on sides of the gallery (photo: Amman and Cole 1983).

pairs would emerge. Or expressing it another way, each tree killed this year would be represented by 92 trees killed the next year, 8,464 trees killed the second year and over 70,000,000 trees killed in the fourth year. However, such population expansions would not occur because of egg, larval, pupae, and adult mortality related to predation, parasites, competition, weather (both heat and cold), and phloem (food) quantity (fig. 18). Phloem quantity is the main factor in brood production and phloem drying is one of the deciding factors causing beetle populations to return to endemic levels (Cole and Amman 1980). Drying is usually more pronounced in small diameter trees compared to ones with larger diameters. Also, trees with extensive blue-stain fungi brought to the tree by MPBs tend to have more moisture compared to those with sporadic and spotty fungal infestations. Trees with abundant beetle attacks tend to be drier than trees with fewer galleries present (Amman and Cole 1983). Nevertheless, the potential for beetle epidemics is immense as the potential for millions of beetles to be produced and infest pines is very plausible (Blackman 1931).

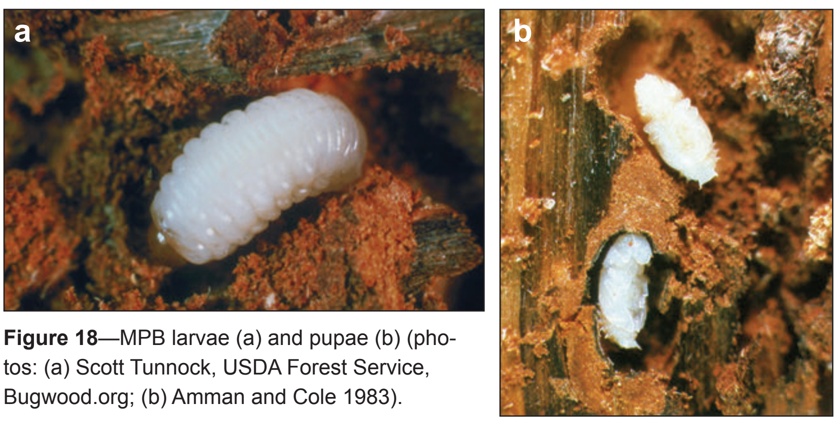

Figure 18—MPB larvae (a) and pupae (b) (photos: (a) Scott Tunnock, USDA Forest Service, Bugwood.org; (b) Amman and Cole 1983).

The only way during the fall and winter to identify a beetle-infested tree is by the presence of pitch tubes and boring dust present on and at the base of the tree (Beal 1939). In the spring as the needles of the tree are turning red, beetle development resumes and the larvae turn into pupae (pupation) (fig. 15). Later the pupae (i.e., immature form between larva and adult) transform into brownish callow adults that feed in the inner bark enlarging a section of the gallery. When the density of new adults is high, their feeding chambers may coalesce. Then when a beetle chews an exit hole through the bark to emerge, all beetles within the common chamber emerge through the single hole in July and early August (Amman and Cole 1983). As adult bark beetles leave, an open exit hole remains and the cycle begins once more (Miller and Keen 1960; Negrón and Fettig 2014) (figs. 15, 18, 19, 20).

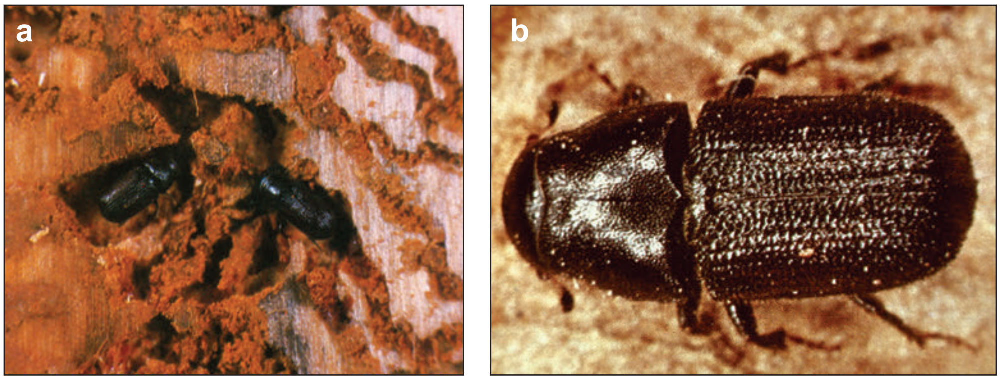

Figure 19—Over a year through tree attack, egg laying, larvae, and pupation, the MPB is ready to start the cycle once again (photos: (a) Amman and Cole (1983); (b) USDA Forest Service, Region 4, Intermountain Archive, USDA Forest Service, Bugwood.org).

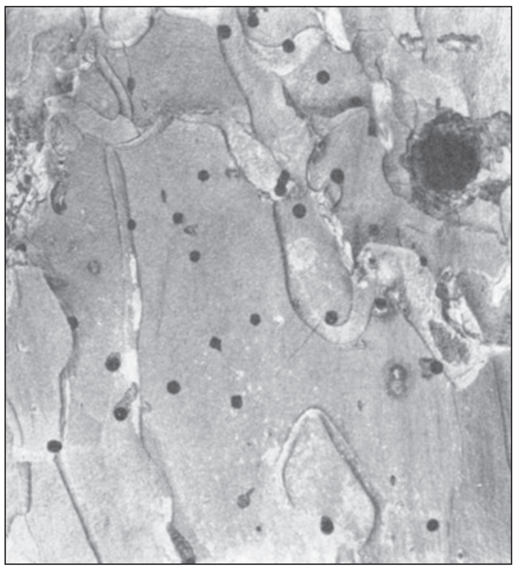

Figure 20—The new bark beetle adults excavate exit holes and leave the tree in late July and early August and the cycle commences once again. Pictured here are the exit holes in a ponderosa pine tree left by western pine beetles and an associated excavation of a woodpecker, no doubt looking for bark beetle larvae (photo: Miller and Keen 1960).

Mountain Pine Beetle Predators and Parasites

Over 100 species of insects are predatory or parasitic to MPBs, with larvae of the *Medetera* fly and braconid wasp larvae being consumers of MPB larvae (Amman and Cole 1983; Furniss and Carolin 1977; Wegensteiner et al. 2015). The checkered and trogossitid beetles prey on both MPB adults and larvae making them an important predator of western bark beetles and wood borers (Boone et al. 2008; Dahlsten and Stephen 1974; Furniss and Carolin 1977; Wegensteiner et al. 2015). At least 17 species of birds, woodpeckers being the most conspicuous, consume bark beetle eggs, larvae, pupae, and adults (Amman and Cole 1983; Wegensteiner et al. 2015). The effects these predators and parasites have on MPB populations vary widely and their impacts are usually dependent on whether the MPB infestation is endemic, epidemic, or post-epidemic (Amman 1984).

Several different braconid wasps are parasitic to MPB larvae. The larvae of the *Coeloides dendroctoni* and *C. rufovariegatus* wasps are also important natural enemies of MPBs (Amman and Cole 1983; Furnis and Carolin 1977; Wegensteiner et al. 2015) (fig. 21a). Compared to the *Medetera aldrichii* that preys on the early life stages of MPBs, the *Coeloides* larvae parasitize nearly full grown MPB larvae in the spring that are ready to pupate. MPB larvae that reach this stage are likely to become adults unless parasitized (De Leon 1935). In lodgepole pine forests, the *C. dendroctoni* has three reproductive strategies. The principal (95 percent of wasps produced) brood over winters in dead MPB killed trees and require nearly a full year to develop while a small summer generation goes from egg to adult in ≈60 days (late May to late July), and another small over-winter generation goes from egg to adult in ≈9 months (September to May) (De Leon 1935).

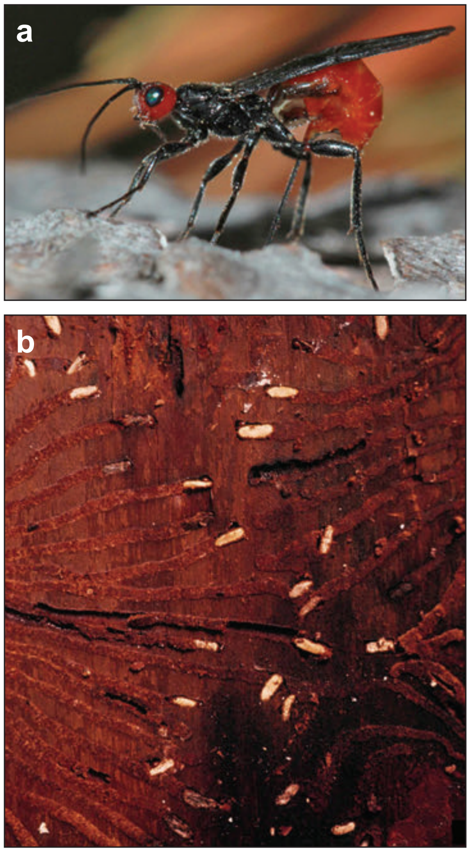

Figure 21—Several braconid wasps (a) are parasitic to MPB larvae as they attach their eggs on MPB larvae under the bark. Upon hatching, the wasp larvae feed on the MPB larvae and then spin cocoons (b) (photo: (a) Javier E. Mercado; (b) Norm Johnson, USDA Forest Service, Bugwood.org).

For each wasp brood, the males emerge before (≈9 days) the females in late May, from a tree with MPB larvae (small number) or from a tree that MPBs emerged from the previous year. The females mate immediately upon emerging with one of the 12 to 15 males that await her arrival. The female promptly flies to a tree, if available, that was mass attacked the previous August and contains MPB larvae more than half-grown. She crawls over the surface "sounding" with her antennae for larvae feeding under the bark. Upon locating a MPB larvae she pierces the tree bark and the skin of the larvae with her ovipositor, paralyzing it, and attaches an egg to the MPB larvae; this process can take from 12 to 50 minutes (De Leon 1935). Those eggs hatch in 27 hours to 4 days and the *C. dendroctoni* larvae begin feeding on the paralyzed MPB larvae. The wasp larvae grow fast and by the first week of July they have spun a cocoon (fig. 21b). A small number pupate very soon (summer generation) after they spin their cocoons, mate, and attach eggs on newly formed MPB larvae in late August and early September. The eggs of this small, over-winter generation hatch in late August and early September and the wasp larvae spend mid-September through late May in their cocoons and as adults they emerge in May joining the principal brood of *C. dendroctoni* adults to start the cycle once again (De Leon 1935).

Although these *C. dendroctoni* wasps on the surface show great promise for controlling MPBs, there are several factors that limit their effectiveness. *Coeloides* are most often found in Ips[2] (*Ips pini*)-infested material and their numbers are insufficient during the first few years of a MPB infestation to destroy many of the larvae. The main generation of *Coeloides* stays in the tree almost a year after the host MPB has been killed. Then, instead of being able to parasitize new infestations of MPBs, the wasps stay within the original epicenter of the MPB attack so their numbers increase slowly. It is fascinating how the female *Coeloides* finds and pierces tree bark with her ovipositor, but these parasites are insignificant in

[2] *Ips pini* (pine engraver) is a very common bark beetle in North America and at times a serious pest. It is most commonly found attacking and killing ponderosa, Jeffrey, and lodgepole pines. Large numbers develop in such host material as windfalls, freshly cut logs, limbs, and tree tops of killed trees and most notably, those killed by *Dendroctonus* beetles. When suitable host material is plentiful, they frequently develop in such numbers to attack healthy living trees (Cognato 2015; Furniss and Carolin 1977).

attacking bark beetles in the thick barked ponderosa, sugar, and Jeffrey pines. Nevertheless, these wasps frequently parasitize MPB larvae within lodgepole and western white pines, which have thinner bark (Amman and Cole 1983; De Leon 1935).

The long-legged fly in the genus *Medetera* are highly, if not solely, dependent on their association with bark beetles to complete their life cycle (Nagel and Fitzgerald 1975) (fig. 22a). Larvae in this group of flies spend their entire lives in the galleries of bark beetles where they prey upon the immature stages of bark beetles and associated insects. Species of the genus have evolved to be associated with different species of bark beetles. *Medetera aldrichii* is a major predator of both western and mountain pine beetle eggs and immatures, especially in ponderosa, lodgepole, and western white pine trees (DeMars and Roettigering 1982; Nagel and Fitzgerald 1975). These predators have developed so that their life cycle coincides with that of bark beetles, allowing them to thrive and have a major impact on bark beetle populations (Beaver 1966).

M. aldrichii larvae are major predators of MPB larvae in both ponderosa and lodgepole pine trees throughout the Rocky Mountains (Amman 1984) (fig. 22b). They have been estimated to destroy 40 to 50 percent of the bark beetle broods available to them by consuming or partially consuming MPB eggs and larvae (Nagel and Fitzgerald 1975; Schmid 1971). Because their life cycle coincides with that of MPBs, *M. aldrichii* adults usually emerge from a MPB-infested tree in late July or early August. Since they use the same exit holes through the bark as MPBs, they need a MPB adult to excavate an exit hole before they can emerge (Amman and Cole 1983; Schmid 1971). Because of this dependency on MPBs to excavate their exit holes, many *Medetera aldrichii* adults likely do not emerge and perish under the bark (Schmid 1971).

Peak numbers of *M. aldrichii* flies usually emerge from MPB-infested trees 20 to 30 days prior to the mass exodus of MPBs. However, their exit can fluctuate considerably and overlap with the emergence of MPBs. The numbers of emerging flies and emerging MPBs do not appear to be related (Schmid 1970). It is very likely that *M. aldrichii* use the pheromones of MPBs and the volatiles of their associated microbial symbionts

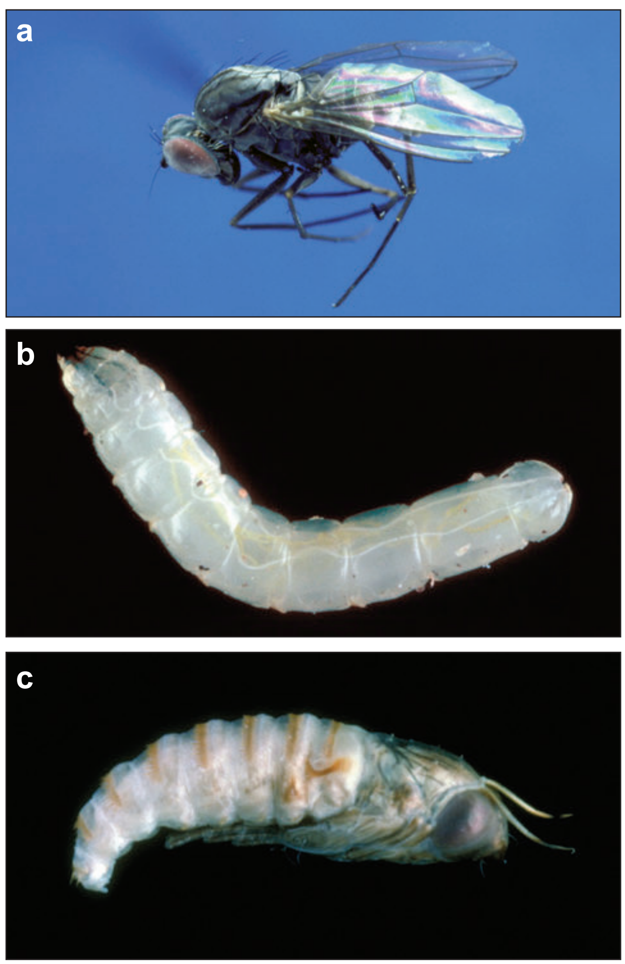

Figure 22—Long-legged fly (a), larvae (b), and pupae (c) are major consumers of MPB larvae (photos: Gerald J. Lenhard, Louisiana State University, Bugwood.org).

as kairomones (i.e., a semiochemical, emitted by an organism, that mediates interspecific interactions in a way that benefits an individual of another species that receives it, and harms the emitter) since they find attacked trees very soon after the MPB infestation has begun (Wegensteiner et al. 2015). *M. aldrichii* mating occurs on the trunks of MPB-infested trees. Females, after examining many locations on the tree bole, deposit their eggs in degenerate resin ducts that occur in crevices and under scales of tree bark (Bedard 1933; Schmid 1970; 1971; Wegensteiner et al. 2015) (fig. 22a). The female *M. aldrichii* usually deposits 2 eggs per resin duct but occasionally 7 or more eggs are placed (Schmid 1971). Interestingly, the location the female *M. aldrichii* selects to deposit her eggs is close to the entrance of a MPB gallery.

After about 9 to 15 days, with the mean time being 11 days, the worm-like *M. aldrichii* larvae emerge from the exposed end of the egg (Bedard 1933; Schmid 1971) (fig. 22b). Just before hatching, the young larva can be observed in the egg, with the last few abdominal segments bent so that the larva forms a "J" (Bedard 1933). The mechanism that the *M. aldrichii* larvae use for finding the MPB gallery entrance is unknown, but it is efficient, as the larvae would die from dehydration if they did not quickly find a gallery after they left the egg (Schmid 1971). Even though entrances to the galleries are plugged, the *M. aldrichii* larvae are able to enter and move freely in the gallery likely using body expansions and contractions as they leave fine compression tracks within galleries (Nagel and Fitzgerald 1975; Schmid 1971). *M. aldrichii* larvae feed on almost any species of larva, including their own, and cannibalism may reduce *M. aldrichii* populations as *M. aldrichii* larvae have no natural enemies (Amman and Cole 1983). The larvae move freely along the sides of the gallery through frass (refuse and excrement of wood boring insects) but they are unable to travel through unmined phloem or areas filled with resin or frass mixed with resin. Within 3 days from the time they leave the egg, *Medetera aldrichii* larvae begin preying on small bark beetle larvae or eggs from which bark beetle larvae would soon emerge (Nagel and Fitzgerald 1975; Schmid 1971).

M. aldrichii larvae can quickly move through bark beetle galleries loosely packed with frass enabling one larva to consume 12 to 25 MPB eggs per day (Schmid 1971) (fig. 22b). *M. aldrichii* larvae can easily attack 2 to 4 MPB larvae in rapid succession and most MPB larvae were completely consumed with the exception of the head before the *M. aldrichii* larvae moved on to new feeding sites (Nagel and Fitzgerald 1975) (fig. 18). Large prey are approached cautiously with the *M. aldrichii* larvae often retreating into the frass between brief attacks of 10 to 30 seconds duration. The bark beetle larvae are not defenseless and the *M. aldrichii* larvae avoid bark beetle larva mandibles by attacking along the posterior margin of the head or on the abdomen, while exposing only the tip of their head through the frass (Nagel and Fitzgerald 1975). *M. aldrichii* larvae can also attack bark beetle larvae and pupae (fig. 18). They rupture the prey's skin with their mandibular hooks and suck out the fluid within (Aukema and Raffa 2004a). Interestingly Aukema and Raffa (2004a) suggest that before feeding, the larvae of *Medetera* spp. immobilize their prey with a toxin. These large prey were often consumed over a 5 to 7 day period with the predator retracting into the frass during frequent non-feeding periods. Also, the *M. aldrichii* larvae moved persistently through the bark beetle galleries indicating they were attracted by the mining activity of bark beetle larvae (Nagel and Fitzgerald 1975).

By late October and early November, MPB larvae usually go dormant depending on the weather and most likely the larvae of *M. aldrichii* do also. In April, as temperatures increase, larvae of both species become active and commence feeding (Amman and Cole 1983; Schmid 1970, 1971). *M. aldrichii* larvae densities in the Black Hills peaked in May and June with Schmid (1971) finding 37 larvae per square foot of bark in the lower 15-foot portion of MPB-infested ponderosa pine trees (fig. 22b). Pupae of *M. aldrichii* start forming in late June and are found most commonly clustered in chambers underneath the bark near the exit holes in the bark initiated by the previous generation of adult MPBs (fig. 22c). After 14 to 33 days, the pupae develop into adult *M. aldrichii* flies and Schmid (1970) found densities of emerging adults averaged less than 1 per square foot of bark and never exceeded 6 per square foot (fig. 22a). With the adult flies emerging and coinciding with the emergence of adult MPBs, the *M. aldrichii* cycle commences once again (Schmid 1971).

Predaceous beetles, especially the checkered beetles or the beetles of the family Cleridae, consume both bark beetle adults and larvae (fig. 23). Known as "clerids," the genera *Enoclerus* and *Thanasimus* contain several important MPB predators. The blackbellied clerid (*Enoclerus lecontei*) is a major predator of WPBs and the redbellied clerid (*Enoclerus sphegeus*) is an effective predator of MPBs (Furniss and Carolin 1977). The *Thanasimus undatulus* clerid and the trogossitid beetles *(Temnochila chlorodia* and *T. virescens)* also frequently prey on MPBs (Amman and Cole 1983; Boone et al. 2008; Furniss and Carolin 1977; Wegensteiner et al. 2015). Similar to the *Medetera*, these predacious beetles are attracted to bark beetle-infested trees by pheromones and tree volatiles and their larvae are able to enter plugged bark beetle galleries (Aukema and Raffa 2004a,b; Boone et al. 2008; Wegensteiner et al. 2015). These predaceous beetles are considered habitat specialists but feeding generalists, in that they develop almost exclusively in trees killed by bark beetles but feed on many different insects they encounter (Boone et al. 2008). Also, these predaceous beetles tend to be cannibalistic both as larvae and adults (Wegensteiner et al. 2015). In contrast to other insect predator/prey relationships, the clerids, *E. sphegeus* and *T. undatulus*, do not show the typical density-dependent response. That is, they are more prevalent when MPB populations are endemic compared to when MPB populations are epidemic. As a result,

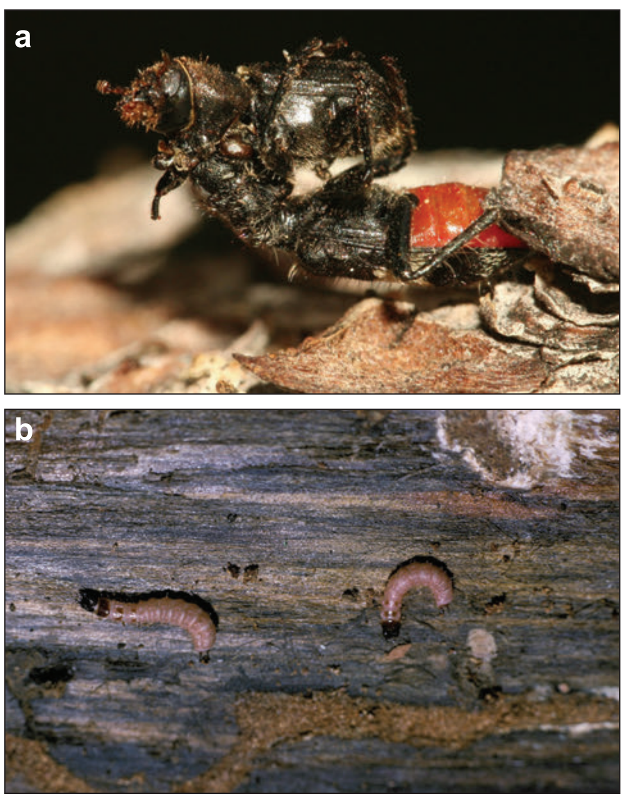

Figure 23—The clerid beetles both as adults (a) and larvae (b) prey on MPB larvae and adults. Photograph (a) shows an adult redbellied clerid eating an adult MPB (photos: (a) Javier E. Mercado; (b) USDA Forest Service, Rocky Mountain Region, Bugwood.org).

most predaceous beetles minimally impact epidemic populations of MPBs but would likely be a MPB controlling agent during endemic periods (Amman 1984; Amman and Cole 1983). The possible exception is the trogossitid beetles, which are long-lived (2 plus years) and nearly spend their entire lives under tree bark, where they likely impact epidemic populations of bark beetles (Reeve 1997; Wegensteiner et al. 2015).

The redbellied adult clerids (*E. sphegeus*) are attracted to MPB-infested trees in late May and early June that contain over-wintered MPB broods (fig. 23) (Böving and Champlain 1920). On the bark surface they mate and feed on small insects they encounter, especially bark beetles. They are able to attack and consume prey three times their own size, but prefer smaller victims (fig. 23a). Adult clerids often live 4 to 5 months during warm summers allowing each clerid to readily consume 25 or more adult bark beetles (Böving and Champlain 1920; Person 1931). Soon after emerging, the female clerid deposits eggs in bark crevices and under scales similar to the *Medetera* near a MPB gallery entrance (Aukema and Raffa 2002; Böving and Champlain 1920; Wegensteiner et al. 2015). One female clerid routinely produces 100 to 300 eggs but 1,000 eggs produced per female is not extraordinary (Wegensteiner et al. 2015). The eggs need to hatch soon after being laid, as the larvae must develop before the adult MPBs emerge in late July and early August (Amman and Cole 1983; Böving and Champlain 1920).

After hatching on the bark surface, the clerid larvae quickly locate and enter the gallery containing half to full grown MPB larvae (fig. 23b). Being voracious feeders, the clerid larvae grow rapidly and easily consume 40 to 60 bark beetle larvae and additional bark beetle pupae before they leave the infested tree (Böving and Champlain 1920; Kenis et al. 2004) (fig. 18). Beginning in late July and early August, the MPB adults emerge leaving the full grown clerid larvae. These mature larvae most likely use the same exit holes created by bark beetles, but they are capable of chewing their way through to the bark surface (Böving and Champlain 1920; Person 1931) (fig. 23b). Redbellied larvae do not over-winter in MPB galleries as they migrate at night to the base of the tree for hibernation. They enter the ground and burrow for several inches in depth close to the base of the tree and begin to construct their pupal cells. They over-winter in these cells in the larval stage. The cells are made in the dirt and debris, in bark crevices, or any suitable place. The cell is lined with the exudation, foam-like and of a silvery luster. This tends to hold all loose particles together, especially when the cell is made in the soil, and provides a smooth surface for the larva and pupa to rest upon as well as a protective covering. The pupal stage of clerids is rather short (≈30 days) and, after transformation, the adults may remain for a time in their cells and emerge in May with peak numbers in June to start the cycle once again (Böving and Champlain 1920; Person 1931).

Trogossitid beetles are important predators of MPBs and are strongly attracted to MPB pheromones (Amman and Cole 1983; Boone et al. 2008; Wegensteiner et al. 2015) (fig. 24). In contrast to the clerids, the trogossitids spend nearly their entire life beneath the bark and they are more specialized in their choice of prey (i.e., bark beetles) compared to the clerids, which consume a wide variety of insects (Wegensteiner et al. 2015). Adult trogossitids prey on adult bark beetles and the larvae feed on bark beetle larvae and pupae (figs. 18, 19, 24). Females can easily produce 200 eggs each and trogossitids over-winter both as adults and larvae, making them a year-long predator of MPBs. Adding to their effectiveness in consuming bark beetles, the *T. virescens* has a lengthy larval stage and adults can live for 2 years, which is approximately 4 times that of most clerids (Wegensteiner et al. 2015) (fig. 24).

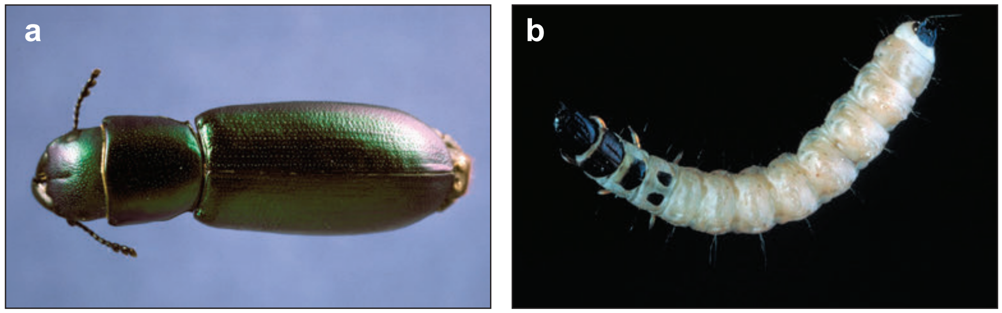

Figure 24—The trogossitid or bark-gnawing beetle adults (a) prey on adult MPBs and their larvae (b) consume MPB larvae and pupae (photos: Gerald J. Lenhard, Louisiana State University, Bugwood.org).

At least 20 bird species prey on bark beetle adults and larvae ranging from crows to sparrows with flycatchers being able to prey on bark beetles in flight (Amman and Cole 1983; Wegensteiner et al. 2015). Woodpeckers are by far the most significant group of birds preying on bark beetles with the three-toed (*Picoides tridactylus*), hairy (*P. villosus*), and downy (*P. pubescens*) woodpeckers being the most important (Amman and Cole 1983) (fig. 25). Often woodpecker populations are related to bark beetle populations. However, increasing prey availability does not necessarily increase the reproductive capacity of woodpeckers. In addition to insect consumption, woodpeckers thin and/or remove tree bark exposing MPB broods to desiccation and exposure causing the death of many more (Amman 1984; Amman and Cole 1983; Fayt et al. 2005; Wegensteiner et al. 2015). During epidemics, even though

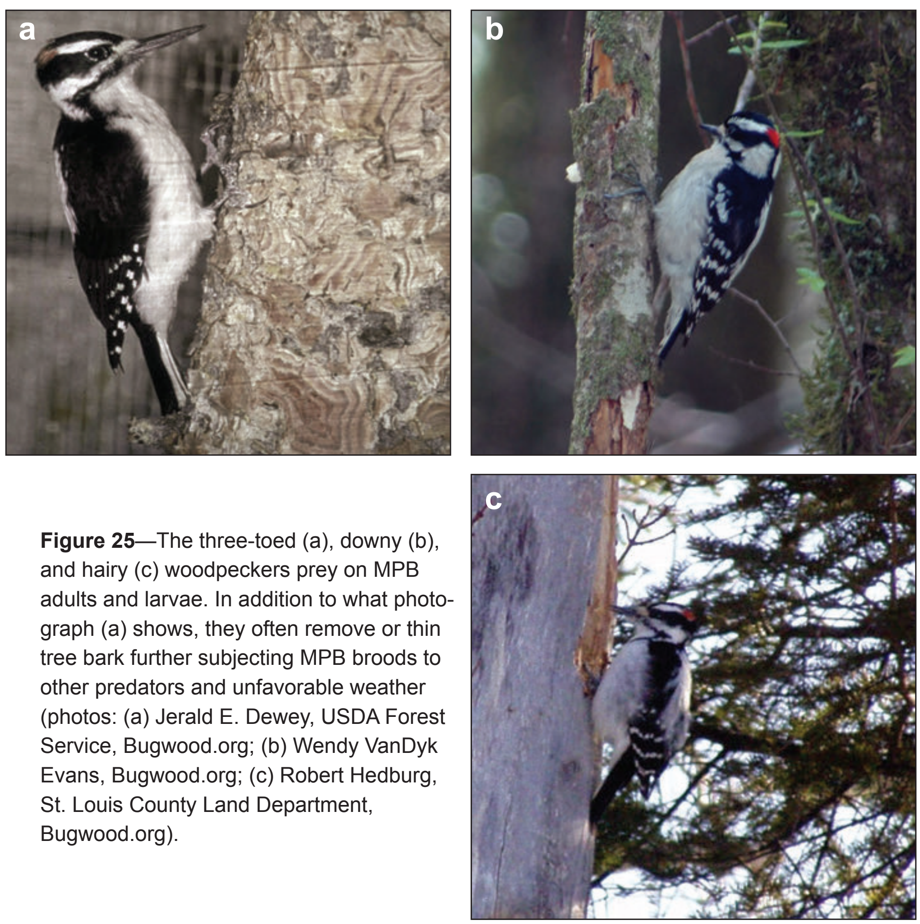

Figure 25—The three-toed (a), downy (b), and hairy (c) woodpeckers prey on MPB adults and larvae. In addition to what photograph (a) shows, they often remove or thin tree bark further subjecting MPB broods to other predators and unfavorable weather (photos: (a) Jerald E. Dewey, USDA Forest Service, Bugwood.org; (b) Wendy VanDyk Evans, Bugwood.org; (c) Robert Hedburg, St. Louis County Land Department, Bugwood.org).

woodpeckers consume large quantities of MPBs, they are believed to have an insignificant effect on MPB production. However, during endemic periods, they may play an important role in keeping bark beetle populations in check (Amman 1984; Amman and Cole 1983; Wegensteiner et al. 2015).

The three-toed woodpecker is consistently listed as an important consumer of bark beetles (Amman and Cole 1983; Fayt et al. 2005; Wegensteiner et al. 2015). The three-toed is the largest of the three primary woodpecker predators, having a larger bill and more hammering power, which allows deeper penetration through bark. Using this assumption, the three-toed would be the most effective at preying on bark beetles, followed by the hairy, and lastly the downy (Reynolds 2015, personal communication). In addition, populations of three-toed woodpeckers readily rise to increases in bark beetle populations (Fayt et al. 2005).

Woodpeckers consume adult, pupae, and larva forms of bark beetles and most notably they are major predators during the winter (Amman 1973, 1984; Wegensteiner et al. 2015). Prey size is an important factor affecting MPB predation by woodpeckers. Trees containing small larvae tend to be avoided and woodpeckers concentrate on trees containing large larvae. At high elevations in northwestern Wyoming, woodpeckers preyed mostly on parent MPBs because the larvae were small (Amman 1973). During the winter, alternate woodpecker prey are less available and often woodpecker diets consist of mostly bark beetles (Amman 1973; Wegensteiner et al. 2015). Amman (1973) found woodpeckers consuming MPB larvae more frequently on tree boles 12 feet above ground level compared to 4 feet, most likely because of snow depth. However, during the initial stages of bark beetle attacks, woodpeckers tend to feed over the entire tree bole, but when bark beetle numbers increase they tend to prey where bark beetle density is greatest (Wegensteiner et al. 2015).

Woodpeckers consume large numbers of adult, pupae, and larva forms of bark beetles but also through their pecking and dislodging bark they can indirectly cause bark beetle brood death (Amman 1984; Fayt et al. 2005; Wegensteiner et al. 2015). Woodpeckers flake, puncture, excavate, and remove tree bark as they feed and frequently reduce bark thickness, which can make the brood susceptible to cold and injury and expose bark beetle larvae to parasitism by wasps (fig. 25a). As mentioned earlier, the female braconid wasp needs to penetrate the bark with her ovipositor to attach her egg on an MPB larvae and the thinner the tree bark, the easier it is for her to attach the egg (fig. 21). Also, depending on the intensity of feeding by woodpeckers, enough tree bark may be removed that the MPB brood could be killed by desiccation as the phloem dries or over winter by freezing (Amman 1973; Amman and Cole 1983; Wegensteiner et al. 2015).

Associated Microorganisms of Mountain Pine Beetles

Amman and Cole (1983), Mercado et al. (2014), and Wegensteiner et al. (2015) list the wide array of bacteria, mites, algae, viruses, nematodes, yeasts, and fungi that the MPB carries from tree to tree as it completes its life cycle (fig. 26). These associated microorganisms can be both beneficial and detrimental to the MPB. With many different species of each organism and all of the possible interactions among them and their host tree, a very complex and minimally understood realm occurs under the bark of a MPB-infested tree. In the following narrative, we highlight the excellent discussions that Amman and Cole (1983), Mercado et al. (2014), Wegensteiner et al. (2015), and Hofstetter et al. (2015) provided on these organisms and their relations with MPBs.

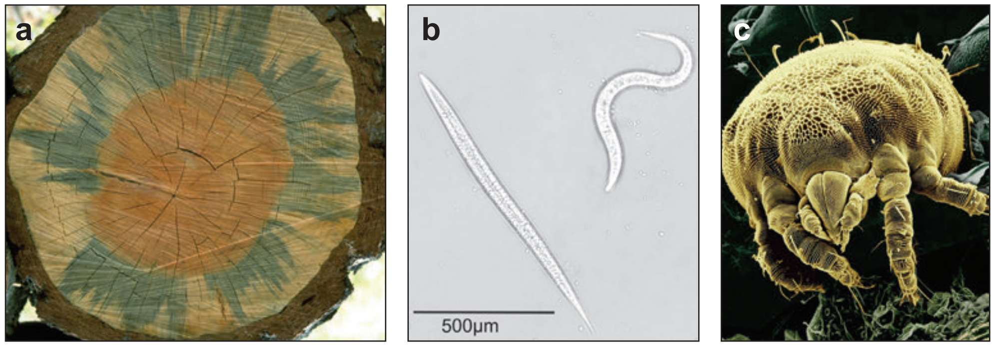

Figure 26—MPBs carry with them a number of bacteria, mites, nematodes, and fungi with the blue-stain fungi being the most notable. (a) As shown in this picture, blue-stain fungi does not weaken the lumber but the blue color devalues it (photo: Sandy Kegley, USDA Forest Service, Bugwood.org). (b) Unidentified nematode from inside of an MPB. Note the spores floating on the medium around the nematode (photo: Javier E. Mercado). (c) Yellow mite (*Lorryia formosa*) enlarged 850 times (photo: Eric Erbe, USDA Agricultural Service, Bugwood.org).

Blue-stain (*Ophiostoma montium, Leptographium longiclavatum*, and *Grosmannia clavigera*) are the most notable and intriguing fungi that MPBs carry from tree to tree (Beal 1939; Mercado et al. 2014; Rumbold 1941; Six and Bracewell 2015) (fig. 26). These fungi do not weaken the wood by coloring the wood blue, but the lumber loses its commercial value. Both blue-stain fungi and MPBs have developed strategies that benefit each other in their establishment, growth, and reproduction within their hosts before the tree dies. Killing a tree before the MPBs have fully occupied it would be detrimental to both fungi and MPB because both colonizers benefit from minimal competition as they become established in a tree (Khadempour et al. 2012; Kim et al. 2005; Mercado et al. 2014). The time it takes for a girdled conifer to die is highly variable but often exceeds 1 year (Noel 1970; Wilson and Gartner 2002). However, pines completely and successfully colonized by MPBs and its associated blue-stain fungi typically die within 1 year after the attack (Hubbard et al. 2013; Mercado et al. 2014; Yamoka et al. 1990).

The relationship between the blue-stain fungi and bark beetles is rather distinctive, as each contributes to the death of the tree. The blue-stain fungi benefit from this relationship as the MPB moves them from tree to tree that provide them with food and shelter. Six and Wingfield (2011) postulated that tree mortality is the result of fungal invasion into the xylem disrupting water flow or fungal invasion into the phloem depriving the tree of photosynthates (e.g., simple sugars) or other defenses allowing for successful bark beetle colonization. Disruption of pitch and water flow prevents the tree from pitching out the bark beetle (Kane and Kolb 2010; Mercado et al. 2014) (fig. 27). Transpiration within lodgepole pine trees can be reduced within 10 days of a MPB attack, which corroborates the notion that blue-stain fungi quickly impacts xylem tissue function (Hubbard et al. 2013; Six and Wingfield 2011). In addition to being impacted by blue-stain fungi, phloem is consumed by MPB larvae and its quality and quantity are major determinants of larvae development. For 3 weeks after hatching, young MPB larvae consume phloem tissue as they extend their feeding galleries 1.0 to 1.2 inches horizontally (Amman and Cole 1983). As a result of ≈5,000 to 10,000 larvae building lateral galleries, 500 to 1,000 feet of the galleries in the average infested tree in the Black Hills (12.6 inches diameter breast height-DBH, 20 feet of bole infested, 80 to 150 larvae/foot^2 of bark) cause the tree to be girdled and contribute to its death (Amman and Cole 1983) (fig. 16).

Figure 27—As the MPB excavates galleries in ponderosa pine, the tree releases pitch (photo: USDA Forest Service, Rocky Mountain Region, Bugwood.org). If the amount is sufficient, occasionally a tree repels an attack and the beetles are “pitched out” and the tree survives. The illustration on the right was produced by Hopkins after he visited the Black Hills in 1901 (Hopkins 1902).

In addition, blue-stain fungi can contribute to nutrition, metamorphosis, sexual maturation, and other important physiological processes of MPBs (Bentz and Six 2006; Bleiker and Six 2007; Hofstetter et al. 2015; Mercado et al. 2014; Six and Paine 1998; Wegensteiner et al. 2015;). MPBs also transport bacteria internally but it can be excreted in the beetle’s frass or secreted orally (Cardoza et al. 2006). Bacteria roles are not well understood, but some species have been found to have fungicidal, nutritional, and antagonistic effects on fungi present in other bark beetle systems (Cardoza et al. 2006; Mercado et al. 2014).

Currently, 13 species of nematodes are known to be associated with MPBs (fig. 26) (Mercado et al. 2014). Massey (1974) found approximately 25 nematodes of one species in one bark beetle. Nonparasitic nematodes are typically transported externally by the beetle, while parasitic nematodes are normally transported internally. Nematodes have various relations with MPBs that can be phoretic (MPB transports them), parasitic (living off the MPB), necromenic (completing their development after natural death of MPB), or predatory (killing and consuming MPBs) (Hofstetter et al. 2015; Massey 1974). Nematodes can reduce MPB fitness and can affect bark beetle populations. Also, nematodes interact with the other microbes that MPBs carry, further confounding their exact role in MPB population dynamics (Hofstetter et al. 2015; Mercado et al. 2014).

The number of mites carried on an individual beetle can vary from none to hundreds (fig. 26) (Hofstetter 2011). In the Black Hills, Reboletti (2008) found 10 mite species on MPBs that can prey on nematodes, other mites, bark beetle eggs, and young larvae (Hofstetter et al. 2013). Because mites can reduce flight speed and wing-beat frequency of bark beetles, they potentially decrease MPB dispersal and tree colonization by MPBs. Mites can alter the presence and abundance of antagonistic or mutualistic fungi, yeast, bacteria, nematodes, or other invertebrates associated with MPBs. In particular, mites have been linked with blue-stain fungi, suggesting that they carry fungal spores among and within trees. Thus, mutualism (the way relationships among different species exist in which each individual benefits from the activity of the other) is a good term for the relationship between mites, fungi, and MPBs with some exceptions where mites are MPB predators and parasites (Hofstetter et al. 2015; Mercado et al. 2014).

As the preceding discussions described, the life cycle of the MPB is far more complex than it appears on the surface (fig. 15). In its simplest terms, the MPB attacks a tree late in summer, lays eggs, the eggs hatch, and new MPBs exit the dead tree the next summer to attack new trees. However, adding all of the associated predators, parasites, and microorganisms and their interactions both among themselves and with the attacked trees, the complexity of the MPB lifecycle is difficult to comprehend. Add more complexity with woodpeckers, weather variations, climate fluctuations, and the unknown impacts of climate change, it is not surprising that all efforts over the last 100 years to directly control bark beetles have been futile.

Bark Beetle Control

Upon describing the MPB from a 4-day trip to the Black Hills, Hopkins (1902) immediately began devising methods to control the damage it caused. However, he recognized that when an infestation had been going on for 6 or 7 years and had reached epidemic levels, unless some natural agents appeared to either modify or check it, control was beyond all human effort. Using knowledge from his work in the Appalachian Mountains and knowledge of the spruce beetle, he recognized that bark beetle-killed trees were the source of bark beetles for tree attacks. He determined that it was only necessary to reduce bark beetle numbers to the point where they could no longer overcome tree resistance to attack (Hopkins 1902). Hopkins (1909) refined this thinking and stated "if 75 percent of the brood was killed, the remaining 25 percent will most likely die of natural causes." He estimated that about 75 percent of infected trees could be located and treated at a reasonable cost. As such, Hopkins' 75 percent rule had as much to do with the logistics of applying treatments as it was with the efficacy of controlling bark beetle infestations.

Direct Control

In the Black Hills, using the knowledge gained by Webb on MPB biology and seasonal history, Hopkins recommended killing MPBs on the spot or transporting the infested trees out of the forest by train (Furniss 1997; Hopkins 1905, 1910). It was thought that if MPB killing were done thoroughly over a large enough area, the amount of timber killed by MPBs would be negligible. Timing was a deciding factor, so during the winter, when bark beetle broods were maturing, these individual tree control efforts would be done (Miller and Keen 1960). However, it was illegal to cut live trees in the Black Hills until 1906 so no infested trees were removed. Even when the law was changed there was no market for blue-stained lumber and again infested trees remained in the forest. As a second option, Hopkins (1905) suggested the bark be removed from infested trees to expose the MPB broods while they were immature. At first, trees were felled and bark was removed and later a debarking tool was developed to remove the bark on standing trees at heights of 6 to 20 feet. Other control suggestions included electrocution and spreading a fungus that appeared to be associated with some of the infested trees (Furniss 1997). Similarly, in California, understanding and control efforts of the WPB began (Smith 1966, 1990). Very much like the work conducted in the Black Hills, trials were started to control the WPB, considered to be the most damaging bark beetle in the western United States in the early 1900s (Miller and Keen 1960).

Methods for protecting living trees from attack were readily dismissed because they would be required to be applied over large areas and, even if they could be developed, they would be cost prohibitive. As a result, bark beetle destruction was the primary control strategy. The attitude during the early 1900s progressed from one of optimism by applying Hopkins' 75 percent rule, to one of determination to get every bark beetle by using a variety of individual tree treatments (Smith 1990). Even though Hopkins suggested the cutting of 10,000 to 15,000 MPB infested trees would quell the ≈1900 MPB epidemic in the Black Hills, it was unsuccessful and the insects killed millions of trees. This epidemic foreshadowed many similar events that would follow over the coming decades in the Black Hills (Furniss 1997).

Trap Trees

Hopkins directed Webb in 1902 to test the effect of trap trees. Trees were felled, hack girdled (notches cut through the bark), girdled to the heartwood, belt girdled, and hacked and peeled at intervals of 5 or 6 days between June 2 and October 30 (Furniss 1997). The assumption was that trap trees would attract MPBs and when the larvae were about full grown, the removal and burning of the bark would effectively destroy the broods. If living trees in the immediate neighborhood of the trap trees were attacked, they were treated the same as trap trees (Webb 1906). However, Hopkins (1905) indicated that no method of preparing trap trees attracted enough bark beetles to warrant its adoption. While many of the trees were attacked, the percentage and density of the infestation was no greater than in nearby or distant healthy stands. As a result, trap trees proved to be futile and Hopkins (1905) looked to other methods of controlling MPBs.

Fell, Peel, and Burn

Another option Hopkins (1905) suggested was locating trees that were attacked during the summer and fall and prior to May l of the following year, fell the trees, and remove the bark to kill the bark beetle brood (fig. 28). However, during fall and winter, in contrast to the

Figure 28—Peeling a large ponderosa pine in California to kill WPB broods under the bark (photo: Miller and Keen 1960).

spring, the bark on large ponderosa pine trees tends to be tight and difficult to peel. Many attempts were made to treat tight-barked trees without peeling them by piling the limbs and other fuel material over the log to create a very hot fire. The heat generated by such fires had little effect on the brood on top of the log. The fires being concentrated on the sides of the logs and insulating properties of ponderosa pine bark prevented sufficient heat to kill broods. Only along the bottom and lower sides of the log where the fire was banked between log and ground was there an effective kill in the unpeeled bark (Hopkins 1909; Miller and Keen 1960; Smith 1990).

Burning

Hopkins (1909) proposed decking and burning infested logs, a treatment most likely used in conjunction with felling, peeling, and burning. This control method was most applicable when a group of trees rather than single trees needed to be treated and it was more economical to burn the unpeeled logs in piles than to peel and treat each separately. The decking method usually required additional fuel to get the fire started. In the larger decks, the bottom logs were often entirely consumed (Evenden et al. 1943). However, the decking and burning method was impractical without equipment capable of hauling and piling large logs. Using kerosene to burn logs and standing ponderosa pine trees was also tested but insufficient heat was generated to kill the broods underneath the bark (Miller and Keen 1960). Standing lodgepole pine with thinner bark was burned and did produce enough heat to kill the broods (Evenden et al. 1943).

After World War II, an incendiary “goop” made of finely ground magnesium, magnesium impurities, asphalt, and kerosene became available. This surplus putty material burned very hot, producing temperatures between 2,000 and 3,000 °C. Even with these temperatures, felled logs needed to be covered with metal or dirt to generate enough heat to kill the broods under the bark of mature ponderosa and sugar pine trees. The surplus supply of goop was quickly exhausted and because of its propensity to spontaneously combust, no operational use of the material occurred. Nevertheless, trials using these materials once again demonstrated how resilient and protected bark beetle broods are beneath tree bark (Miller and Keen 1960).

Solar Heating

Solar heating to create lethal temperatures to kill bark beetle broods was tried as a substitute for burning. Experiments conducted on bark beetle eggs and larvae indicated that lethal temperatures ranged from 115 to 120 °F (Miller and Keen 1960; Mitchell and Schmid 1973). Ponderosa pine trees in California were peeled and the bark spread to expose it to the sun to produce lethal temperatures. Being able to treat trees in the summer would extend the season in which infested trees could be treated. But spreading peeled bark to ensure it got full sunlight was difficult, especially when trees were located on northern slope aspects or where other trees shaded the area. Unless air temperatures approached 85 °F, the required lethal bark temperatures could not be reached. Using Keen’s suggestion in 1924, infested ponderosa pine trees were felled on the Kaibab National Forest in northern Arizona and arranged to maximize their heating by the sun and rolled to ensure all sides of the trees were heated. Also, trees were felled and lodged in adjacent trees to elevate the boles to encourage both heating and drying to kill the broods. In both instances broods were not killed and their numbers actually increased in trees that were felled (Blackman 1931). In contrast, Negrón et al. (2001) showed that MPB brood survival was reduced by solar heating especially when a single layer of tree boles were exposed to the sun. Success of using the sun to reduce or kill broods in ponderosa pine and especially in thin-barked lodgepole pine was improved if the logs were rolled to make sure that each face was exposed to the sun (Negrón et al. 2001; Patterson 1930; Smith 1990; Wickman 1987).

Toxic Chemicals

Fire heat proved to destroy bark beetles but required the bark to be removed at least partially; alternatively, fires of sufficient intensity were needed to create lethal temperatures under the bark (Blackman 1931; Evenden et al. 1943; Miller and Keen 1960). The use of fire had complications and risks, so alternatives were sought that had greater application flexibility for killing bark beetle broods. As a result in 1932, in cooperation with Standard Oil, the search for bark beetle insecticides began (Miller and Keen 1960).

Oils and Insecticides

In the early 1930s, a variety of light oils were used to spray on felled logs with varying success at killing brood (fig. 29). It was found that light distillates caused the highest mortality and that their effect was increased by the addition of insecticides such as naphthalene, creosote, and paradichlorobenzene. Penetrating sprays containing a toxic chemical and mixed with diesel fuel or a water emulsion were found to be more effective in killing broods than oil alone. The sprays were applied liberally to the bark surface to penetrate to the inner bark tissue (Lyon 1965). Larval mortality resulting from the use of the oil-naphthalene

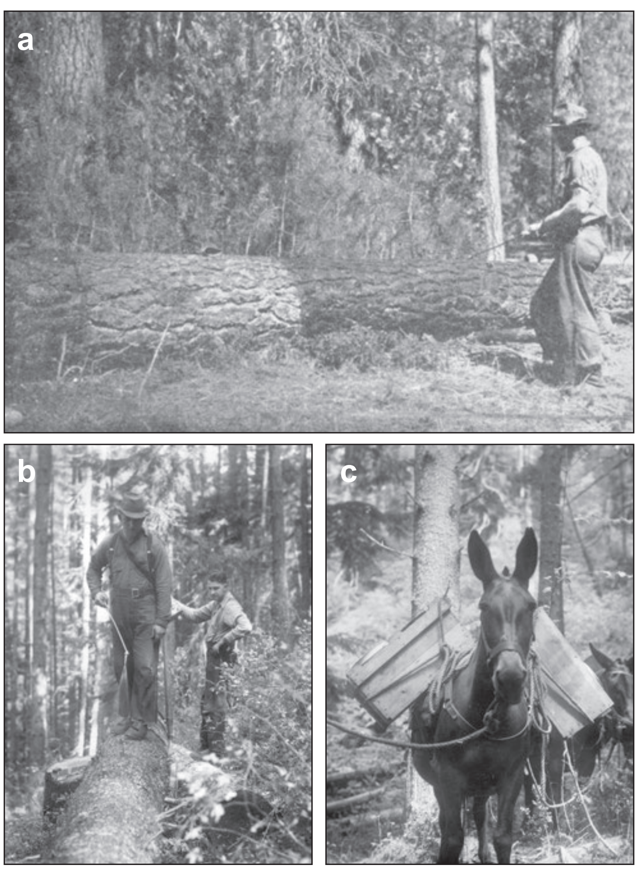

Figure 29—(a) Light oils were sprayed on felled trees under the assumption that they would penetrate the bark and kill bark beetle broods. However, the success of such treatments was highly variable and they were used only for a short time (photo: Miller and Keen 1960). (b) Insecticides (i.e., orthodichlorobenzene, Ethylene dibromide, lindane) were combined with oils and applied to both standing and felled trees to kill bark beetles as they landed and emerged from trees. (c) Where access was limited, mules in pack trains were used to keep spray crews supplied.

formula was found to depend upon the depth and rate of oil penetration into the outer bark. This varied greatly among individual ponderosa pines, primarily because of differences in bark texture. Higher brood mortality resulted where large larvae, pupae, or new infestations occurred. It was shown that the penetrating oil control method could only be used on thin-barked trees and that it was impossible to obtain satisfactory control unless the logs were rolled and the bottom half given a separate treatment. In addition, the difficulties with the transportation of supplies and the high cost of the treatment compared to peeling-burning treatments limited their use. However, a variety of insecticides were tried including DDT, chlordane, and toxaphene and several became widely used to control bark beetles in felled and standing trees throughout the Western United States (Cole and Amman 1980; Lyon 1965; Miller and Keen 1960; Smith 1990).

Orthodichlorobenzene/Ethylene dibromide

By the 1930s and 1940s, building on the use of fuel and kerosene oils in combination with poisonous chemicals, orthodichlorobenzene (i.e., solvent) was used for direct control of bark beetles (Cole and Amman 1980; Evenden et al. 1943; Miller and Keen 1960). Sprays had been developed that penetrate the bark of infested lodgepole pine trees and could be applied on both felled and standing trees (Wickman 1987). This method eliminates the objectionable use of fire and permits bark beetle control to occur during June and July. Four parts diesel oil and one part of orthodichlorobenzene was used extensively on lodgepole pine and to some extent on western white pine and ponderosa pine trees into the late 1950s (Furniss 2007; Miller and Keen 1960; Thompson 1975). In 1957 Ethylene dibromide[3] was added to the chemicals used for treating both standing and felled trees (Evenden et al. 1943; Thompson 1975) (fig. 29).

Lindane

Starting in the late 1950s another approach for direct insecticide control of bark beetles was developed. Instead of having the toxic substance penetrate the bark and kill the brood, the insecticide would be sprayed lightly on the bark surface and the adult bark beetle would contact a lethal dose as it emerged or attacked a new host tree. Attention turned to testing lindane, also known as gamma-hexachlorocyclohexane and erroneously known as benzene hexachloride (BHC). It was a widely used insecticide and bark beetles were killed when they crawled over filter papers coated with the equivalent of one-twentieth of a pound of lindane per acre (fig. 29). A pilot test involving 100 acres was set up in the Black Hills where up to two pounds of lindane per acre was applied repeatedly for a period of 2 or 3 days as MPBs began exiting infested trees. "The foliage and bark of the trees literally glistened with the insecticide" and most notably more trees were infested by MPBs in the treated areas then the untreated areas (Furniss 2007; Larson 1979). Nevertheless, lindane proved to be cost effective in controlling and preventing bark beetle attacks, as it gave trees protection for up to 3 years (Koerber 1976; Lyon 1965; Lyon and Swain 1968; Smith 1976a,b). As a result, it was used widely in the 1960s and had strong support for protecting timber resources and for protecting recreation sites (Koerber 1976; Roettgering et al. 1976; Swain 1976). Because of

[3] Ethylene bromide, EDB, 1, 2-Dibromoethane, ethyl bromide, and Glycol dibromide are names that have been used for the insecticide Ethylene dibromide (Barsan 2007).

its side effects, the use of lindane for controlling bark beetles diminished by the mid-1970s and once again harvesting, felling, and other mechanical bark beetle control strategies were used (Smith 1990).

Lindane was first registered in the United States in the 1940s and was used as a bark beetle insecticide and used to protect a variety of fruit and vegetable crops. In 1977, the Environmental Protection Agency (EPA) disallowed its use for home fumigation and in 1985 they asked for information as to why its registration should continue. Between 1993 and 1998, long-range transport and environmental concerns about lindane increased and lindane registrants voluntarily cancelled all registered uses in 1998 and 1999, except for treating some seeds. In 2002 only 6 lindane seed treatments were available and in 2006 the EPA suspended lindane use in the United States (U.S. Environmental Protection Agency 2006).

Silvisar

Creating trap trees and injecting chemicals into trees after they have been attacked by bark beetles began in the 1930s. However, a limitation to injecting chemicals into the sap stream of bark beetle-infested trees is the presence of the blue-stain fungi. The fungi can interrupt xylem flow in southern pines in 3 to 5 days after bark beetles attack, effectively blocking the toxic chemicals from killing the bark beetles. Successful control of the broods, however, can be obtained for 60 or even up to 90 days after western white pine trees have been attacked (Craighead and St. George 1938). Bedard (1938) developed and evaluated different methods for injecting copper sulfate into the conductive tissues of western white pine and killed over 90 percent of MPB broods.

In 1964 Silvisar (fast-acting herbicide) was injected into trees to test its effectiveness in killing bark beetle broods. Silvisar 510 was used for thinning stands of conifers and hardwoods and the lethal component was cacodylic acid, a highly water-soluble arsenic compound (Schmid and Frye 1977). The exact way the herbicide acts on bark beetles was not known. The herbicide may kill the cambium layer, making the habitat unfavorable for the insect or may have direct insecticidal properties (Chansler and Pierce 1966). The chemical was inserted into the sap stream around the full circumference of the tree about 5 to 10 inches above ground level in trees that were recently attacked. At first an injector was used to apply the chemical but later it was placed in a frill or notch cut with a hand axe through the bark and applied by using a squeeze bottle (Buffam 1971; Chansler and Pierce 1966) (fig. 30). Using Silvisar for controlling bark beetles directly was very encouraging as Chansler and Pierce (1966) killed 99 percent of the MPB broods in the trees they treated.

Direct Control of Mountain Pine Beetles in the Black Hills

1900–1910

In 1897, Graves found MPBs in the Black Hills and in 1901 Hopkins began devising ways to control them (Furniss 1997; Graves 1899; Hopkins 1902). This was the beginning of one of the, if not the, longest and continuous efforts to directly control bark beetles anywhere in North America (fig. 31). In 1902, Webb, who was employed by Hopkins to study the MPB, treated 200 live trees by dousing them with kerosene, girdling them, and felling them in an effort to attract beetles. After the MPBs were concentrated in these trap trees, the trees would be harvested or other means would be used to destroy the MPBs. Trap trees did

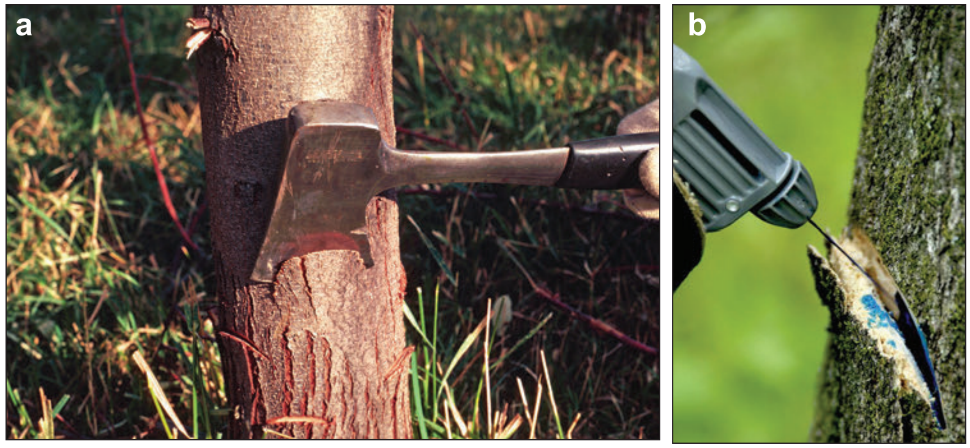

Figure 30—Silvisar, an herbicide was widely used to control unwanted woody vegetation. The bark was notched and the frill was sprayed with Silvisar. This “ hack and squirt” method was used on the entire circumference of ponderosa pines to kill broods of bark beetles in standing trees with limited success (photos: (a) Steve Manning, Bugwood.org.; (b) Steve Dewey, Bugwood.org).

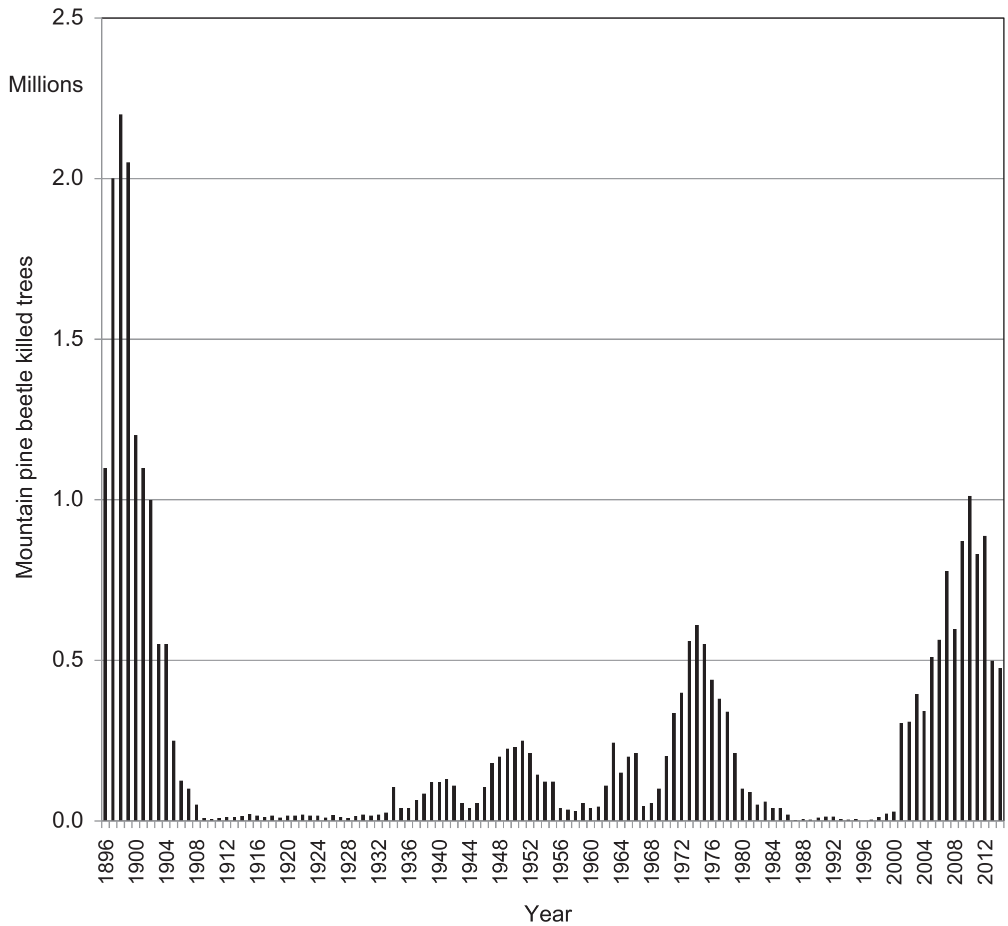

Figure 31—Within the forests of the Black Hills, there has been a continuous endemic and several epidemics of MPBs over the last 129 years. There is an uncertainty about how many trees were killed but the above graph provides estimates from descriptions and values provided by Graves (1899), Hopkins (1910), Murdock (1910), Furniss (1997), Thompson (1975), Lessard et al. (1987), Freeman (2015), Harris (2003, 2004, 2005, 2006, 2010, 2011, 2012, 2013, 2014), and Harris et al. (2001, 2002).

not work and felling, peeling, and burning attacked trees became the method of choice for controlling MPBs (Hopkins 1905, 1909). By 1906, a total of 300,000 board feet of timber had been cut and 350 standing trees had their bark peeled for $0.27 per tree in an effort to control MPBs (Thompson 1975). Between 1906 and 1908, 10,000 to 15,000 trees had been cut and the broods had been destroyed. In the Black Hills from 1900 through 1910 it was estimated that 251.3 million board feet were harvested out of 2 billion board feet attacked (Thompson 1975) (fig. 32). Nevertheless, there was no doubt in Hopkins' mind that the peeling and tree cutting was the primary means of ending the bark beetle epidemic in the Black Hills. He went on to say "there is no trace of doubt in my mind that if my recommendation in 1901 and 1902 had been promptly adopted and carried out, there would have been no further loss of timber from the work of the beetles" (Furniss 1997).

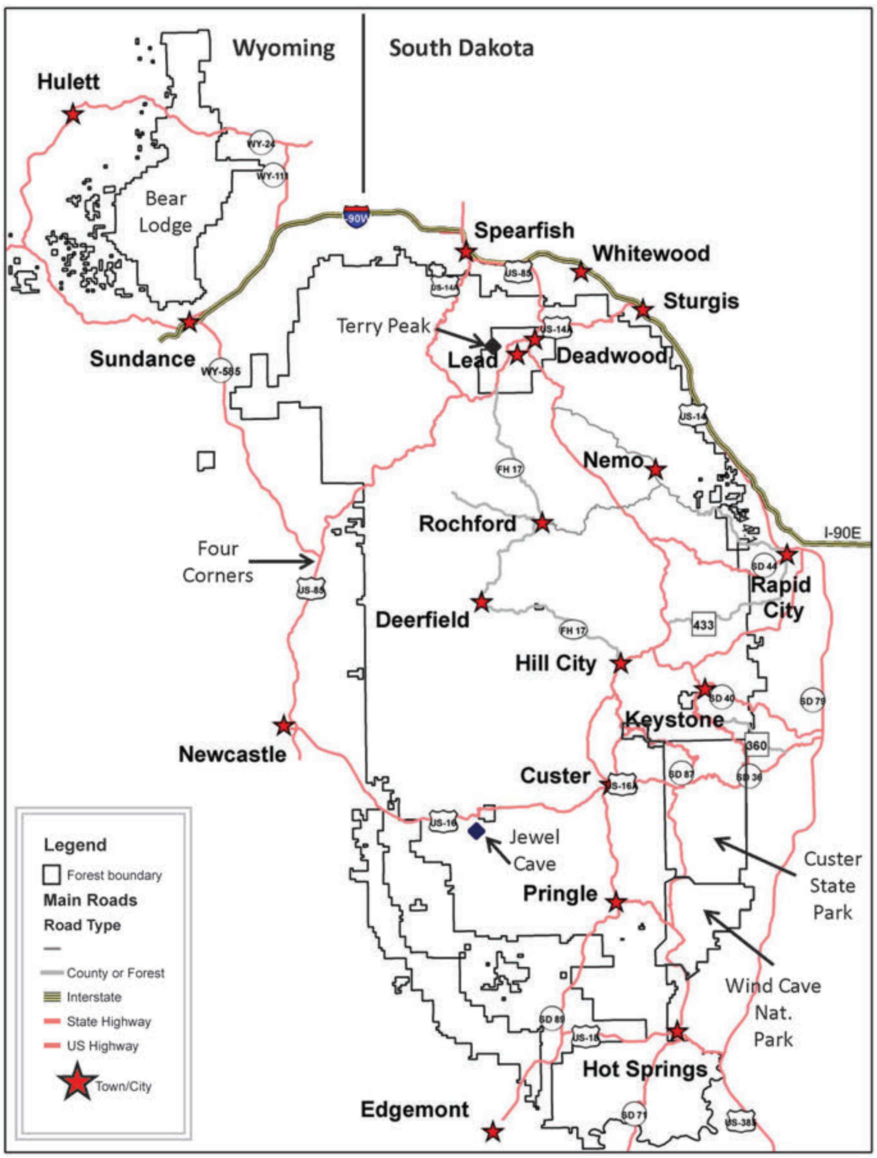

Figure 32—Beginning in 1902, direct control of MPBs occurred throughout the Black Hills of South Dakota and the Bear Lodge Mountains of Wyoming.

1911–1935

With the MPB epidemic that began in the late 1800s ending by ≈1910, the next two-and-a-half decades saw spotty and endemic levels of bark beetle activity. Between 1914 and 1923, 740,000 board feet were harvested, with much of it associated with MPB infestations[4] (fig. 31). MPB infestations were scattered throughout the Black Hills with patches of trees killed and treated. The minimal activity is exemplified in 1930 when only 29 trees were reported as being felled, piled, and burned (Thompson 1975). To control MPBs in 1932, 1,452 trees were harvested over 1,810 acres that contained 176,000 board feet of timber. In 1934, 1,300 trees were treated and in 1935 no infestations were discovered and only 2 trees were felled, peeled, and burned.

1936–1945

In 1937, 137 trees were treated across the Black Hills by felling, peeling, and burning. Widespread infestations of MPBs occurred throughout the northern Hills in 1938. Near Spearfish, groups of trees were being attacked in the 6- to 10-inch diameter breast height (DBH) range, aided by considerable snow damage that occurred in 1937. Also, areas in the central Hills were being attacked and Custer State Park and Jewel Cave National Monument had between 1,000 and 2,000 trees attacked. Across the Black Hills National Forest, 16,882 acres containing 2,358 attacked trees were treated in 1938 (Thompson 1975) (fig. 32).

There was a considerable increase in MPB activity in 1939 throughout the Hills with 10,758 newly attacked trees occurring on 77,910 acres; 10,461 trees were treated primarily by harvesting (fig. 33). In 1940 and 1941, newly discovered infestations (see footnote 4) covered 73,446 acres and 5,536 trees were removed by harvesting. From 1942 through 1945 an additional 30,965 acres were infested and the attacked trees were rather scattered as 1,795 trees were harvested. However, it was observed that MPB infestations were increasing near Spearfish and east into Wyoming (Thompson 1975) (fig. 32).

Figure 33—Harvesting of MPB infested trees was frequently used in the 1930s and 1940s as shown here in the Moskee, Wyoming, area.

[4] "Infested acres" does not indicate that every tree in the infested area was attacked and killed. For example, from 1911 through 1935, 1,810 acres were described as infested but attacked trees were scattered and 1,452 MPB attacked trees were harvested. Also from 1942 through 1945, 30,965 acres were infested and MPB-attacked trees were scattered.

1946–1955

The northern Black Hills and Bear Lodge Mountains in Wyoming had a rapid increase in MPB infestations beginning in 1946. The Rochford and Bear Lodge Districts were especially affected in 1946 but infestations were occurring throughout the Hills (figs. 31, 32). World War II reduced the amount of funds that could be used for direct control, and this reduction was given as a reason for the building of the MPB epidemic. In 1946, 7,005 new acres were infested and the number of acres infested each year increased with 350,000 new acres infested in 1950 at the peak of the epidemic (fig. 31). By 1951 the newly infested acres decreased to 157,000 and through 1955 only small additional groups of attacked trees were detected covering minimal acres. Nevertheless, during the period of 1946 through 1955, over 1.4 million acres were deemed to have been infested by MPBs and additional patches of trees were attacked through the entire Black Hills (figs. 31, 32) (Thompson 1975).

In 1947 a special appropriation of $235,000 was passed by Congress so treatment could begin in an effort to control a pending epidemic. In contrast to earlier control efforts of peeling, burning, or harvesting attacked trees, orthodichlorobenzene was sprayed on standing trees (fig. 34). By July of 1948, 45,949 trees had been sprayed over 177,000 acres. Spraying of attacked standing and felled trees was the control method of choice from 1949 through 1955 but some harvesting was also used. As a result, from 1946 through 1955, 93,333 attacked trees had been treated primarily by spraying with orthodichlorobenzene (fig. 31) (Thompson 1975).

The years of 1946 through 1955 show how quickly MPB populations can increase and also show how quickly their populations diminish (fig. 31). Also, this epidemic shows how difficult it is to influence MPB populations by direct control. When Hopkins came to the Hills in 1901 he recognized that “when a trouble has been going on six or seven years and has reached the magnitude of the one under consideration [i.e., 1901 infestation], it is very

Figure 34—Beginning in the 1940s orthodichlorobenzene (an insecticide) mixed with diesel fuel was used throughout the Black Hills to kill MPBs as they landed or emerged from standing trees. These photographs show fully protected employees spraying trees in 1948 (photos: R.A. Lerchen, USDA Forest Service, Deadwood Ranger District).

plain that unless some natural agencies appear to either modify or check it, its control is beyond all human effort" (Hopkins 1902). Prior to this Black Hills' wide epidemic, the last major Black Hills MPB epidemic occurred in the early 1900s. From the time when Hopkins visited in 1901, through 1955, the Black Hills had a consistent and rigorous MPB control program, except when it was limited during World War II (fig. 31).

1956–1961

From the end of 1955 through 1957, MPB control efforts were described as maintenance through harvesting and with 1,399 trees sprayed with Ethylene dibromide and lindane, two new insecticides (fig. 35). Also, in 1957, 18,000 new acres of MPB infestations were discovered but nearly all of it was described as light. In 1958 a total of 35,100 acres of new MPB infestations were discovered southwest of Hill City but again most of the acres were described as lightly infested and 4,085 trees were treated (figs. 31, 32). Similarly in the same area in 1960, 20,000 trees were treated and the infestation was controlled. In 1961 south and southwest of Spearfish, numerous infestations were discovered with the trend described as having a build-up ratio of 1:3.5, indicating that for every attacked tree one year an additional 3.5 trees were attacked the following year. The drought that had occurred for several years prior to 1961 was suggested as contributing to this trend and trees 17.9 inches DBH and greater were preferentially being killed. No large control efforts occurred and maintenance level activities continued (Thompson 1975).

Figure 35—Beginning in 1957, standing trees were sprayed with the insecticides Ethylene dibromide, lindane, and Sevin (2% Carbaryl) to kill MPBs when they landed on or emerged from trees (photo: Malcom Furniss).

1962–1981

In 1962, MPB infestations within the Black Hills continued to increase in area and intensity (fig. 31). The northern Hills near Spearfish, Lead, Deadwood, and west into Wyoming were severely infested with MPBs (fig. 32). The State of South Dakota and the Forest Service planned joint control projects that resulted in 20,680 trees being treated. Trees being attacked averaged 14.1 inches DBH and it was noted the 250,000 acres cleaned (i.e., precommercial thinned) by the Civilian Conservation Corp in the 1930s was in need of thinning as the MPB epidemic was mushrooming (fig. 36). Control efforts were urgently needed to keep the infestations at the endemic level (Thompson 1975).

In 1963 the MPB epidemic transcended the Black Hills from Custer, South Dakota, to the Bear Lodge in Wyoming (figs. 31, 32). At least 25 million board feet of timber had been killed and 16,800 trees had been treated. It was estimated that 243,400 trees were attacked with the greatest number located in the area north of Rochford, near Deadwood and Lead, and extending throughout the northern Hills. Large chemical treatment projects

Figure 36—Between January 1, 1933, and December 1, 1938, the Civilian Conservation Corp (CCC) cleaned (e.g., precommercial thinned) 237,188 acres in the Black Hills and a total of over 250,000 acres were cleaned in the 9 years that the CCCs operated in the Black Hills (photo: Sanders 2004).

were used with 25,000 trees being treated. Again, it was recognized that there was a large amount of dense forests occurring across the Hills that were in need of thinning that would reduce the risk of MPB infestations (Thompson 1975).

In 1964 the MPB epidemic worsened all across the Hills with increased ratios of 1:2 to 1:4 being reported. Areas near Spearfish, Terry Peak, Four Corners, and Rochford were highly infested with MPBs (figs. 31, 32). The urgency of treating the epidemic was exemplified by the use of wildfire terminology such as "*suppression by all land managers was needed in areas of the epidemic*" and "*scattered infested areas needed complete mop-up work.*" During 1964 in Wyoming and South Dakota, 34,000 attacked trees were harvested, 118,000 were oiled and burned, and 86,000 were treated with insecticides (Thompson 1975).

An intensive suppression program was planned for 1965 where 79,000 attacked trees were to be treated. However, only 18,700 trees were treated. Infestations still persisted on the west side of Terry Peak, near Deadwood and Lead, and on State and private lands in the Four Corners area (figs. 31, 32). Again, it was noted that there was a need for thinning overstocked stands in the northern Black Hills. An emphasis for treating MPB-infested areas continued, to insure against further outbreaks. Cold and wet weather persisted throughout the Hills in August and September, which likely helped suppress the epidemic. Also clerid beetles and the *Medetera* fly preyed on MPB larvae, which also contributed to controlling the epidemic. A total of 285,785 attacked trees were treated between 1963 and 1965 in the Black Hills and this work was credited for bringing the epidemic under control (fig. 31). Predictions for coming years were static to a declining trend of MPB activity in the Hills (Thompson 1975).

MPB activity reports for 1966 indicated that tree losses were low (fig. 31). Many attacked trees remained on State and private lands and infestations were expanding near activity centers that existed in the previous years. Mortality caused by MPBs was still apparent on Terry Peak, near Deadwood and Lead, and the Four Corners area (fig. 32). Harvesting and other direct control measures were used in these areas to avoid further losses, but the amount and kind of treatment is unknown (Thompson 1975).

In 1967, attacked trees were treated on State, private, and Federal lands throughout the Black Hills. Nevertheless, the northern Hills in general saw large increases in MPB infestations with the area near Lead and Deadwood continuing to be a major center (figs. 31, 32). Also, predictions were for the MPB infestation to increase. Harvesting was used throughout the Hills to control the MPBs but it was used intensively in the Lead and Deadwood area. Chemical control of MPBs wherever possible was replaced by thinning of pole sized stands with pulp wood harvesting and salvage harvesting of large trees (fig. 37). Thus the use of chemicals for controlling MPBs that began in 1947 started to decline (Thompson 1975).

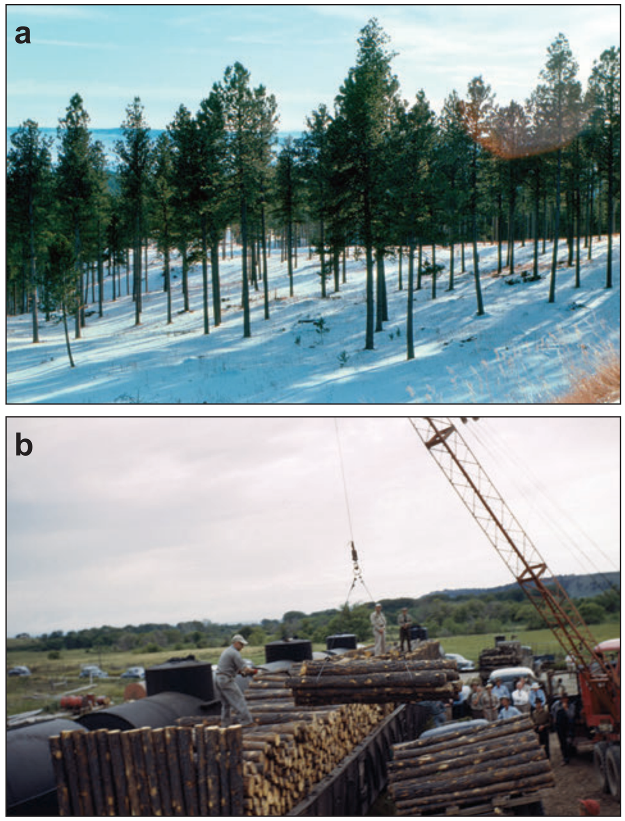

Figure 37—(a) Thinning pole sized stands to a tree density of 100 feet^2 of basal area per acre was used as a MPB control measure beginning in the mid-1960s. (b) The harvested pulp was shipped to paper mills in Wisconsin (Freeman 2015).

In 1968, the Black Hills reported approximately 21,000 attacked trees on State and private lands and 35,000 attacked trees on National Forest lands. Direct control was used in several areas where timber harvesting could not keep pace with the increasing MPB infestations. In the Bear Lodge of Wyoming and possibly in other areas of the Hills, individual attacked trees were treated using Silvisar. In the Bear Lodge, approximately 2,500 to 3,000 large trees were hand frilled and Silvisar applied with a plastic squeeze bottle (Graham 2015a, personal communication) (fig. 30). Even with harvesting and chemical treatments, MPB infestations throughout the northern Hills were increasing but past infestations were light and scattered. Heavy infestations occurred on private lands near Lead and Deadwood and on Forest Service lands within the Spearfish Creek watershed (Thompson 1975) (figs. 31, 32).

MPB infestations in 1969 tended to be static, but tree mortality remained high due to the number and extent of the trees attacked the previous year. Heavy infestations remained on Terry Peak and near Lead and Deadwood. Mixed land ownership patterns throughout the northern Hills limited coordinated and intensive direct control activities (fig. 31). Harvesting, burning, and chemicals were used in the infested areas and 17,000 attacked trees were treated on 200,000 acres of Forest Service lands and 20,000 attacked trees were treated on State and private lands (Thompson 1975).

MPB infestations in the Black Hills remained static in 1970 with 30,000 newly attacked trees located on 250,000 acres (fig. 31). Most of the infestations occurred on National Forest and South Dakota Department of Game, Fish, and Park lands (fig. 32). A major change in MPB control occurred in 1970 as no direct control of MPBs was proposed unless the losses were intolerable. As such, direct control of MPBs in the Black Hills that was so strongly advocated by Hopkins in 1902 greatly diminished.

From 1902 through 1969, over 13.1 million trees were either harvested, peeled, burned, or sprayed with chemicals in an effort to control the damage the MPB was causing in the Black Hills. These treated trees occurred on 3.1 million acres. With the Black Hills National Forest being 1.25 million acres in size, many acres were infested twice and more likely multiple times over this period. Over 3 million dollars were spent from 1946 through 1969 in the

Black Hills to individually treat over 525,000 trees attacked by MPBs. Treatments possibly had local impacts on MPBs but did not appreciably alter bark beetle dynamics across the Black Hills (fig. 31).

Efficacy of Direct Control of Bark Beetles

After Hopkins' 1901 trip to the Black Hills and having Webb devise direct control strategies, he was confident they would work (Furniss 1997). Hopkins (1909), after reviewing several direct bark beetle control projects in Maine and Colorado, solidified his opinion on the success of controlling bark beetles by treating individual trees. He went on to say:

> "One, that a very extensive outbreak by one of the *Dendroctonus* beetles can be controlled without expense, and even at a profit, whenever the conditions are favorable for the utilization of the infested timber; and the essential details, recommendations, and expert advice can be successfully carried out by a manager of a private forest and by the rangers of National and State forests. It also indicates quite conclusively that the widespread depredations in the Black Hills National Forest could have been prevented with very little expense to the Government if the matter had received prompt attention in 1901, when the first investigations were made and recommendations submitted. But, through the lack of public appreciation of the importance of the problem at the time, and the lack of sufficient authority and funds later, it was allowed to extend beyond practical control, and in consequence a large percentage of the timber on the entire National Forest has been killed."

As mentioned earlier, Hopkins also indicated it was not necessary to kill all of the bark beetles in an infested area and only 50 to 75 percent of them needed to be destroyed to bring them under complete control (Hopkins 1909). However, Blackman (1931) questioned this rule noting the great ability of the MPB to reproduce and that populations can increase at rates of 500 to 1,000 percent each generation. As a result, he suggested the rule would only be applicable when bark beetle populations were decreasing from natural causes. Similarly, the early results with WPB cast serious doubt about the 75 percent rule in California and it was not followed for long. Instead, early workers tried diligently to locate all infested trees and treat them (Smith 1990). Blackman (1931) also indicated that MPB could be controlled by direct methods as evidenced by successful efforts on the Kaibab Plateau in northern Arizona. Beal (1939) called these individual tree treatments "preventative" rather than "control" because he suggested they needed to be applied continually to keep bark beetle populations in check.

F. Paul Keen used 80,000 acres of ponderosa pine located on the Sierra National Forest of California to evaluate the effectiveness of directly controlling WPBs (Miller and Keen 1960). Keen was an entomologist with the Bureau of Entomology and Plant Quarantine in Ashland, Oregon. Keen, like Hopkins, was a pioneering entomologist and bark beetle expert (fig. 38). He had both formal forestry and entomological training at the University of California, Berkeley. For the first 5 years they attempted to treat every infested tree on the 80,000 acre area. In the subsequent 4 years they did maintenance control work by treating as many trees as they could and, as a result, they only treated about 40 to 50 percent of new infestations each year. Also, they tried to eliminate all infestations on 3,600 acres each year.

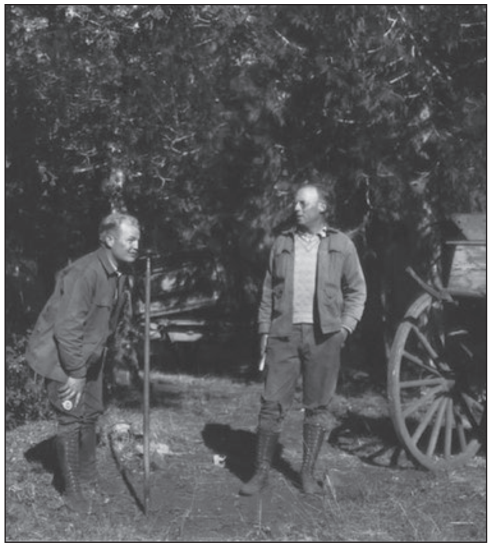

Figure 38—F. Paul Keen (right) was a pioneering entomologist of western forest bark beetles and is shown with his assistant Walter Buckhorn (left) developing bark beetle survey methods (photo: FPK 343 Western Forest and Insect Work Conference).

But once again they discovered only about 90 percent of the new infestations each year and found that such treatment intensity was impractical and was ineffective in stopping new infestations. As such, they concluded in 1920 that it was difficult if not impossible to prevent insect epidemics by any direct control methods (Miller and Keen 1960).

Not fully satisfied with the results of his 1920 work, Keen took on a much larger project to control WPBs on 1,276,000 acres of ponderosa pine on the east side of the Sierra Mountains of California. At the time, and even now (2015), this was the largest single undertaking of its kind. The fell-peel-burn method was applied uniformly with about the same efficiency throughout the area providing a good test of its application. From January 1922 to the end of the project in 1924, 1,276,000 acres were surveyed, 393,507 acres treated, and 31,512 trees treated costing $144,880. As a result of this work Keen summarized his findings, which varied by season, that for every tree treated one tree was saved (Miller and Keen 1960).

Large direct bark beetle control projects continued in California and in Oregon into the 1940s. In 1931 and 1932, on the Modoc National Forest, WPB infestations were increasing and direct control by cutting, piling, and burning was applied and the season after treatment some trees were saved from infestation. On the east side of the Sierra Nevada Mountains in 1934, two large control projects were undertaken with one showing some good short-term results. However, the other did not decrease timber losses. Such divergent results illustrate the erratic response of bark beetle infestations to the effects of control work. Throughout California during the early 1930s, with the use of Civilian Conservation Corp labor, 41 projects treated 560,000 acres. The results once again showed that projects undertaken at the peak of an infestation do little or no saving of timber. In addition, the results were temporary and limited by funding, making it imperative that a more consistent, effective, permanent, and cheaper method of forest insect control be found. From 1932 through 1940 on the Warm Springs Indian Reservation in Oregon, 57,731 attacked ponderosa pine trees were cut, piled, and burned on 320,000 acres. However, once again the benefits of the control work were temporary and the infestation resumed to its normal course after the work was done (Miller and Keen 1960).

As mentioned earlier, the direct control of bark beetles was often framed in terms related to fire control and suppression and the organizations that developed around bark beetle control projects resembled those associated with large wildfires (Blackman 1931; Smith 1990; Thompson 1975). Other than the Black Hills where the control projects were well defined and confined, Crater Lake in west central Oregon also has a history of MPB control. Keen exemplified the war philosophy taken when attempting to control bark beetles in Crater Lake National Park. He described progress in 1930 as:

> ". . . the tide of the control battle has ebbed and flowed. The control forces have given the enemy repeated setbacks, but until recently the beetles on the southern front have had their forces strengthened by reinforcements from the north. The northern reserves are now depleted, and the remnants of the beetle army are widely dispersed and rendered ineffective with only a few concentrated groups operating in territory outside the former battlefields. The ultimate victory is now in sight" (Wickman 1987).

The MPB was attacking lodgepole pine trees in and around Crater Lake National Park. In 1925 the urgency facilitated an appropriation from Congress that allowed for direct control of MPBs. The Bureau of Entomology in Ashland, Oregon, responded to the Park Service while John Patterson of the Bureau took charge of the Park MPB control project. The beetles were moving into the Park from the north and felling, peeling, and burning was the control method of choice. The treatments applied in 1925 were called a success and more funds were required to finish the work the next year. In general, each year the norm was acquiring the funding, getting to the Park because of snow, finding attacked trees, and not treating all of the attacked trees (fig. 39). Thousands of trees were treated in and adjacent to the Park, and even though the reports each year were very optimistic, the MPB continued to kill lodgepole pine trees.

Figure 39—Crawler tractors and sleds were used for moving men and equipment within Crater Lake National Park in 1929 to directly control MPBs (photo: 9845 by J. E. Patterson, Western Forest and Insect Work Conference).

In July 1929, Keen assumed leadership of the Bureau of Entomology Crater Lake project because of his major experience in the field of bark beetle control. Lessons that he learned at Crater Lake added to his interest in developing ways to prevent insect outbreaks rather than combat them directly. Keen developed three strategies for use in the Park: do no control work, control MPBs in as much of the Park as possible, and control MPBs only along roads and within special areas. Keen recommended the last alternative of protecting valuable areas as being the most feasible (Wickman 1987).

In 1929, the struggles between pessimism and optimism of trying to control MPBs in Crater Lake National Park escalated. In his thorough reports, Keen tended to be optimistic that the Bureau control work was making progress in controlling the MPB. For example, Keen finished his 1930 report with the statement, "The completion of this work should leave the lodgepole stands in very good shape except for an endemic infestation which should be watched for a few years and controlled if it develops active characteristics." In contrast, Solinsky, who led the Crater Lake Park's efforts to control the MPB, argued that from 1929 through 1931 the Park spent over $33,000 and cut 48,238 trees with minimal effect on the MPB populations. He went on to say "unless a complete cleanup of the control units was done the battle with the bark beetles would not be won" and if this approach was not followed he recommended stopping the control efforts. Also, Park personnel discovered thousands of attacked trees that the Bureau control project had missed, intensifying the pressure on Keen from Craighead, Chief of Forest Insect Investigations in Washington, DC, to show progress. This pressure is exemplified by an introduction of a letter Craighead sent to Keen: "We have failed so miserably on this project that it has reacted very unfavorably on our work in the region." Even with this pessimism, control work continued and the MPBs continued to kill trees in and around the Park (Wickman 1987).

Whether there was a lack of preferred trees for MPBs to infest or possibly the realization that the control efforts to protect the mature and old lodgepole pine were futile, fewer and fewer trees were being treated in 1932 and 1933. The control efforts may have delayed the killing of large old lodgepole pine trees in high use recreation areas, but most of them died during the eight years of MPB control in the Park or in ensuing years. Killing MPBs by cutting and heating trees by the sun or by piling and burning them perhaps slowed the progress of the epidemic, but the outcome was inevitable. When MPB populations are epidemic over large areas of susceptible lodgepole pine trees and the weather remains favorable for infestation, there really is no way to stop it until almost all the susceptible trees are either killed or removed by harvesting (Wickman 1987).

The Civilian Conservation Corp and Park personnel were the only ones mentioned in 1933 as being involved with MPB control work, indicating that Keen and the Bureau were no longer actively involved (Wickman 1987). In reviewing Keen's work with direct control efforts of WPBs in California in the 1920s that were far from positive, it is hard to understand his optimistic reports on the MPB control work in the Park. However, this experience added to his earlier work would make his perception that the direct control of bark beetles was ineffective. It would be 30 to 40 years before many forest managers recognized the futility of trying to control MPB in dense, over-mature pine stands.

Evenden et al. (1943) suggested the efficacy of directly controlling bark beetles was dependent on bark beetle population size and the amount of the population that was eliminated or reduced. If an insect outbreak were building at a ratio of 1:3, then for each tree treated, 3 trees would be saved from attack the following season. However, if one attacked tree was missed 3 trees would be subsequently destroyed. After a peel and burn WPB control was conducted in 1922 through 1923 in northern California and Southern Oregon, Keen completely inventoried 29 sections (18,560 acres) for past and current WPB attacked trees. He found that if 5 attacked trees were missed in a section, up to 36 trees could be found attacked the next year and if 30 trees were missed then up to 44 attacked trees could be found the next year (fig. 40). As such, whether trying to control or prevent bark beetle infestations, the locating and killing of broods was an insurmountable task. Missed trees combined with bark beetles flying in from outside the treated area further exacerbated the problem. As a consequence of this and the previous work discussed by Keen, the futility of trying to directly control bark beetles was well established by the 1920s but such efforts continued for decades.

Even though the evidence was to the contrary beginning with Hopkins in 1909, there has been continued reasoning for directly controlling bark beetles. For example, Smith (1990)

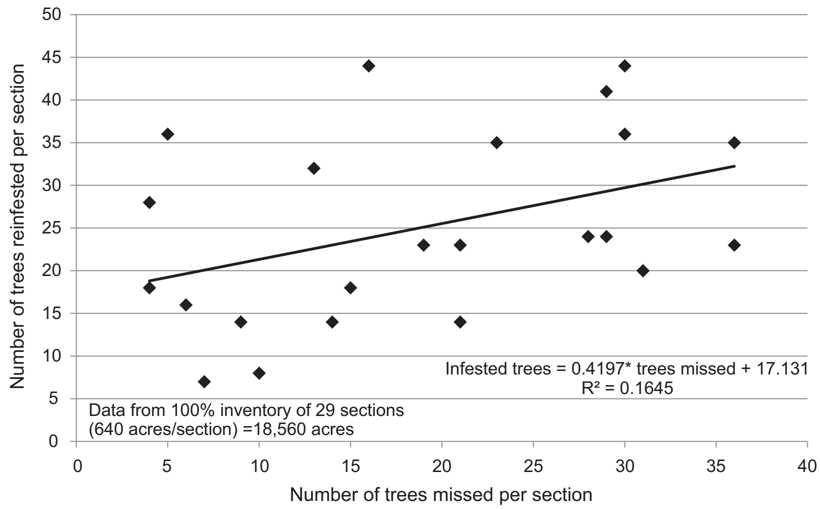

Figure 40—In 1922, Keen inventoried 18,560 acres of ponderosa pine in northern California and southern Oregon and showed that if WPB beetle infested ponderosa pine trees were missed, the next year more trees would be infested (Miller and Keen 1960).

suggested that decades of control programs have satisfactorily shown that direct control of WPBs is feasible, effective, and economical. However, he qualified this assertion by saying that the results of direct control are still variable, uncertain, usually temporary, and no less so now than 40 to 50 years ago. Similarly, Roettgering et al. (1976) and Swain (1976) argued strongly that the insecticide lindane was an effective method of controlling bark beetle populations and that its registration for such use should remain. In contrast Browne et al. (1976) contended that control of bark beetle populations with lindane has never been demonstrated adequately and its registration should be discontinued. Klein (1978), summarizing the direct control of MPBs in lodgepole pine, suggested that at the very best it was no more than a delaying action. Once control was terminated, the infestation will run its course and tree mortality will be essentially the same as that in uncontrolled areas (Amman and Baker 1972). Within the Black Hills, Harris (2013) reported that cutting and chunking was partially related to the lower ponderosa pine mortality in Custer State Park in western South Dakota, but again the treatment had little effect on overall MPB dynamics in the Black Hills.

We've tried for over 100 years to directly control bark beetles throughout the Western United States, and Craighead's conclusions circa 1920 ring as true today as they did then:

> "The direct control of bark beetles at the peak of an infestation saves no timber. The control work of one season may have no effect on beetle activity the next season. Because the results are temporary and inconsistent, it is imperative that more consistent, effective, permanent, and cheaper methods of forest insect control be secured" (Miller and Keen 1960).

Indirect Bark Beetle Control

Direct control of bark beetles for the most part entailed finding an attacked tree usually by detecting pitch tubes on tree boles, boring dust at tree bases, or fading foliage, and then killing the brood of adults, larvae, or pupae under the bark. Cutting, chunking, peeling, burning, spraying with oils and insecticides, and solar heating were used to kill the broods. Heat, cold, desiccation, and poison were the modes of death that these methods inflicted upon the bark beetle. Direct control proved to be ineffective in controlling bark beetles for multiple reasons but it also was not economically viable. Treating individual trees was costly and the control effects were temporary at best (Craighead et al. 1931). As these methods were being used for decades, several foresters and entomologists and, in particular Keen, suggested and tested ways of modifying the forest conditions and/or identifying tree characteristics that could be used to reduce bark beetle losses. Forest density and the many tree and environmental characteristics it influences became a focus of indirect control as did tree characteristics such as diameter, phloem thickness and temperature, and tree vigor (Miller and Keen 1960; Schmid et al. 1993). Also, depending on how they were applied, the use of semiochemicals (e.g., pheromones) could be either a direct or indirect method of bark beetle control (Progar et al. 2014).

Semiochemicals

Chemical cues of bark beetles and of the hosts they attack are major drivers of bark beetle behavior. As such, these chemicals have been used in direct and indirect bark beetle control methods for decades. Progar et al. (2014) provide an outstanding synthesis of semiochemical (i.e., chemical substance or mixture that carries a message for purpose of communication) based tools and tactics to protect trees from mortality attributed to MPBs of which we can only highlight.

Upon successfully boring into a suitable host, the pioneering female beetle releases a pheromone that signals other beetles to "mass attack" the tree to ensure the beetles can overcome the tree defenses and successfully colonize the tree and produce offspring. The main aggregation pheromones the beetles produce are *trans*-verbenol and *cis*-verbenol that attract more females and males to the tree. As the number of males increase, both males and females release antiaggregation pheromones such as *exo*-brevicomin, frontalin, and verbenone which causes the tree to lose attractiveness, avoiding bark beetle overcrowding (Amman and Cole 1983; Progar et al. 2014). These chemicals have been used to manipulate bark beetle behavior.

Some of the earliest trials for killing bark beetles with trap trees that relied on volatiles produced by stressed or felled trees proved to be ineffective (Hopkins 1909). However, by synthesizing aggregation pheromones (i.e., *trans*-verbenol) and placing them on a sticky surface or some other form of a trap, or by adding an insecticide to the trap, bark beetles could be attracted and subsequently die (Progar et al. 2014). Or a tree could be treated with an attractant and when fully attacked, much like Hopkins (1909) suggested, it would be removed or destroyed. Because the attraction caused by pheromones is rather short, attracting and controlling beetles over large areas with this method is problematic (Progar et al. 2014).

Antiaggregation chemicals have been used to dissuade bark beetles from attacking trees. Verbenone and other antiaggregation compounds can be broadcast in a stand or individual trees can be treated to reduce their susceptibility to bark beetle infestation (Amman and Cole 1983; Progar et al. 2014; Rudinsky et al. 1974). Pouch formulations can be attached to trees to protect individual trees and if pouches are distributed throughout a stand, bark beetle protection may be obtained over larger areas (fig. 41). Within the Black Hills, verbenone was used to protect individual limber pines in Custer State Park with good success (Harris 2013).

Flakes and pellets containing verbenone have been developed for application with helicopters and modified fertilizer spreaders. In the Pacific Northwest, applying the antiaggregative pheromone (MCH) has been very successful in protecting both windblown and standing Douglas-fir (*Pseudotsuga menziesii*) trees from bark beetles (McGregor et al. 1984; Ross et al. 2006). However, complexity of the host selection process, stand composition and structure, levels of inhibition, bark beetle population size, and several other barriers occur that confound and impact the effectiveness of using such techniques (Progar et al. 2014).

Figure 41—Verbenone (antiaggregation pheromone) pouches have been shown to protect trees from attack by MPBs. However, their use has been limited to protecting high value trees and is not recommended for treating large areas (photo: Rob Progar).

Tree Characteristics

Instead of killing broods or using chemicals to discourage bark beetles from attacking a tree, Keen pioneered the concept of removing susceptible trees from a stand to make the stand more resilient to bark beetle attack. Trees injured by lightning, fires, top-killing insects, girdling, or mechanical bark injuries are frequently attacked by bark beetles (Evenden et al. 1943). Keen (1928) postulated that very few lightning-struck trees escape death if bark beetles are present in any numbers and unless lightning-struck trees were completely shattered, they rarely die unless attacked by insects. Also, the Douglas fir beetle and pine engraver thrive in downed trees, which are the major vector for these beetles to attack living trees (Furniss and Carolin 1977; Furniss et al. 1981). As such, the removal of damaged or otherwise inferior trees was a prudent stand treatment for decreasing bark beetle risk (Miller and Keen 1960).

For selecting such trees, Keen used observations and studies of what trees were preferred by bark beetles (Keen and Salman 1942). Bark beetles use various cues in attacking trees, which vary considerably depending on bark beetle populations, tree species, stand conditions, weather, and tree condition (Amman and Cole 1983; Blackman 1931; Person 1931). Tree age was often associated with risk to bark beetle attack, but just because a tree was old did not necessarily make it a high bark beetle risk, as the character of its crown and its position in the stand were much more important considerations (Miller and Keen 1960). Large, injured, diseased, slow growing trees and trees with low vigor have been identified as being preferred by bark beetles (Beal 1943; Chojnacky et al. 2000; Miller and Keen 1960; Progar et al. 2014). The MPB usually selects the largest lodgepole pine trees in a stand to infest, at least during the few years preceding and during a major epidemic (Amman and Cole 1983). When the WPB was presented with ponderosa pine trees ranging from 10 to 54 inches DBH, they preferred to attack trees in the 20 to 32 inch DBH range (Miller and Keen 1960). Particularly with lodgepole pine, a MPB selecting a tree with a large DBH would likely ensure a thick phloem, which also is an important host selection criterion (Amman and Cole 1983). Tree growth rates are also considered a determinant of bark beetle attacks (Blackman 1931; Person 1928). However, many slow growing trees have survived years without being attacked but those slow growing trees as a result of drought were often attacked (Beal 1943). Of the tree attributes associated with bark beetle susceptibility, tree crown condition evolved as being the tree characteristic most related to a ponderosa pine tree's susceptibility to bark beetle attack.

In the 1930s, radial growth of trees was the standard for estimating tree vigor and its response to the environment. However, the root, shoot, and leaf are major locations of growth within trees. Miller and Keen (1960) indicated that up until the 1940s most tree growth research concentrated on radial and shoot growth because these two attributes made the largest contribution to producing forest products. Based on different soil treatments, Miller and Keen concluded that no single growth metric was fully adequate in determining tree vigor. The term "vigor" describes a tree's physiological ability to grow and its relative resilience to stressors such as insects, diseases, weather, and climate (Kaufmann 1996; Thomson 1940; Waring 1987). The best visible expressions of a tree's physiological condition are crown form; relative size of crown to tree height (i.e., crown ratio); needle retention; foliage color, and its abundance in terms of weight and length; crown density, and the color; and thickness and texture of the bark (Dunning 1922, 1928; Hornibrook 1939; Keen 1943; Taylor 1937).

In the early 1900s, entomologists and foresters working in California and Oregon were noting that ponderosa pine stands containing large numbers of large, old, and slow growing trees had more bark beetle attacks than stands dominated by fast growing trees. WPB infestations were making periodic thinnings by attacking and killing susceptible suppressed, intermediate, and codominant trees. Thinnings made openings for regeneration and stimulated the growth of young trees. The result was an uneven-aged forest composed of even-aged groups of trees and the WPBs were determining the natural development of ponderosa pine stands. With these clues, foresters began developing silvicultural systems for ponderosa pine that included the natural habits of the tree and the role the WPB played in forest ecology (Miller and Keen 1960).

To facilitate the development of these selection systems, Dunning (1928) developed a tree classification for use in uneven-aged ponderosa pine forests of the Sierra Nevada Mountains of California (fig. 42). He defined seven tree classes based on age, tree position

Figure 42—Dunning's tree vigor classes were used in selection stands and suitable for all-aged forests. Classes 1, 2, and 6 represent young or thrifty mature trees; classes 3 and 4 mature trees; and classes 5 and 7 represent mature or over-mature trees. Formation of top, crown width and length, and position of the crown in the canopy are other determining characteristics (illustration: Dunning 1928).

in the canopy, and crown form. Also, trees having Dunning's poorest vigor classification had the highest rates of mortality caused by bark beetles so he was able to relate his classification to bark beetle risk (Miller and Keen 1960). Hornibrook (1939), for use in the Black Hills, and Keen (1943), for use in California and Oregon, refined Dunning's classifications for selecting trees to remove to increase forest resistance to bark beetles (fig. 43). Keen's and Dunning's classifications were used so extensively in selection (uneven-aged) silvicultural systems within Oregon and California that Meyer (1934) and Roe (1952) produced yield tables that could be applied to these heterogeneous forests.

Although widely used for developing silvicultural systems for virgin stands of ponderosa pine and providing some long-term bark beetle resilience, Hornibrook and Keen's classifications did not adequately describe the immediate risk (≈1 year) of a tree being attacked by bark beetles (Keen and Salman 1942). Keen (1936) classified 27,465 WPB killed trees in southern Oregon and northern California with his crown vigor classes. He found that 72 percent of the volume lost to bark beetles occurred in classes 3B, 3C, 4B, and 4C, which were also very valuable as lumber (fig. 43). If these trees were removed due to their high risk to bark beetles, considerable value could be lost. This demonstrated the need for a bark beetle risk rating for individual trees.

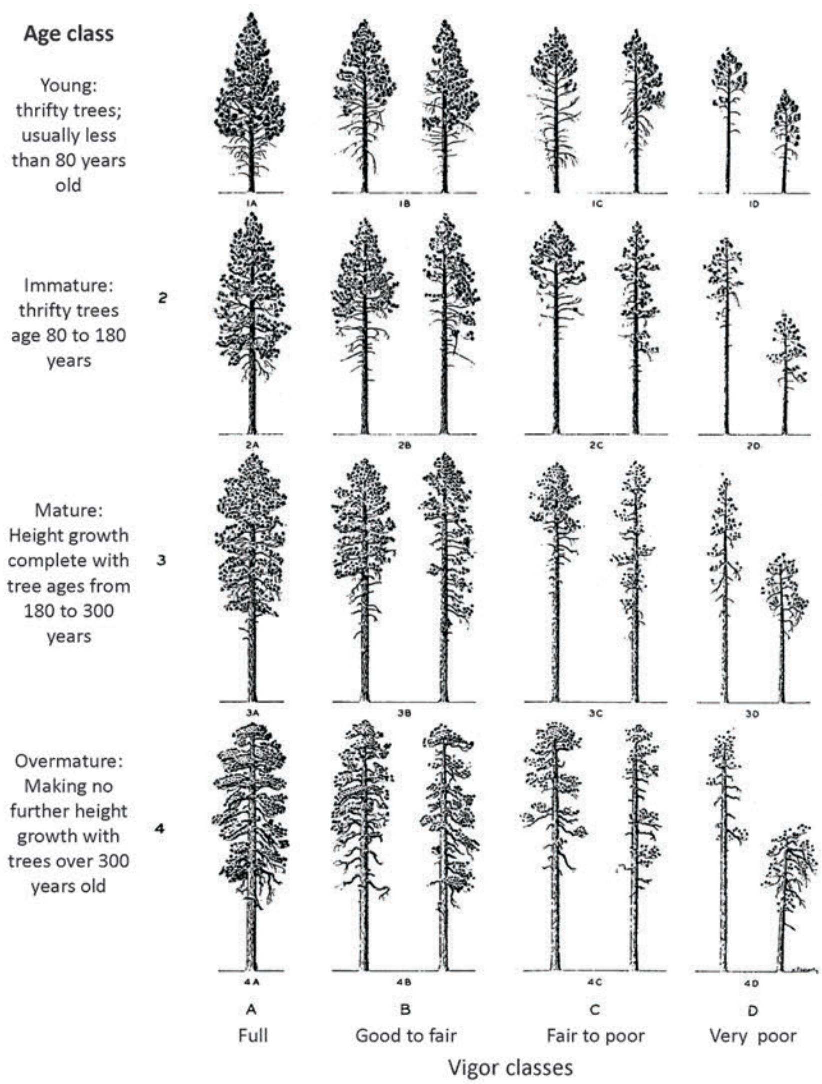

Figure 43—Keen's (1943) ponderosa pine vigor classes.

In response, Salman and Bongberg (1942) felled and described 973 WPB attacked trees and 2,026 green trees on the Lassen and Modoc National Forests in California. From this work they described classes of trees that were low, medium, high, and very high risk of being attacked by bark beetles. As a result, a visual assessment of risk to bark beetle infestations for individual ponderosa pine trees could be used to select trees for removal to increase stand and forest resilience to bark beetles (fig. 44). Throughout the Western United States, depending on the character of the forest and in particular those that had a large component of old and mature ponderosa pine trees, choosing trees for removal relied heavily on these risk classes. Moreover, the crown vigor classes of Keen and Hornibrook were used throughout the West in young and mid-aged forests for executing a variety of even- and uneven-aged silvicultural systems aimed at reducing bark beetle losses or to increase the general fitness of a forest stand to develop and produce commercial products.

a

b

Figure 44—Salman and Bongberg (1942) provided drawings (a) of ponderosa pine trees and their risk of being attacked by bark beetles. Whiteside (1951) provided color pictures (b) of the different classes of ponderosa pine trees at risk of being attacked by bark beetles.

Under epidemic conditions, bark beetles attack groups of trees regardless of tree position, crown class, size, age, or vigor. However, in each group there is usually a tree to which the beetles are first attracted and on which they concentrate during the first phase of the attack. This initial “key” or “ focus” tree as a rule exhibits one or several of the symptoms of susceptibility such as suppressed growth, deteriorated crown, or some special injury to the trunk, crown, or roots (i.e., high and very high risk trees) (Eckberg et al. 1994; Miller and Keen 1960) (fig. 44). Once the beetles have occupied the bark area of “key trees,” more beetles coming to the vicinity attack adjacent trees. These attacks are usually unrelated to tree condition, until the beetle population coming to that particular center of attraction has been absorbed.

Stand Characteristics

As these risk and vigor systems were used in many pine forests in the Western United States, bark beetles, and in particular the MPB, continued to be endemic to epidemic causing large losses of trees throughout the area (Amman et al. 1988b; Bartos and Amman 1989; Cole 1978; Graham 1980; Wellner 1952). Again through observation of bark beetle attacks throughout the West, the thought was emerging that stand density not only affected tree vigor and growth but it also affected the impact of bark beetles as well as stand resistance (Eaton 1941, 1959; Keen 1950; Keen and Salman 1942). This increased resistance to bark beetle attack was attributed for the most part to increased tree vigor and the removal of receptive trees based on crown vigor or by bark beetle risk (Miller and Keen 1960; Whiteside 1951). Tree density, expressed as basal area per acre of stands containing trees greater than 5 inches DBH, became the metric for describing a MPB susceptible stand.

Sartwell and Stevens (1975) described susceptible ponderosa pine stands to MPBs as those of pure or nearly pure ponderosa pine, even-aged, 50 to 100 years of age, having 8- to 12-inch DBHs, and a tree density in excess of 150 feet^2 of basal area per acre. Schmid (1987), using Berryman’s (1978) model based on phloem thickness, indicated that lodgepole pine stands with over 100 feet^2 of basal area per acre were highly susceptible to attack by MPBs and those with over 120 feet^2 of basal area per acre were extremely susceptible to MPB attack. Using these thresholds, Mata et al. (2003) evaluated different thinning densities ranging from 40 to 120 feet^2 of basal area per acre in lodgepole pine stands located in northern Colorado and southern Wyoming. They indicated that thinning lodgepole pine stands to a residual of 80 feet^2 of basal area per acre offered considerable options and protection from MPB attack and those thinned to 40 feet^2 of basal area per acre might be resistant to MPBs but were very prone to wind-throw. In Montana, Bollenbacher and Gibson (1986) recommended thinning lodgepole pine stands to a residual of 80 to 100 feet^2 of basal area per acre to increase their resistance to MPBs.

McGregor et al. (1987) showed that when lodgepole pine stands in western Montana were thinned to 80, 100, and 120 feet^2 of basal area per acre, significantly fewer trees were killed by bark beetles over 5 years compared to untreated stands with 109 to 246 feet^2 of basal area per acre. In contrast, Amman and Baker (1972) had very mixed results with thinning lodgepole pine stands to reduce MPB mortality in Idaho, as 25 to 67 percent of the trees were killed by MPBs in stands with 44 to 101 feet^2 of basal area per acre. They suggested, as did Roe and Amman (1970) that in lodgepole pine forests diversity in tree ages, DBH, and density across landscapes would reduce MPB impacts. Being less precise, Cahill (1978) suggested that removing 50 percent of the basal area in lodgepole pine stands was a prudent

MPB prevention strategy. Amman and Logan (1988) postulated that changes in microclimate when thinning lodgepole pine stands were more important than increasing tree vigor in reducing tree losses to MPBs (Bartos and Amman 1989).

By observing tree and stand characteristics of those attacked by MPBs and comparing them to those that were not attacked, researchers developed a better understanding of MPB dynamics. Amman and Schmid did experimental cuttings in both lodgepole and ponderosa pine forests to validate the findings of Sartwell and Stevens (1975) and those modeled by Berryman (1978) (Amman et al. 1988a,b; Schmid 1987). The Black Hills was to become the center of studying the effects that stand density have on MPB dynamics in ponderosa pine forests.

Indirect Methods of Controlling Bark Beetles in the Black Hills

Indirect control of bark beetles in the Black Hills was always considered a control tactic, but as in the rest of the Western United States, the emphasis tended to be on direct control of MPBs (Blackman 1931; Freeman 2015; Hopkins 1902; Thompson 1975). The burning, spraying, cutting, and harvesting of individual trees continued until the early 1970s when such efforts were minimal and only used within special areas or unique situations (Thompson 1975). During this era, in the Black Hills, as in the rest of the West, the need for modifying forest structure to promote tree growth and vigor was recognized. Within the Hills, as exemplified by the 250,000 acres of young forest that were cleaned (precommercial thinned) by members of the Civilian Conservation Corp in the 1930s, the need for forest tending[5] was recognized (Freeman 2015; Sanders 2004; Thompson 1975). In addition, a variety of selection silvicultural systems was used in the early 1900s, leaving a variety of forest structures that often could not be distinguished in appearance or effect of two-step shelterwoods (fig. 45). In both systems, MPB attacked trees and those with defect or having poor vigor were to be removed (Harmon 1955; Newport 1956; Thompson 1975). This was the beginning of indirectly controlling MPBs in the Black Hills by selecting individual trees to leave, remove, or protect based on crown vigor, stand characteristics, or applying pheromones.

Semiochemicals in the Black Hills

Semiochemicals are chemical substances or mixtures that carry a message for the purpose of communication. As described earlier, bark beetles emit pheromones to both attract and dissuade bark beetles from attacking trees (Progar et al. 2014). Verbenone, an antiaggregation pheromone, was tried in 1989 within the Black Hills as a method of protecting ponderosa pine trees from being attacked by MPBs. Verbenone bubble capsules were stapled to trees in MPB attacked stands of ponderosa pine at densities of 10, 20, 40, and 68 capsules per acre. A failure of the capsules for protecting trees was attributed to the above-average air temperatures occurring after the capsules were placed; and, possibly, the verbenone

[5] Any forest treatment designed to enhance growth, quality, vigor, and composition of the stand after regeneration or establishment and prior to final harvest (e.g., cleaning, weeding, precommercial thinning, thinning).

Figure 45—A variety of cuttings were used in mature ponderosa pine forests of the Black Hills in the early to mid-1900s leaving a variety of structures and frequently relying on vigor classes and bark beetle risk rating for selecting trees to remove or leave.

formulation was incorrect (Bentz et al. 1989; Lister et al. 1990). Within the Black Hills in 2000, Negrón et al. (2006) released verbenone from plastic capsules (containing 0.8 g verbenone) at a density of 25 and 64 per acre and in 2002 they released verbenone by using plastic pouches containing 5.0 g of verbenone at a density of 30 and 50 pouches per acre. In both releases and in untreated areas they placed *trans*-verbenol, exo-brevicomin, and myrcene bark beetle attractants in the center of the areas to ensure the treated and control trees received MPB pressure as insect populations were endemic. For both years (2000 and 2002) and verbenone release methods, they found no difference in the number of trees attacked, number killed, or where the bark beetles were pitched-out among the treated trees and untreated trees (Negrón et al. 2006). As a result Bentz et al. (1989), Lister et al. (1990), and Negrón et al. (2006) recommended that verbenone treatments for protecting ponderosa pine trees not be used until further testing produced effective methods and/or chemical formulations that reduce MPB-caused tree mortality.

Even though certain formulations of verbenone were proved to be ineffective in protecting ponderosa pine stands under endemic levels of bark beetles, it was used in an attempt to save rare limber pines growing in Custer State Park. Relic stands of limber pine located in the Cathedral Spires area of the Park are highly valued. There was concern that the expanding MPB population from the adjacent Black Elk Wilderness Area, where nearly all mature ponderosa pine trees were killed, might spread into these stands and eliminate the species in the Hills. Infections of white pine blister rust (*Cronartium ribicola*) and competition from white spruce trees were stressing the limber pines so that even unsuccessful MPB attacks would likely result in significant limber pine mortality. In 2012, verbenone was used to protect these relic stands of limber pines and was very effective as less than 1 percent of the trees were lost despite a high infestation of MPBs in the area (Harris 2013).

Using Tree Characteristics in the Black Hills to Control Mountain Pine Beetles

A variety of selection systems was used to manage mature ponderosa pine forests in the Black Hills beginning in the early 1900s and continued in various forms into the 1960s. After the 1960s and because of large expanses of young and mid-aged forests throughout the Hills, a variety of even-aged silvicultural systems dominated by two-step shelterwoods were used (Boldt and Van Deusen 1974; Graham 2015b, personal communication; Hornibrook 1939; Newport 1956). Both the selection and even-aged systems relied on crown vigor classes and bark beetle risk ratings for selecting trees to leave and remove to improve the forest's resilience to MPBs.

Keen (1936) described the relative susceptibility of ponderosa pine trees to bark beetle attack based on age and tree and crown characteristics. His vigor classes could be used for selecting trees to leave or remove when implementing both intermediate and regeneration silvicultural methods. Hornibrook (1939) modified Keen's tree classes for use within the Black Hills for managing ponderosa pine (fig. 46). However, he was unsure how bark beetle infestations would be impacted by using his classification and suggested that direct control of MPBs was preferred. Nevertheless, tree vigor and recently needle retention have been used in the Black Hills to select trees for retaining in both uneven- and even-aged silvicultural systems to increase or maintain forest resilience to MPBs (Boldt and Van Deusen 1974; Harmon 1955; Jain et al. 2014; Jain 2015, personal communication; Shepperd and Battaglia 2002).

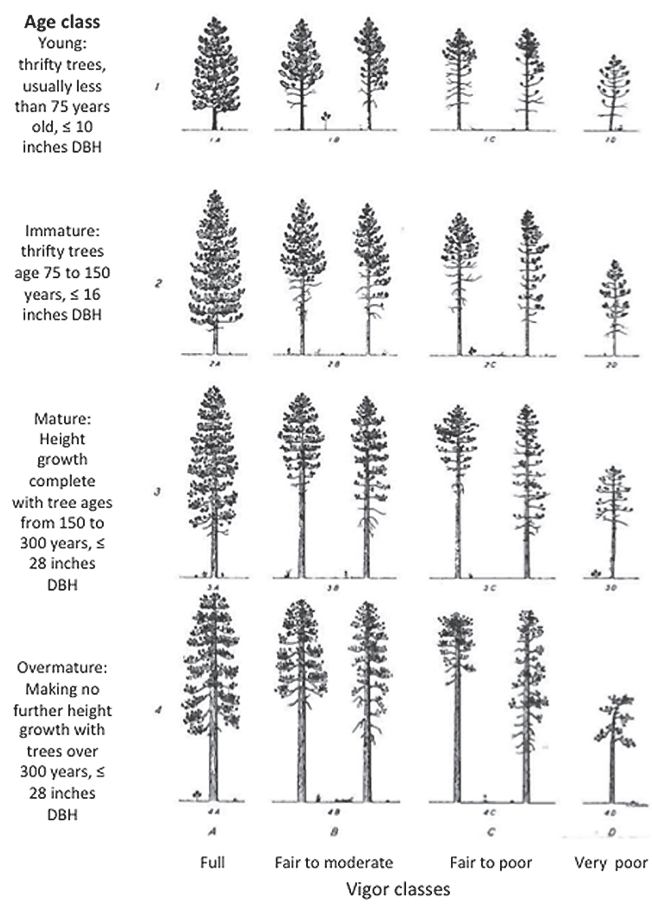

Figure 46—Hornibrook (1939) modified Keen's (1936, 1943) vigor classes for use in the Black Hills refining the age classes, tree sizes, and crown architecture (see fig. 43).

By the mid-1970s, the Black Hills had only small remnants of old ponderosa pine forest structures as most of the operable ground had received at least one commercial harvest and many areas had received multiple harvests (Alexander and Edminster 1981; Boldt and Van Deusen 1974; Shepperd and Battaglia 2002). In the 1940s, Keen's individual tree risk ratings were used to select trees in the Black Hills for removal in mature stands but on a trip to the Black Hills in the 1950s Keen suggested that his risk ratings would not work in the mid-aged (80- to 150 year-old) forests that dominated the Black Hills (Furniss 2007). Similar to the failure of trying to directly control MPBs in the Black Hills, the use of tree vigor and risk as criteria for leaving or removing susceptible trees also failed to stem the periodic epidemics of MPBs (fig. 31) (Thompson 1975).

As recognized in the 1930s, stand tending was desirable to shape how the forests in the Hills would develop, as exemplified by the extensive stand cleaning (e.g., precommercial thinning) accomplished by the Civilian Conservation Corp. By 1962, it was suggested that these same areas were in need of tending to increase their resilience to MPB attacks (Thompson 1975). Another development in forest management in the Black Hills was emerging pulp wood markets that provided value to the 6- to 10-inch DBH trees that needed to be removed in thinnings (Harmon 1955; Thompson 1975). As a result, stand density control in the Black Hills, as a measure to influence bark beetle dynamics, came to the forefront.

Using Stand Characteristics to Control Mountain Pine Beetles in the Black Hills

Eaton (1941), Graham (1959), Keen (1958), and Sartwell and Stevens (1975) were among the pioneers that indicated stand density, and in particular stand density expressed by basal area per acre, was related to the susceptibility of a stand to an attack by bark beetles. Within the Black Hills, basal area was considered an important metric in 1970 for evaluating MPB risk, and in 1972, 70 feet^2 per acre was suggested as a residual thinning target for minimizing MPB risk (Thompson 1975). Stands in the Black Hills harvested for pulp wood in the 1960s left ≈100 feet^2 of basal per acre and rather uniformly spaced trees (Graham 2015c, personal communication) (fig. 37). Stevens et al. (1980), using observations of MPB-caused mortality, suggested stands with densities less than 80 feet^2 of basal area per acre were at a low risk for attack by bark beetles, those with densities between 80 and 150 feet^2 per acre were of moderate risk, and those with densities over 150 feet^2 of basal area per acre were at high risk for MPB infestation. With the near 100-year history of MPB-caused tree mortality and forest management occurring in the Black Hills, it was the ideal location for studying the impact that different stand densities had on MPB dynamics. Also, the environments created by different stand structures could be described and how these environments affected MPBs could be evaluated. In 1984, John Schmid and Stephen Mata set out to define the relationship between stand density and MPB-caused mortality in Colorado, Wyoming, and the Black Hills (Furniss 2007). This was the start of very fruitful research that added significantly to the knowledge and understanding of MPB dynamics for nearly three decades.

Silvicultural Treatments for Reducing Losses to Mountain Pine Beetles in the Black Hills

Schmid and Mata established several study areas for testing different stand density relationships with MPB attacks within the South Dakota portion of the Black Hills National Forest. The study was designed to provide a more definitive understanding of how stand density described by square feet of basal area per acre influenced MPB dynamics for refining or revising the differing MPB stand hazard ratings. The areas where they sought to establish plots were at least 10 acres in size and contained trees with mean diameters equaling or exceeding 8 inches and tree densities equaling or exceeding 120 feet^2 of basal area per acre (Schmid and Mata 1992).

Study Plots

Schmid and Mata had ponderosa pine plots thinned to different tree densities and paired them with unthinned plots throughout the northern and central portions of the South Dakota portion of the Black Hills National Forest (fig. 47). In 1985, the first plots they had thinned and established were located at Custer Crossing and Brownsville and in 1994, the last plots they had thinned and established were located near Custer Peak. Their locations ranged from north and east of Deadwood to north and west of Custer and west to the Wyoming border and south and east of Lead (fig. 47). Four plots near Jewel Cave were burned by a wildfire in 2000 and three plots near Sturgis were not thinned. At most locations three stand densities were created by thinning and an untreated plot was established. Most plots were 2.5 acres in size and trees were tagged and described on 1.2 acres in the center of the plot except for the

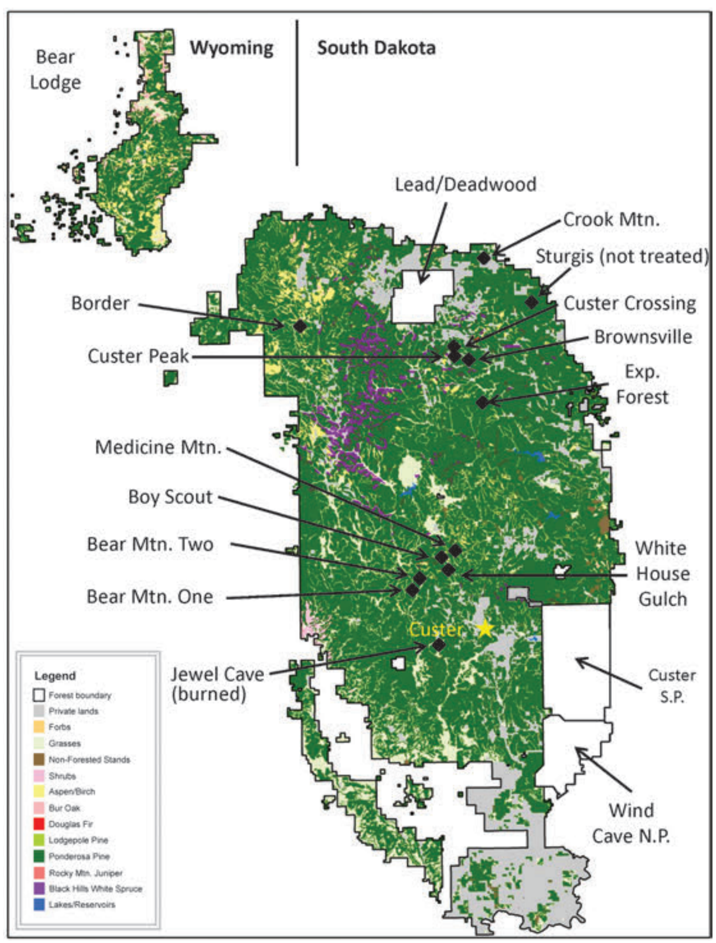

Figure 47—Beginning in 1985, Schmid and Mata established 46 study plots within the South Dakota Black Hills that contained different densities of ponderosa pine trees to evaluate the effect forest structure would have on MPB dynamics (Schmid and Mata 1992). However, 4 plots near Jewel Cave were lost to wildfire in 2000 and 3 plots near Sturgis were not treated leaving 39 MPB study plots.

Custer Crossing plot, which was 2.5 acres in size, and the White House Gulch plot, which was thinned to 80 feet^2 per acre of basal area per acre and had 1.07 acres of trees tagged and described. At installation, and when the plots were revisited, the diameters were measured and the status (e.g., alive or dead) of each tree and its condition (e.g., MPB activity-infested, strip attack, pitch out, other insect activity, other damage and cause, and occurrence of disease) were recorded. With these data, stand density index, volume per acre (board feet and cubic feet), tree density (trees and basal are per acre), and DBH (quadratic mean diameter—the diameter of the tree with the mean basal area) were computed for each one of the tree conditions by using the Forest Vegetation Simulator (FVS) (Dixon 2002). After thinning, the treated plots had densities ranging from 44 to 127 feet^2 of basal area per acre and DBHs ranging from 7.8 to 13.8 inches. In the unthinned plots the tree densities ranged from 108 to 199 feet^2 of basal area per acre and the DBHs ranged from 8.6 to 12.9 inches (figs. 48, 49).

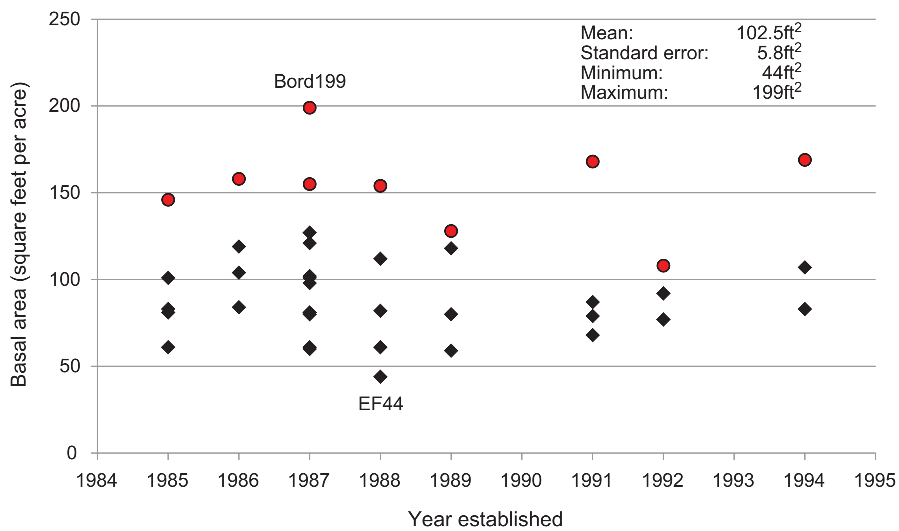

Figure 48—Stand density of the MPB plots, expressed as basal area per acre, when they were established. The diamonds are the plots that were thinned and the circles are the untreated plots.

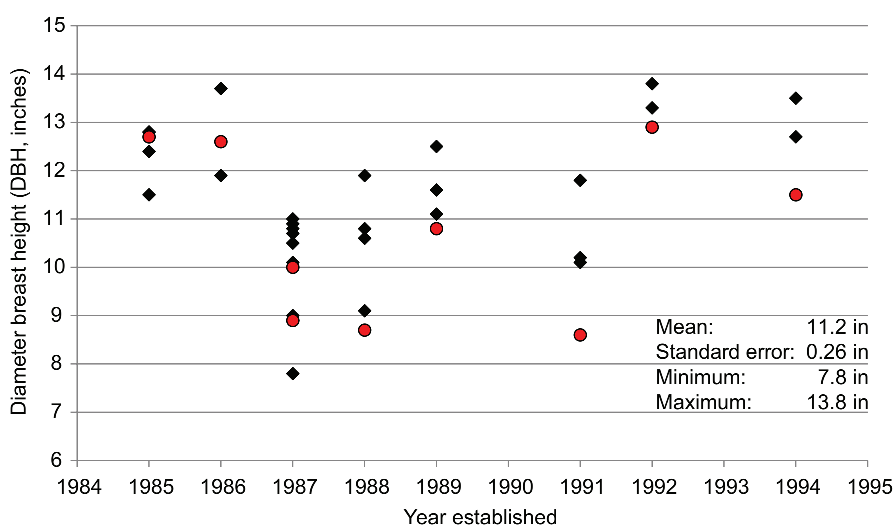

Figure 49—Diameter breast height (DBH, 4.5 feet from the forest floor; quadratic mean diameter; i.e., the diameter of the tree with the mean basal area) of the MPB plots when they were established. The diamonds are the plots that were thinned and the circles are the untreated plots.

Crook Mountain (CMt)

Near the northern border of the Black Hills National Forest are the Crook Mountain plots (figs. 47, 50). They are located off Highway 79, the Boulder Canyon Road accessed by the Louis Road, which is located approximately 5.25 miles from where Highway 79 exits Interstate 90 near Sturgis. There the Louis Road tracks north 0.4 miles where it intersects with the Warren Loop road tracking to the west. In roughly 0.3 miles the Warren Loop road intersects with the Florence Place Road on the right and the Crook Mountain plots are on the left in 0.14 miles (fig. 51).

- Coordinates: 44° 24' 10" N and 103° 37' 32" W
- Established and measured: 1986, 1996, 2004, 2006, 2010, 2012
- Elevation: 4,459 feet
- Habitat type: bur oak
- Stand age in 1986: 100 years
- Site index (100 year): 66
- 4 plots (table 1)

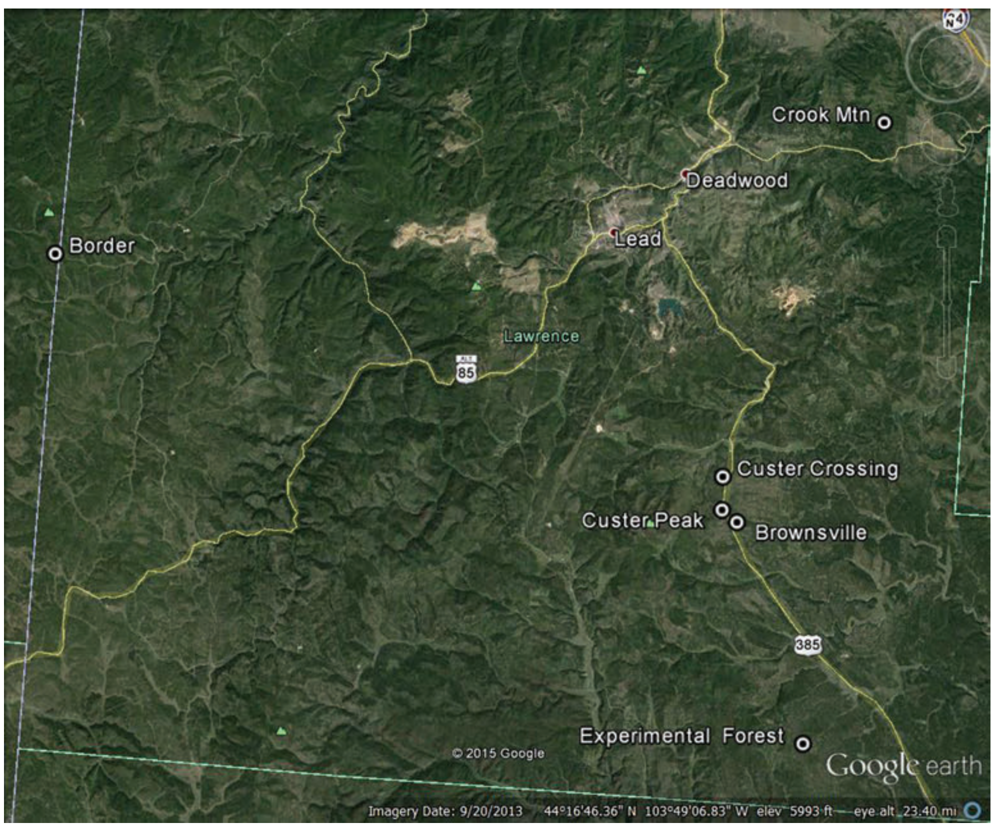

Figure 50—The most northern plots that Schmid and Mata established within the South Dakota portion of the Black Hills National Forest ranged from north and east of Deadwood to the Wyoming border and south to the Black Hills Experimental Forest west of Highway 385 (see fig. 47).

Figure 51—Crook Mountain plots are located north of the Boulder Canyon Highway (79) and adjacent to the Florence Place Road. The plots were thinned in 1986 leaving tree densities of 84, 104, and 119 feet^2 of basal area per acre and the untreated plot had 158 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Border (Bord)

The border plots are located just west of the Wyoming border adjacent to road 104 (fig. 47). They can be reached by road 222, the Roughlock Falls Road, which leaves the Spearfish Canyon Highway (Alt-14) some 5.25 miles north of Cheyenne Crossing and Highway 85. Road 222 intersects with the Tinton Road (134) approximately 5.25 miles from Alt-14. Turning left on 134 it intersects with the Wagon Canyon Road (105) in about 1,000 feet and the Border plots are located on the right in 3.0 miles on Road 104 (figs. 50, 52).

- Coordinates: 44°19’ 10” N and 104° 3’ 23” W
- Established and measured: 1987, 1997, 2004, 2006, 2010, 2012
- Elevation: 6,243 feet
- Habitat type: common juniper
- Stand age in 1987: 87 years
- Site index (100 year): 65
- 4 plots (table 1).

Table 1—Descriptors of the plots and the trees contained in them at the time they were established.

Name[a]	Year est	Age yrs	SI[b]	Trees /ac	DBH[c] in	Std[d] in	Num obs[e]	BA[f] ft^2	SDI[g]	Volume[h] ft^3	bd ft
Black Hills Experimental Forest—kinnikinnick[i]											
EF44	1988	95	61	71	10.6	1.99	304	44	79	916	3,173
EF61	1988	95	61	79	11.9	1.67	88	61	104	1,359	5,310
EF82	1988	95	61	128	10.8	1.91	98	82	145	1,711	6,046
EF112	1988	95	61	246	9.1	1.97	158	112	213	2,086	5,383
EF154	1988	95	61	375	8.7	1.91	463	154	299	2,775	7,026
Bear Mountain One—common juniper[i]											
BM161	1987	92	70	93	11.0	2.22	210	61	108	1,377	5,115
BM181	1987	92	70	146	10.1	1.52	115	81	148	1,671	5,374
BM1101	1987	92	70	170	10.5	1.54	180	101	183	2,161	7,268
BM1155	1987	92	70	284	10.0	1.75	351	155	284	3,204	9,964
Bear Mountain Two—common juniper[i]											
BM2102	1987	87	64	230	9.0	2.45	284	102	195	1,974	5,358
BM2121	1987	87	64	282	8.9	1.67	348	121	232	2,207	5,107
BM2127	1987	87	64	381	7.8	1.26	471	127	257	2,062	2,380
Border—common juniper[i]											
Bord60	1987	87	65	93	10.9	1.40	196	60	107	1,334	4,881
Bord80	1987	87	65	125	10.8	1.46	115	80	142	1,773	6,443
Bord98	1987	87	65	159	10.7	1.84	155	98	176	2,180	7,754
Bord199	1987	87	65	462	8.9	2.02	571	199	382	3,902	10,676
Boy Scout—kinnikinnick[i]											
Boy68	1991	120	73	123	10.1	3.33	142	68	124	1,461	5,067
Boy79	1991	120	73	139	10.2	2.42	152	79	143	1,621	5,415
Boy87	1991	120	73	115	11.8	2.99	172	87	150	2,031	8,070
Boy168	1991	120	73	417	8.6	2.97	515	168	326	3,219	9,292
Brownsville—common juniper[i]											
Brn61	1985	110	74	73	12.4	1.05	140	61	103	1,439	5,763
Brn81	1985	110	74	112	11.5	1.54	90	81	140	1,811	6,912
Brn101	1985	110	74	113	12.8	1.29	138	101	168	2,424	10,012
Brn146	1985	110	74	167	12.7	1.92	206	146	243	3,543	14,861
Custer Peak—common juniper[i]											
CP83	1994	112	64	83	13.6	1.40	151	83	136	2,391	10,943
CP107	1994	112	64	122	12.7	1.42	103	107	179	2,785	11,777
CP169	1994	112	64	234	11.5	1.61	289	169	293	4,388	17,977
Custer Crossing—common juniper[i]											
CC83	1985	99	61	92	12.8	1.51	231	83	137	1,985	8,160
Medicine Mountain—kinnikinnick[i]											
MMt77	1992	104	73	74	13.8	2.36	117	77	125	2,064	9,179
MMt92	1992	104	73	95	13.3	1.90	92	92	150	2,361	10,158
MMt108	1992	104	73	118	12.9	2.23	146	108	179	2,752	11,825
White House Gulch—kinnikinnick[i]											
WHG59	1989	89	73	69	12.5	1.73	171	59	98	1,423	5,828
WHG80	1989	89	73	119	11.1	1.42	85	80	141	1,771	6,589
WHG118	1989	89	73	160	11.6	1.11	147	118	203	2,670	10,319
WHG128	1989	89	73	202	10.8	1.33	249	128	228	2,766	10,028

(continued)

Table 1—(Continued)

Name[a]	Year est	Age yrs	SI[b]	Trees /ac	DBH[c] in	Std[d] in	Num obs[e]	BA[f] ft^2	SDI[g]	Volume[h] ft^3	Volume[h] bd ft
				Crook Mountain—bur oak[i]							
CMt84	1986	100	66	82	13.7	1.83	167	84	136	2,228	9,915
CMt104	1986	100	66	135	11.9	2.38	143	104	179	2,543	10,174
CMt119	1986	100	66	116	13.7	1.89	101	119	193	3,162	14,116
CMt158	1986	100	66	181	12.6	2.88	224	158	264	4,116	17,969

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and Cmt = Crook Mountain.

[b] SI = Site index base 100 years.

[c] DBH = Quadratic mean diameter (i.e., diameter of the tree with the mean basal area).

[d] Std = Standard deviation of the mean DBH.

[e] Num obs = number of trees on the plot.

[f] BA = Basal area (feet^2 per acre).

[g] SDI = Stand density index.

[h] Volume = Volume per acre in cubic feet (feet^3) and Scribner board feet (bd ft).

[i] Location of where the plots were located and the habitat type of the plot.

Figure 52—Border plots, located on the Wyoming border, are reached from the Spearfish Canyon Highway and the Roughlock Falls Road. The plots were thinned in 1987 leaving tree densities of 60, 80, and 98 feet^2 of basal area per acre and the untreated plot had 199 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Custer Crossing (CC)

The Custer Crossing plot is approximately 8.5 miles south on Highway 385 from the Lead/Deadwood junction (figs. 47, 50). The area where the plot was established had been lightly harvested in 1982 through 1983. The plot is located on the west side of Highway 385 across from the Rockland Road (539) junction (fig. 53). In contrast to the other plots, the Custer Crossing plot was established in a treated stand resulting in an initial tree density of 83 feet^2 of basal area per acre.

- Coordinates: 44° 15’ 50” N and 103° 41’ 53” W
- Established and measured: 1985, 1996, 2004, 2006, 2010, 2012
- Elevation: 5,737 feet
- Habitat type: common juniper
- Stand age in 1985: 99 years
- Site index (100 year): 61
- 1 plot (table 1)

Figure 53—The Custer Crossing plot is located 8.5 miles south on Highway 385 from the Lead/Deadwood junction. The plot was thinned in 1985 leaving a tree density of 83 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Custer Peak (CP)

The Custer Peak plots are located approximately 8.6 miles south on Highway 385 from the Lead/Deadwood junction (figs. 47, 50). They are adjacent to the highway and located on the north side of the Custer Peak Road (216) (fig. 54).

- Coordinates: 44° 15’ 5” N and 103° 41’ 50” W
- Established and measured: 1994, 2004, 2006, 2010, 2012
- Elevation: 5,770 feet
- Habitat type: common juniper
- Stand age in 1994: 112 years
- Site index (100 year): 64
- 3 plots (table 1)

Figure 54—The Custer Peak plots are located 8.5 miles south on Highway 385 from the Lead/Deadwood junction. The plots were thinned in 1994 leaving tree densities of 83 and 107 feet^2 of basal areas per acre and the untreated plot contained 169 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Brownsville (Brn)

Brownsville plots are located approximately 9.0 miles from the Lead/Deadwood junction on Highway 385 and about 0.5 miles south from the Custer Peak plots on the north side of the Halso Road (523.1), which tracks to the east (figs. 47, 50). The plots are about 0.2 miles from Highway 385 (fig. 55).

- Coordinates: 44° 14' 50" N and 103° 41' 20" W
- Established and measured: 1985, 1990, 1995, 2004, 2010, 2012
- Elevation: 5,711 feet
- Habitat type: common juniper
- Stand age in 1985: 110 years
- Site index (100 year): 74
- 4 plots (table 1)

Figure 55—The Brownsville plots are located 9.0 miles south on Highway 385 from the Lead/Deadwood junction. The plots were thinned in 1985 leaving tree densities of 61, 81, and, 101 feet^2 of basal area per acre and the untreated plot contained 146 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Black Hills Experimental Forest (EF)

Black Hills Experimental Forest plots are located approximately 14.0 miles from the Lead/Deadwood junction on Highway 385 to the Experimental Forest Road 616 (figs. 47, 50). From Highway 385 on road 616 for 2.25 miles is road 658 to the south. The plots are located 0.3 miles from this junction on both sides of road 658 (fig. 56).

- Coordinates: 44° 9' 57" N and 103° 38' 43" W
- Established and measured: 1988, 1994, 1998, 2004, 2008, 2010, 2012
- Elevation: 5,852 feet
- Habitat type: kinnikinnick
- Stand age in 1988: 95 years
- Site index (100 year): 61
- 5 plots (table 1)

Figure 56—Five plots were established on the Black Hills Experimental Forest. Four plots were thinned in 1988 leaving tree densities of 44, 61, 82, and 112 feet^2 of basal area per acre and an unthinned plot contained 154 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Medicine Mountain (MMt)

Medicine Mountain plots are located off the Reno Gulch Road that leaves Highway 16 to the west approximately 1 mile south of Hill City. The Medicine Mountain Road intersects the Reno Gulch Road in approximately 10 miles from Highway 16 (figs. 47, 57). About 300 feet north on the Medicine Mountain Road, Forest Road 297.3 K enters from the west. It parallels the Medicine Mountain Road in the valley bottom to the east as it tracks to the north and in approximately 2 miles road 297.3 F enters from the left. The Medicine Mountain plots are located near the junction of these two roads (fig. 58).

- Coordinates: 43° 55’ 0” N and 103° 42’ 27” W
- Established and measured: 1992, 2007, 2010, 2012
- Elevation: 6,217 feet
- Habitat type: kinnikinnick
- Stand age in 1992: 104 years
- Site index (100 year): 73
- 3 plots (table 1)

Figure 57—The most southern plots that Schmid and Mata established within the South Dakota portion of the Black Hills National Forest ranged from west of Hill City to southwest of Custer. These plots can be reached from Highway 16 between Hill City and Custer and from Highway 16 west of Custer. The Jewel Cave Plots burned in 2000 and provided no data (see fig. 47).

Figure 58—The Medicine Mountain plots are accessed by the Reno Gulch Road that leaves Highway 16 just south of Hill City and the Medicine Mountain Road. The plots were thinned in 1992 leaving tree densities of 77 and 92 feet^2 of basal area per acre and the untreated plot contained 108 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Boy Scout (Boy)

The Boy Scout plots are located just north of the Medicine Mountain Boy Scout Camp (figs. 47, 57). They can be reached by the Medicine Mountain Road (297) that tracks west from Highway 385 about 3.2 miles north from downtown Custer (intersection of Highways 385 and 16). In 7.25 miles after leaving Highway 385 the Medicine Mountain Road intersects on the west with Bobcat Road (299) and the plots are located on the south side of 299 in 2.6 miles (fig. 59).

- Coordinates: 43° 54’ 20” N and 103° 44’ 5” W
- Established and measured: 1991, 2000, 2004, 2010, 2012
- Elevation: 6,238 feet
- Habitat type: kinnikinnick
- Stand age in 1991: 120 years
- Site index (100 year): 73
- 4 plots (table 1)

Figure 59—The Boy Scout plots were established just north of the Medicine Mountain Boy Scout Camp. Three plots were thinned in 1991 leaving tree densities of 68, 79, and 87 feet^2 of basal area per acre and an unthinned plot contained 168 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

White House Gulch (WHG)

The White House Gulch plots are located south of the Medicine Mountain Boy Scout Camp on Bobcat Road (299) (figs. 47, 57). They can be reached by the Medicine Mountain Road (297) that tracks west from Highway 385 about 3.2 miles north from downtown Custer (intersection of Highways 385 and 16). In 7.25 miles after leaving Highway 385, the Medicine Mountain Road intersects with Bobcat Road (299) on the west and the plots are located on the south side of 299 in 0.6 miles (fig. 60).

- Coordinates: 43° 53’ 8” N and 103° 42’ 43” W
- Established and measured: 1989, 1995, 1999, 2004, 2007, 2010, 2012
- Elevation: 6,224 feet
- Habitat type: kinnikinnick
- Stand age in 1989: 89 years
- Site index (100 year): 73
- 4 plots (table 1)

Figure 60—The White House Gulch plots were established just south of the Medicine Mountain Boy Scout Camp. Three plots were thinned in 1989 leaving tree densities of 59, 80, and 118 feet^2 of basal area per acre and an unthinned plot contained 128 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Bear Mountain One (BM1)

The Bear Mountain One plots can be reached by the Medicine Mountain Road (297) that tracks west from Highway 385 about 3.2 miles north from downtown Custer (intersection of Highways 385 and 16) (figs. 47, 57). In 0.7 miles after leaving Highway 385 the Medicine Mountain Road intersects on the south with Limestone Road (284). In 3.0 miles 284 intersects with the Saginaw Road (285) on the right, which in 0.6 miles intersects with Elliot Road (292) on the left (west). After 3.7 miles Elliot road meets Forest Development Road (291) and tracking north (right) 291 connects to Bear Mountain Lookout Road 293 on the right in 1.2 miles. The Bear Mountain One plots are located on the ridgetop 2.0 miles north on road 293 on the west side of the road (fig. 61).

- Coordinates: 43° 51’ 58” N and 103° 45’ 35” W
- Established and measured: 1987, 1995, 2006, 2010, 2012
- Elevation: 6,871 feet
- Habitat type: common juniper
- Stand age in 1987: 92 years
- Site index (100 year): 70
- 4 plots (table 1)

Figure 61—The Bear Mountain One plots were established just south and west of the Medicine Mountain Boy Scout Camp in 1987. Three plots were thinned leaving tree densities of 61, 81, and 101 feet^2 of basal area per acre and an unthinned plot contained 155 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Bear Mountain Two (BM2)

The Bear Mountain Two plots can be reached by the Medicine Mountain Road (297) that tracks west from Highway 385 about 3.2 miles north from downtown Custer (intersection of Highways 385 and 16) (figs. 47, 57). In 0.7 miles after leaving Highway 385, the Medicine Mountain Road intersects on the south with Limestone Road (284). In 3.0 miles 284 intersects with the Saginaw Road (285) on the right, which in 0.6 miles intersects with Elliot Road (292) on the left (west). After 3.7 miles Elliot road meets Forest Development Road (291) and tracking north (right) 291 connects to Bear Mountain Lookout Road 293 on the right in 1.2 miles. The Bear Mountain Two plots are located on the ridgetop 1.5 miles north on road 293 on the west side of the road (fig. 62).

- Coordinates: 43° 51’ 10” N and 103° 46’ 7” W
- Established and measured: 1987, 1997, 2004, 2007, 2010, 2012
- Elevation: 6,781 feet
- Habitat type: common juniper
- Stand age in 1987: 87 years
- Site index (100 year): 64
- 3 plots (table 1)

Figure 62—The Bear Mountain Two plots were established south and west of the Medicine Mountain Boy Scout Camp in 1987. Three plots were thinned leaving tree densities of 102, 121, and 127 feet^2 of basal area per acre. Plot borders are approximations, limited by GPS accuracy and their placement on the photograph.

Summary of Black Hills Mountain Pine Beetle Plots

To summarize, from 1985 through 1994, Schmid and Mata established 46 MPB plots in the ponderosa pine forests of the Black Hills, of which 39 over 11 sites could be used to evaluate how different forest structures would impact MPB dynamics. Three plots were established near Sturgis that were not treated and four plots established near Jewel Cave were lost to wildfire in 2000. The useable plots were located in the northern and central Hills with one set of plots just across the border in Wyoming at elevations ranging from 4,459 to 6,871 feet. The site indices of ponderosa pine on the plots ranged from 61 to 74 (100 year base) with 4 plots established on a bur oak habitat type, 19 on a common juniper habitat type, and 16 on a kinnikinick habitat type (Hoffman and Alexander 1987; Meyer 1938; Sheppard and Battaglia 2002). From 1985 through 2012, a total of 226 visits were made to the plots and thousands of trees were measured and examined providing abundant information on the fate of each tree. Including both the thinned and unthinned plots at establishment, tree densities expressed by basal area ranged from 44 feet^2 to 199 feet^2 per acre and expressed as trees per acre, densities ranged from 69 to 462. DBHs (QMD) of the trees ranged from 7.8 to 13.8 inches and timber volumes on the plots ranged from 2,380 to 17,977 board feet per acre (table 1). Even though the forests of the Black Hills appear to be rather homogenous, the stand conditions created by Schmid and Mata were rather diverse depending on the metric used to describe the plots. As a result, when MPBs approached the plots they encountered a variety of stand conditions of which, presumably, some would be conducive and some not for tree colonization and brood production.

Mountain Pine Beetles in the Black Hills: 1985–2012

The 1970 to 1981 MPB epidemic, which peaked in 1974 with over 600,000 trees killed, was the last major outbreak of MPBs occurring in the Black Hills before Schmid and Mata established the different levels of stand densities to test their effects on MPB dynamics (fig. 31) (Freeman 2015; Thompson 1975). From 1981 when approximately 90,000 trees were killed, through 1996, MPB activity in the Black Hills was very low. This low level of activity was illustrated as the first MPB-caused mortality within the plots that Schmid and Mata established and occurred on the Custer Crossing plots in 1985 when 1.2 trees per acre were killed. In 1986, 2.4 trees per acre were killed at Crook Mountain. In 1987, 1.0 tree per acre was killed at Bear Mountain One and 1.6 trees per acre were killed on the Border plots. This endemic level of MPB-caused mortality was reflected in 10 of the 11 areas where the plots were established through 1997 (fig. 63). Such endemic levels of MPB-caused mortality prevailed throughout the Black Hills until 1997 when many patches of dead trees could be readily detected by MPB surveys (Harris et al. 2001) (fig. 64).

Although the appearance of a significant MPB epidemic was uncertain in the late 1990s, all signs were showing that a major MPB infestation in the Black Hills was likely (fig. 65). From 1997 through 2000, an additional 13,000 acres were infested and an additional 66,600 trees were killed (Harris et al. 2001, 2002). (Acres infested does not indicate that all trees were killed by MPBs—see footnote 4.) The area west and south of Sturgis saw a major infestation and the rest of the South Dakota side of the Hills and the Bear Lodge had scattered patches of dead trees (fig. 66).

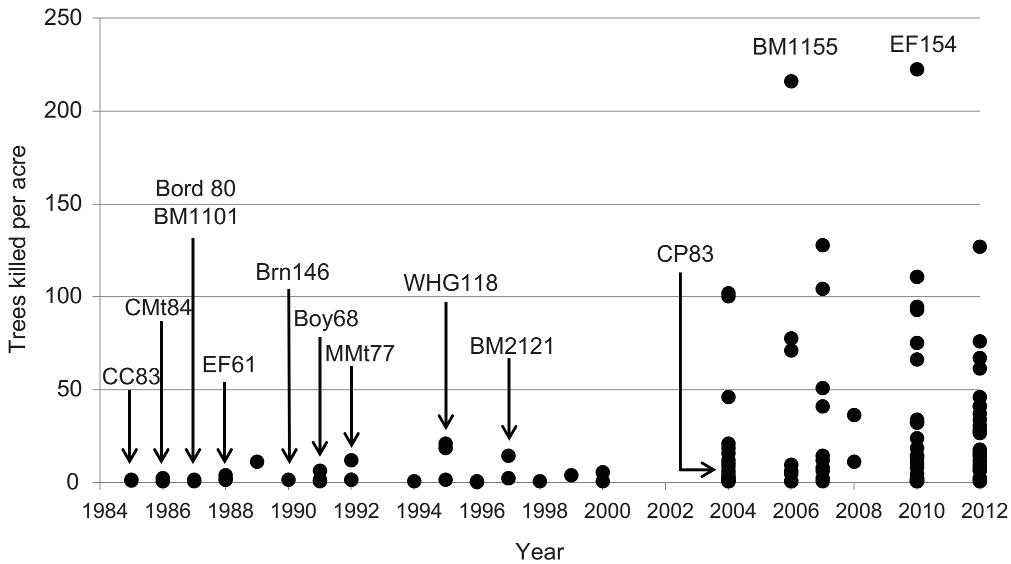

Figure 63—The timing and number of trees per acre killed by MPBs on each of the 39 plots was highly variable. Among the plots evaluated in the Black Hills for MPB-caused mortality, the first trees died in 1985 on Custer Crossing plot CC83 and 2010 is when mortality peaked with over 220 trees per acre killed by MPBs at the Black Hills Experimental on plot EF154. The first occurrence of MPB-caused mortality at each location is highlighted, as well as the plot on which the mortality occurred.

Figure 64—In general, from 1981 through 1997 MPB-caused tree mortality was rather low with scattered groups of trees killed.

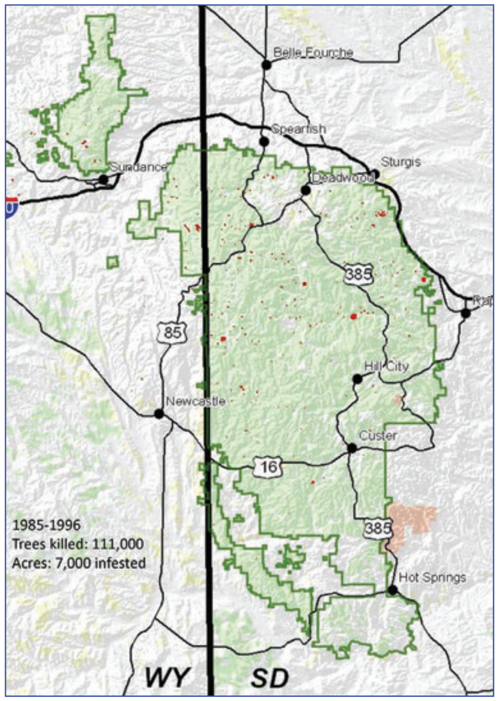

Figure 65—In 1996 there was minimal MPB activity in the Black Hills as indicated by the few areas shaded in red. For the previous 11 years since the MPB plots were established, 7,000 acres had been infested and a mean of 16 trees per acre were killed in those areas.

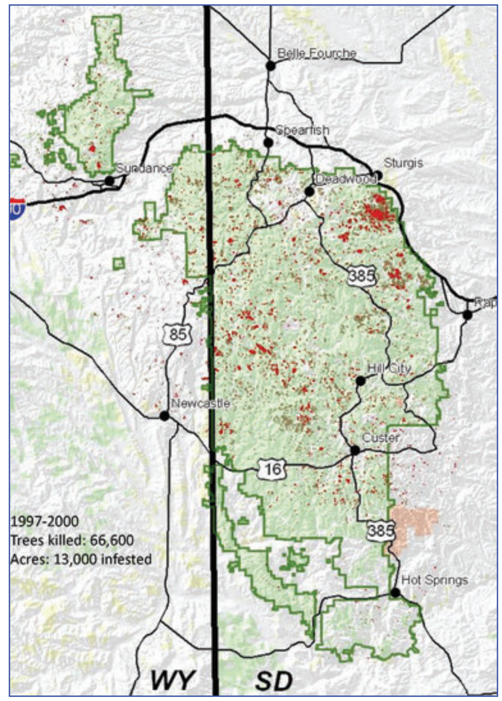

Figure 66—MPB-caused tree mortality became more apparent by 2000 as surveys showed many patches (shaded red) of trees killed that were distributed throughout the South Dakota portion of the Black Hills. The most noticeable epidemic conditions of MPBs occurred south of Sturgis.

By the end of 2004 the central Black Hills, and especially west and north of Hill City to the Wyoming Border, had major infestations of MPBs and from 2001 through 2004 an additional 94,000 acres became infested (Harris 2003, 2004, 2005) (fig. 67). Even though the area infested from 2005 to the end of 2008 by MPBs did not appreciably change, an additional 2,450,000 trees were killed and an additional 128,000 acres were added to the total infested (Harris 2006, 2010) (fig. 68). The epidemic possibly reached its peak between 2009 and 2012 when another 165,000 acres were infested (Harris 2011, 2012, 2013). As a result, the MPB plots representing a variety of stand structures established from 1985 through 1994 were exposed to MPBs with the Medicine Mountain, Boy Scout, White House Gulch, and Bear Mountain One and Two plots most likely the first to be exposed in 2001 (fig. 69). By 2008 all of the plots except those at Crook

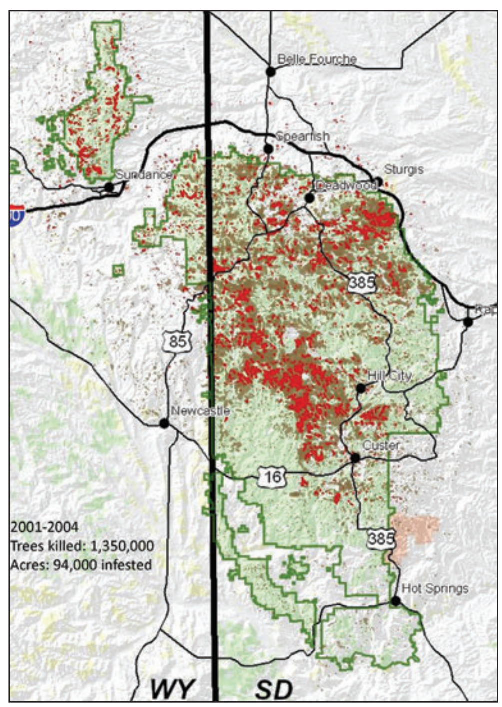

Figure 67—By 2004, a full-fledged MPB epidemic (shaded red) was occurring in the northern and central portions of the Black Hills with approximately 94,000 acres infested.

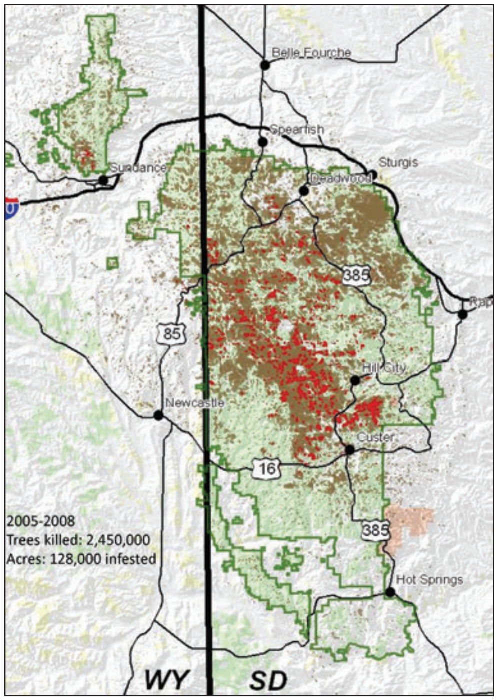

Figure 68—The total area infested from 2004 through 2008 (shaded red) did not appreciably change; however, the number of trees being killed by MPBs continued to increase.

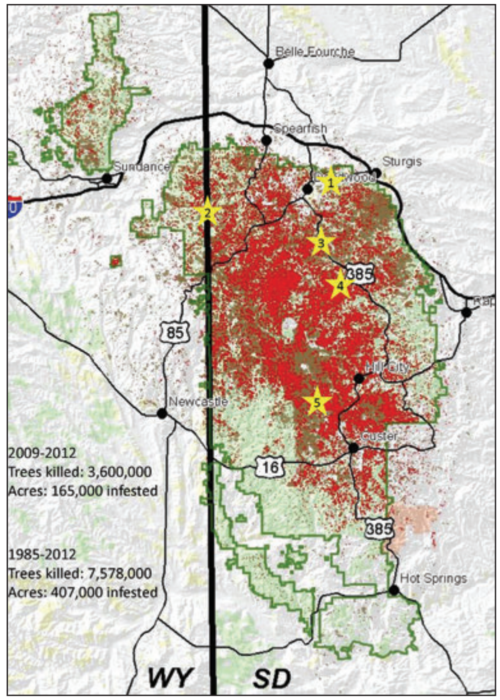

Figure 69—By 2012, the border (2), Custer Crossing, Custer Peak, Brownsville (3), Experimental Forest (4), Boy Scout, Medicine Mountain, White House Gulch, Bear Mountain One, and Bear Mountain Two (5) plots were intensely exposed to MPBs (shaded red). MPBs were in the vicinity of Crook Mountain (1) but minimal MPB-caused mortality occurred on those plots.

Mountain had intense MPB populations near them and by 2012 the intensity of the infestation around these same plots only worsened (fig. 70). The timing of the plots' establishment, and their examinations several times from 1985 through 2012, proved invaluable during one of the largest and intensive MPB epidemics the Black Hills has experienced in the last 100 years. As such, the veracity of stand structures in ameliorating MPB attacks would readily be tested (fig. 71).

Efficacy of Stand Structures Impacting Mountain Pine Beetle Dynamics

Forest development has been studied since the beginning of the 18th Century and there is much uncertainty and lack of understanding of the variables and their infinite interactions that control forest development (Assmann 1970; Liang et al. 2007). Nevertheless, the biophysical characteristics including location, elevation, slope angle, slope aspect, and potential natural vegetation (i.e., habitat type) have been shown to explain a large portion of the variation in how forests develop. Also, the stand characteristics—basal area per acre, basal area percentile distribution, and crown competition factor (CCF), along with the tree characteristics DBH, crown ratio, and the basal area of an individual tree in relation to the total basal area of larger trees—have been shown to explain another large portion of the variation. These relationships were determined from approximately 46,000 tree descriptions gathered over the northern Rocky Mountains (Stage 1973; Wykoff et al. 1982).

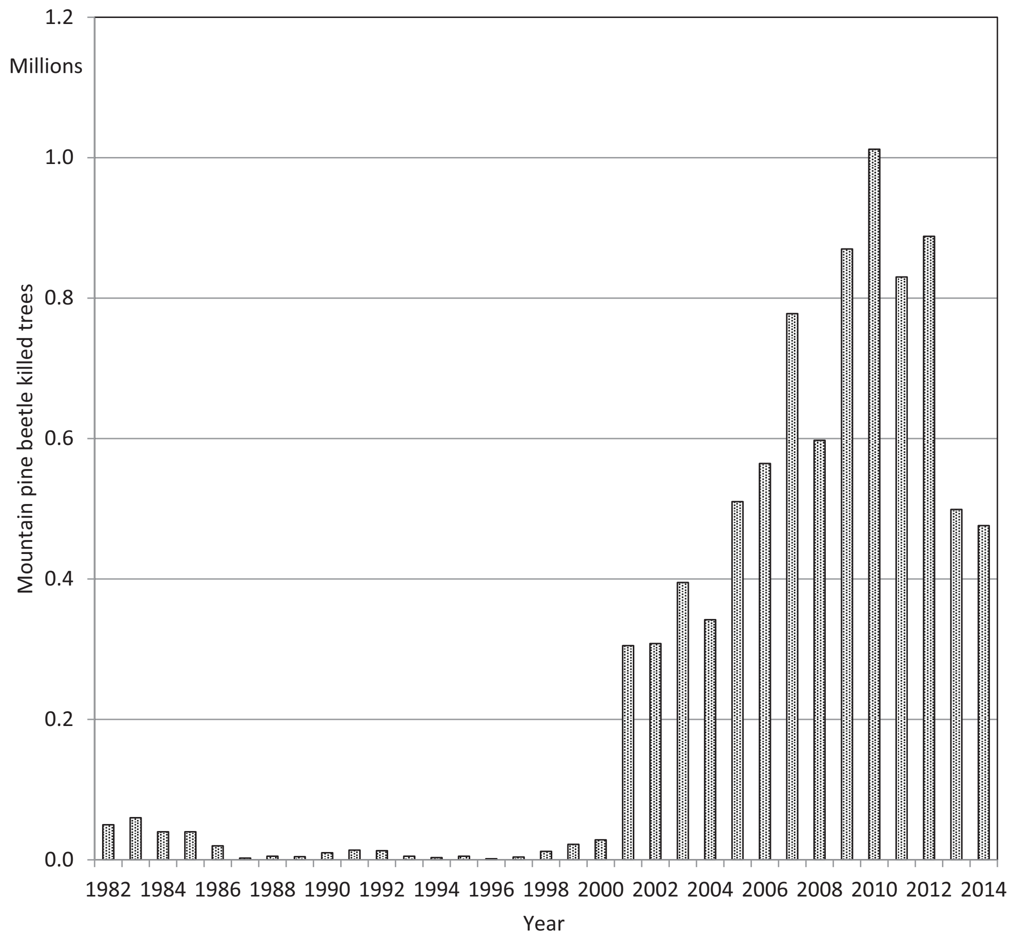

Figure 70—By 2004 a major epidemic of MPBs was occurring in the Black Hills and exceeding the mid-seventies epidemic (Lessard et al. 1987; Harris 2003, 2004, 2005, 2006, 2010, 2011, 2012, 2013, 2014; Harris et al. 2001, 2002) (see fig. 31).

Figure 71—Beginning in 2004, MPBs killed large expanses of ponderosa pine especially in the central Black Hills.

In addition to the above stand descriptors, site index, trees per acre, stand density index (SDI), leaf area index (LAI), growth basal area (GBA), and growing stock level (GSL) have also been used to describe stand structures (Hall 1983; Larsson et al. 1983; Long and Shaw 2005; Meyers 1967). As a result, there are several tree and stand variables that can be evaluated for having a relationship with MPB dynamics in the Black Hills.

Biophysical Setting

Climate, microclimate, geology, and soils are related to location, elevation, slope aspect and angle, and habitat type that influence forest type and development, which in turn can influence MPB dynamics (Amman and Baker 1972; Assmann 1970; Hoffman and Alexander 1987). The Black Hills are not large enough to expect that location within the Hills would likely influence forest development, even including the Bear Lodge (Dixon 2002; Wykoff et al. 1982). In addition, the MPB plots were located in the central and northern South Dakota portion of the Hills, further decreasing the spatial variation among the plots so that no differences in MPB-caused mortality among the plots could be attributed to their location. There is evidence that elevation can influence MPB dynamics since Amman and Baker (1972) found that MPB-caused mortality in lodgepole pine forests was related to 2,000-foot differences in elevations. Within the Black Hills, the elevations of the plots where MPB-caused mortality was monitored ranged from 4,459 to 6,871 feet with the majority of the plots occurring at elevations between 5,700 and 6,300 feet, a difference of only 600 feet. The Crook Mountain plots have the lowest elevation of 4,459 feet and little tree mortality, but MPB activity was minimal in the area compared to MPB activity near the other plots. Also, the beginning of this latest epidemic can be traced to a major outbreak of MPB in 1997 located just east and south of Crook Mountain and its elevations were in the low and mid 4,000-foot range (figs. 31, 66). As a result, no differences in MPB-caused mortality among the plots could be attributed to differences in elevation. McCambridge et al. (1982) in Colorado also found that ponderosa pine mortality caused by MPBs was not influenced by elevation.

Slope angle and slope aspect may impact MPB mortality because they are related to microclimate (Amman and Logan 1998). There is minimal topographic relief in the Hills and the two dominant Black Hills habitat types the plots were located on, ponderosa pine/kinnikinnick (*Arctostaphylos uva-ursi*) and ponderosa pine/common juniper (*Juniperus communis*), are widely distributed and are not readily determined by slope aspect as other habitat types are in more dissected landscapes (Hoffman and Alexander 1987; Pfister et al. 1977). As a result, slope angle and aspect were not found to be related to MPB mortality but habitat type was to a limited extent.

Habitat types or potential natural vegetation are a vegetative classification system that integrates a variety of physical and biological components including climate, soil, geology, and vegetation. Potential vegetation types are identified by species indicative of similar conditions. Due to growth, mortality, and disturbance, many other kinds of vegetation can occur on a given type through time. In some cases the indicator species may not be present, due to disturbance. Ponderosa pine/kinnikinnick is simply a vegetative indicator and a name for a physical and biological environment stratification system useful for predicting response to disturbance (Hann et al. 1997; Hoffman and Alexander 1987; Pfister et al. 1977). Nineteen plots were located on the ponderosa pine/common juniper habitat type, 16 on the ponderosa pine/kinnikinnick, and 4 on the ponderosa pine/bur oak (*Quercus macrocarpa*) habitat type.

Bur oak habitat types tend to occur on calcareous parent materials, kinnikinnick habitat types on metamorphic and granitic, and common juniper habitat types on limestone and igneous parent materials. Sandy loam and clay loam soils weathered from these materials occur within all three habitat types. Sites classified as having a bur oak habitat type receive about 20 inches of precipitation a year, those with a kinnikinnick habitat type receive between 15 and 25 inches of precipitation a year, and the plots located on the common juniper habitat type receive 18 to 20 inches of precipitation yearly (Hoffman and Alexander 1987).

The only trend of MPB-caused tree mortality related to habitat type was that the amount of trees killed peaked at 216 trees per acre in 2006 on the common juniper habitat type and the same number of trees killed occurred 4 years later (2010) on the plots located on the kinnikinnick habitat type (fig. 72). Again, little tree mortality caused by MPBs occurred on the bur oak habitat type, but this could not be related to habitat type as the intensity of MPB activity was minimal in the area of the plots. Similar to the differences in MPB-caused tree mortality related to elevation, differences in lodgepole pine tree mortality among the habitat types were noted (Amman and Baker 1972). Within the Hills there are different habitat types, but differences in the environments they represent are more subtle than those in more topographically diverse and species-rich locales (Hoffman and Alexander 1987; Pfister et al. 1977).

Site quality of a forest is its relative productive capacity determined by climate, soil, topography, and other factors; the higher the site quality, the faster the tree growth. Height in feet of mean-diameter dominant and codominant trees at the age of 100 years is used as an indicator of site quality in the Black Hills (Meyer 1938). The site indexes of the stands where the plots were located ranged from 61 at the Custer Crossing and the Black Hills Experimental Forest to 74 at the Brownsville. There was minimal differentiation in site quality, expressed by site index, similar to the other biophysical characteristics where the MPB plots were located. With this small variation, no differences in MPB-caused mortality could be attributed to site quality, which was also the finding of McCambridge et al. (1982) in Colorado.

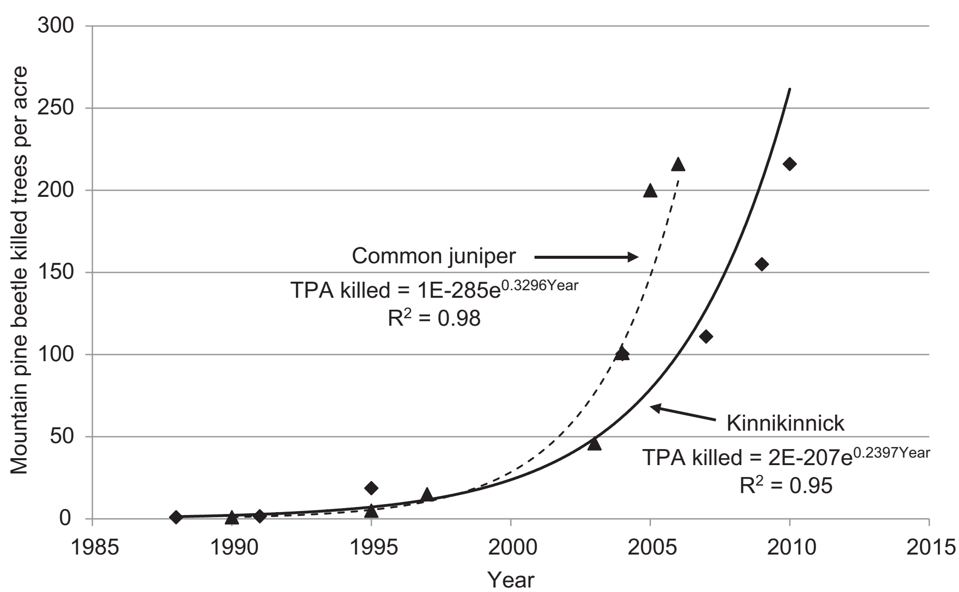

Figure 72—MPB-caused tree mortality started on plots located on both habitat types about the same time but tended to accelerate sooner on the common juniper habitat type compared to the kinnikinnick habitat type. The highest number of trees killed per acre was similar on both habitat types.

In summary, the biophysical settings of the Black Hills seem to have minimal impact on MPB dynamics. The MPB appears to be as destructive and virulent across all sites represented by the plots. These findings are illustrated in the progression of the 1996 through 2012 MPB infestations in the Black Hills as they transcended all locations, slopes, aspects, and elevations (figs. 65-69). Moreover, no area in the Hills has been spared a MPB infestation since Hopkins and Pinchot went to the Hills in 1901 (Hopkins 1902; Thompson 1975).

Tree Diameter

MPBs most often attack ponderosa pine trees that have DBHs in the 8 to 12 inch range (Sartwell, and Stevens 1975). In Colorado, McCambridge et al. (1982) found them preferring 12- to 14-inch DBH ponderosa pines and Alexander (1987) in the Black Hills suggested they prefer pines over 8 inches DBH. Reporting on attacks of ponderosa pine by MPBs in the Black Hills, Schmid et al. (1994) showed they were attacking pines with a mean DBH of 10 inches, in 2005 they attacked pines from 7 to 16 inches DBH, and in 2007 they were attacking pines from 7 to 19 inches DBH (Schmid and Mata 2005; Schmid et al. 2007). These preferences for tree sizes by MPB were readily tempered by the size of MPB populations and the size of available host trees.

The management of the Black Hills forests for over the last 50 years has tended to homogenize the forests and reduce the variation of tree sizes available for the MPB to attack. However, the mean DBHs of the plots after establishment ranged from 7.8 to 13.8 inches and averaged 11.2 inches, readily encompassing the range of ponderosa pine tree diameters that MPBs have been known to attack (fig. 49). MPBs killed a small number of trees in 1985 having DBHs ranging from 11 to 15 inches and in 1991 a tree with a 20-inch DBH was killed and in 1994 a 6-inch DBH tree was killed (fig. 73). From 2004 through 2012 the greatest numbers of trees were killed by MPBs in the Hills and the trend was

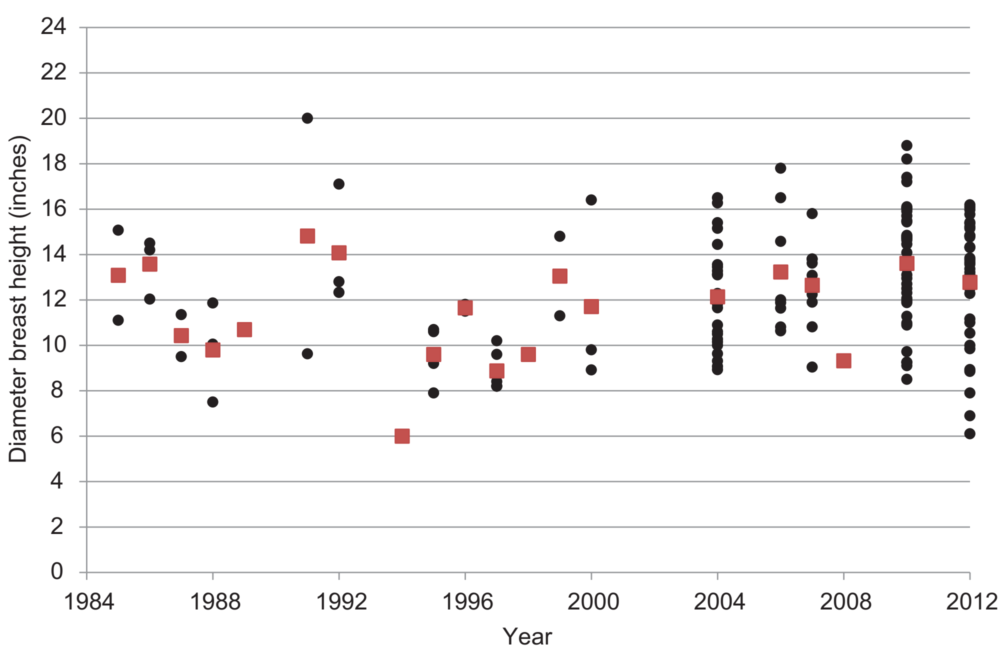

Figure 73—DBH (quadratic mean diameter-QMD at breast height-diameter of the tree with the mean basal area) of trees killed by MPBs from 1985 through 2012 on all of the MPB plots in the Black Hills. Red squares are the mean DBH of trees killed that year.

to have a greater number of small DBH trees killed compared to the years 1985 through 2000. Nevertheless, relatively large trees were still being killed; for example, a tree with an 18.8 DBH was killed in 2010, again illustrating the continued wide variation in tree sizes the MPBs were selecting, even at the outbreak's peak (fig. 73). In those years when MPB-caused mortality was the highest, the mean DBH of the trees killed ranged from 12.1 to 13.6 inches (fig. 73). The DBHs of the trees killed by MPBs were very reflective of the DBHs of the plots as a whole. In other words, the distribution of tree DBHs of trees killed by MPBs was very similar to the distribution of tree DBHs that were not killed (fig. 74). The DBHs of trees killed during the MPB outbreak in the Black Hills were similar to the DBHs that Sartwell and Stevens (1975), McCambridge et al. (1982), and Alexander (1987) suggested MPBs preferred. However, during this MPB epidemic in the Black Hills, trees with DBHs between 9 and 17 inches were the ones most frequently killed (fig. 74).

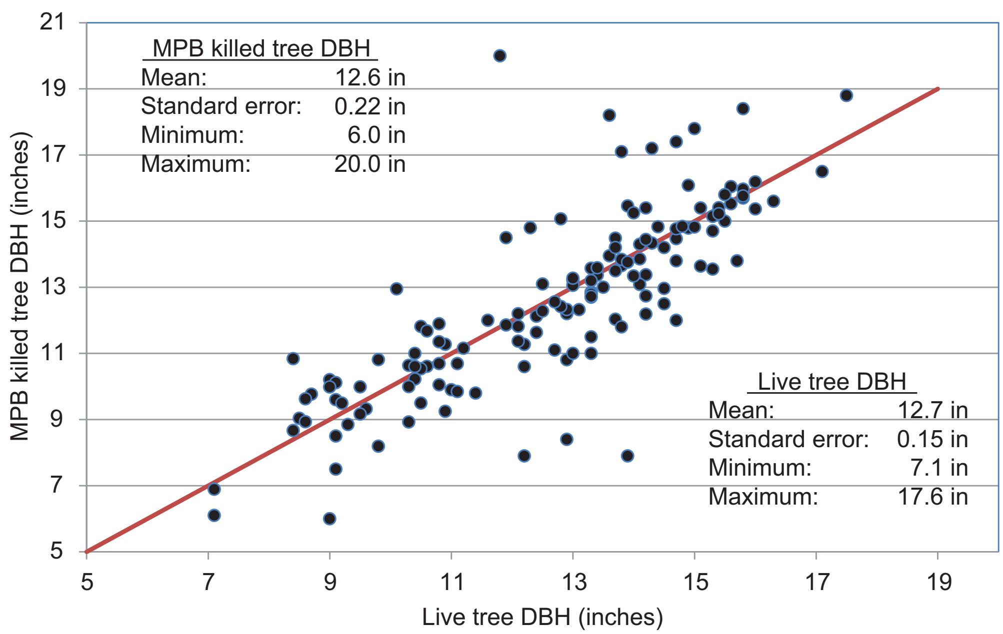

Figure 74—DBH (quadratic mean diameter-QMD) of trees killed by MPBs compared to the DBH of live trees on each plot. Solid line represents the center of the graph.

Stand Density

Within the Black Hills, it was recognized in 1972, if not earlier, that stand density influenced MPB dynamics and 70 feet^2 of basal area per acre was suggested as a target for MPB resistance (Thompson 1975). Sartwell and Stevens (1975) as well as Alexander (1987) indicated even-aged stands of ponderosa pine with ages from 50 to 100 years and having a density of over 150 feet^2 of basal area were particularly susceptible to MPB attacks in the Black Hills. With this knowledge, Schmid and Mata established plots throughout the Hills to test the efficacy of modifying stand structures to influence MPB dynamics (fig. 47). In creating the different stand densities they ensured the tree densities of the plots would transcend those suggested by Sartwell and Stevens (1975) and those suggested by Alexander (1987) for reducing MPB impacts (Schmid and Mata 1992; Schmid et al. 1994). From 1985 through 1994, Schmid and Mata established 46 plots in the Black Hills, of which 39 could be used and were distributed from north and east of Deadwood, west to the Wyoming border and south to north and west of Custer (fig. 47). All of these 39 plots, with the exception of the four Crook Mountain plots near Deadwood, were subjected to intense attack by the MPB, readily testing whether stand density influenced MPB-caused ponderosa pine mortality (fig. 69).

As mentioned before there are several measures of stand density, with basal area per acre and stand density index (SDI) both widely used and offering excellent interpretative power. SDI combines tree diameter and density expressed as trees per acre and is independent of site quality and stand age. SDI can be used to compare levels of growing stock and describe the onset of competition, full site occupancy, when self-thinning occurs, and when maximum density occurs (Long 1985). Long et al. (2010) and Anhold et al. (1996) showed how SDI could be used to develop and compare silvicultural alternatives aimed at reducing tree losses caused by MPBs. Negrón et al. (2008) indicated that ponderosa pine stands infested with MPBs in the Black Hills had SDI values over 192 while uninfested stands had SDIs averaging 157. Of the 35 plots exposed to MPBs reported here, 3 plots with peak SDIs of 121, 123, and 128 had very few trees killed by MPBs and 3 other plots with peak SDIs of 124, 125, and 126 had major tree mortality caused by MPBs. Possibly by combining tree density with DBH, SDI does not provide the differentiation in forest structure that basal area alone provides for, showing the impact of MPBs. In addition, no direct conversion from SDI to basal area per acre is possible, because many combinations of mean stand diameter and number of trees will produce identical SDIs at different basal areas (Oliver 1995). As such, density expressed as basal area in feet^2 per acre was used to show how MPBs impacted trees on the plots over the years; and SDI, volume, and trees per acre further describe the impact the MPBs had in the Black Hills (see Appendix A for MPB dynamics described by SDI).

The establishment stand densities of the 35 plots exposed to MPB ranged from 44 to 199 feet^2 of basal area per acre with the majority of the plots having tree densities within the range of 60 to 125 feet^2 of basal area per acre (fig. 48). With these different establishment densities, MPB-caused tree mortality, and to a limited extent, the different quality of sites the plots were established on, resulted in a wide range of maximum tree densities that occurred on the plots from 1987 through 2012 (fig. 75). Some of the plots reached their highest tree density in 1987, which ranged from 81 to 155 feet^2 of basal area per acre, shortly after they were established. The highest tree density on a plot was 217 feet^2 of basal area per acre in 2004 and three plots reached their maximum tree density in 2012. As a result of this large amount of variation in establishment and maximum tree densities that occurred on the 35 plots that were exposed to MPBs from 1985 through 2012, the plots were put into stand density clusters that could be used to disclose how each plot was impacted by MPBs. Also, the plots were named for their location and their tree density expressed as basal area per acre when they were established.

The 35 plots that were exposed to MPBs were put into one of 7 similarity clusters depending on their establishment and maximum tree density expressed as square feet of basal area per acre that occurred from 1985 through 2012. As a result of this clustering, overlap of tree densities among the cluster was possible. However, within the cluster, minimum and maximum tree densities expressed as basal area per acre were similar. The tree densities in clusters were: 45 to 80 feet^2, 60 to 90, 80 to 90, 80 to 100, 80 to 125, 120 to 150, and 150 to 220 feet^2 of basal area per acre (table 2). As a result, 3 plots—the Experimental Forest plots with establishment tree densities of 44 and 61 feet^2 of basal area per acre and a single

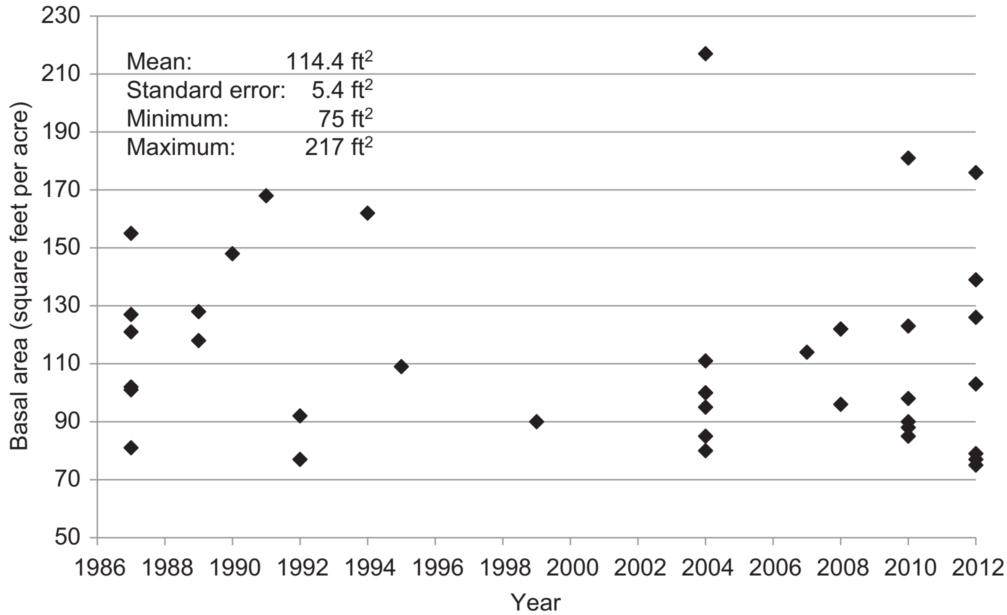

Figure 75—The maximum tree density expressed as square feet of basal area per acre that occurred on the plots from the time they were established through 2012.

Table 2—The 35 plots exposed to mountain pine beetles and experienced major mortality within them or near them were placed into clusters based on the minimum and maximum tree densities that occurred on them expressed as square feet of basal area per acre. Also included in the table are the tree densities of the four Crook Mountain plots when they were established.

Tree densities that occurred from establishment through 2012							
BA 45–80 ft^2/ac		**BA 60–90 ft^2/ac**		**BA 80–90 ft^2/ac**		**BA 80–100 ft^2/ac**	
Plot[a]	**Est BA[b]**	**Plot[a]**	**Est BA[b]**	**Plot[a]**	**Est BA[b]**	**Plot[a]**	**Est BA[b]**
EF44	44	BM161	61	BM181	81	EF82	82
EF61	61	Bord60	60	Boy79	79	BM1101	101
Boy68	68	Brn61	61	MMt77	77	Boy87	87
		WHG59	59	WHG80	80	Brn81	81
						CP83	83
						CC83	83
						MMt92	92

Tree densities that occurred from establishment through 2012							
BA 80-125 ft^2/ac		**BA 120-150 ft^2/ac**		**BA 150-220 ft^2/ac**		**Establishment density Crook Mountain**	
Plot[a]	**Est BA[b]**	**Plot[a]**	**Est BA[b]**	**Plot[a]**	**Est BA[b]**	**Plot[a]**	**BA[b] ft^2/ac**
EF112	112	BM2121	121	EF154	154	CMt84	84
BM2102	102	BM2127	127	BM1155	155	CMt104	104
Bord80	80	Brn146	146	Bord199	199	CMt119	119
Bord98	98	WHG128	128	Boy168	168	CMt158	158
Brn101	101			CP169	169		
CP107	107						
MMT108	108						
WHG118	118						

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1= Bear Mountain One, BM2 = Bear MountainTwo, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est BA = established basal area, feet^2 per acre.

Boy Scout plot with an establishment tree density of 68 feet^2 of basal area per acre—were in the smallest cluster. Eight plots were included in the largest cluster that contained 80 to 125 feet^2 of basal area per acre and were located at Bear Mountain Two, Border, Brownsville, Black Hills Experimental Forest, Medicine Mountain, Custer Peak, and White House Gulch (table 2, fig. 47). By using these density clusters, the fate of the trees on each plot and how the MPBs impacted the trees on the plots from their establishment through 2012 could be readily described. The board foot volumes expressed in the following plot narratives are Scribner.

Plots With Establishment and Maximum Densities Ranging From 150 to 220 Feet^2 of Basal Area Per Acre

BM1155—The Bear Mountain One plots were located on a site with a common juniper habitat type and 92-year-old trees (figs. 47, 57, 61). The site index was estimated at 70 and the plot was exposed to MPBs circa 1990. The untreated plot, when established, had a tree density of 155 feet^2 of basal area per acre, a mean DBH (QMD) of 10.0 inches, and an SDI of 284 (table 1). Even though the plot was not treated, tree DBHs were rather uniform as 68 percent of them ranged from 8.3 to 11.8 (1.75 inch standard deviation) inches. From establishment in 1987 through 2006, 133 feet^2 of basal area per acre and 216 trees per acre were killed by MPBs (fig. 76). Tree density through 2010 remained relatively constant and actually increased to 32 feet^2 of basal area per acre even though another 9 trees per acre succumbed to MPBs. When the plot was measured in 2012, 28 feet^2 of basal area per acre remained distributed over 40 trees per acre. However, visual inspection of the plot in 2013 revealed most if not all of the remaining trees were infested with MPBs. As a result of MPBs in the densest plot established at Bear Mountain One, 139 feet^2 of basal area, 227 trees, and 14,140 board feet per acre were lost by 2012 (table 3, fig. 77).

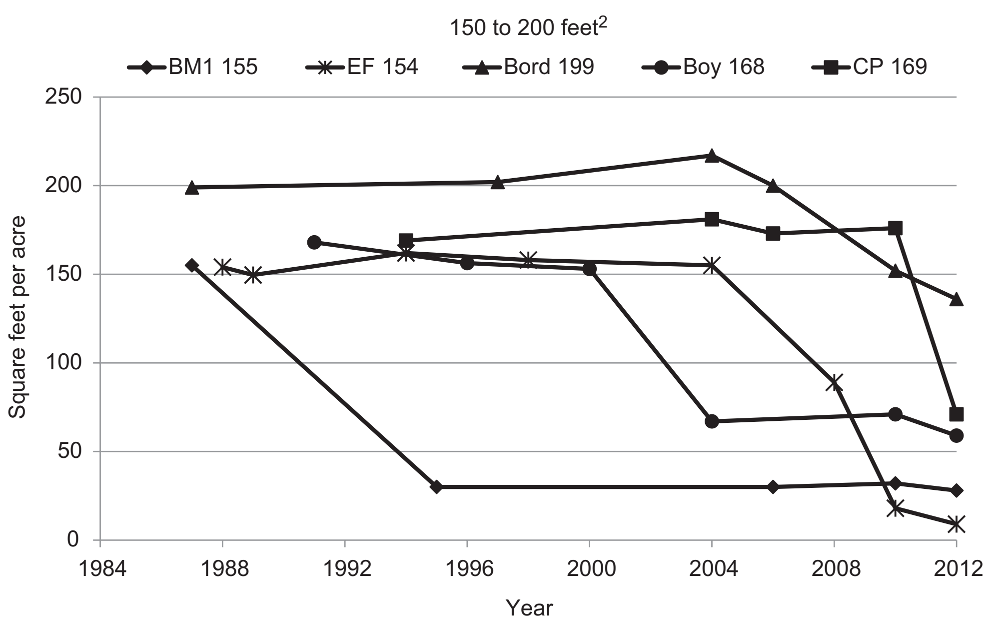

Figure 76—These plots contain tree densities ranging from 150 to a maximum of 220 feet^2 of basal area per acre. They were located at Bear Mountain One (BM1155), Black Hills Experimental Forest (EF154), on the Wyoming border (Bord199), adjacent to the Medicine Mountain Boy Scout Camp (Boy168), and at Custer Peak (CP169). These plots represent the highest tree densities that were exposed to MPBs.

Table 3—Trees (A), basal area (B), cubic volume (C) and Scribner board foot volume (D) per acre removed and lost on the plots from the time they were established through 2012. Also the table shows the number of trees, square feet of basal area, and volume per acre that occurred on the plots in 2012.

Table 3 A. Trees.

Plot[a]	Est trees[b] trees/ac	Year thinned[c]	Trees removed and lost: Thinned[d] trees/ac	Other[e] trees/ac	MPB[f] trees/ac	Total trees/ac	2012 trees/ac
EF44	71		0.0	1.6	0.8	2.4	69
EF61	79	1998	0.8	3.2	6.5	10.5	68
EF82	128	1998	5.7	2.4	21.9	29.9	98
EF112	246	1998	13.8	21.0	164.3	199.1	47
EF154	375		0.0	31.6	309.2	340.8	34
BM161	93	1992	9.7	4.0	22.7	36.4	57
BM181	146	1992	16.2	4.0	76.9	97.1	49
BM1101	170	1992	14.6	10.5	106.8	131.9	38
BM1155	284		0.0	17.0	226.6	243.6	40
BM2102	230	1997	47.8	10.5	111.7	170.0	60
BM2121	282	1997	42.1	9.7	169.2	221.0	61
BM2127	381	1997	48.6	21.9	251.7	322.1	59
Bord60	93	1997	7.3	13.0	13.8	34.0	59
Bord80	125	1997	8.9	17.0	44.5	70.4	55
Bord98	159	1997	3.2	27.5	82.6	113.3	46
Bord199	462		0.0	79.3	147.3	226.6	235
Boy68	123	1996	37.2	10.5	3.2	51.0	72
Boy79	139	1996	29.1	4.0	46.9	80.1	59
Boy87	115	1996	6.5	5.7	61.5	73.7	41
Boy168	417	1991	25.9	62.3	171.6	259.8	157
Brn61	73	1995	4.0	2.4	10.5	17.0	56
Brn81	112	1995	3.2	2.4	48.6	54.2	58
Brn101	113	1995	4.9	0.8	58.3	63.9	49
Brn146	167	1985	0.8	8.9	148.1	157.8	9
CP83	83	1994	0.8	2.4	43.7	46.9	36
CP107	122		0.0	1.6	80.9	82.6	39
CP169	234		0.0	3.2	149.7	153.0	81
CC83	92	1985	0.4	2.4	35.2	38.0	54
MMt77	74	1992	7.3	6.5	42.9	56.7	17
MMt92	95	1992	9.7	4.0	78.5	92.3	3
MMt108	118	1992	2.4	3.2	112.3	118.0	0
WHG59	69	1999	4.0	1.6	30.8	36.4	33
WHG80	119	1999	7.3	22.7	57.5	87.4	32
WHG118	160	1999	16.8	7.5	103.8	128.1	32
WHG128	202		0.0	17.0	160.3	177.3	25
CMt84	82	1996	11.3	5.7	4.0	21.0	61
CMt104	135	1996	8.1	13.0	6.5	27.5	107
CMt119	116	1996	17.1	6.5	3.2	26.8	89
CMt158	181		0.0	30.0	2.5	32.5	148

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and Cmt = Crook Mountain.

[b] Est Trees = the number of trees per acre when the plot was established.

[c] Year thinned = the dates when trees were removed in a thinning after the plot was established.

[d] Thinned trees = the number of trees removed per acre after the plot was established.

[e] Other = trees per acre killed by weather and Ips.

[f] MPB = trees per acre killed by mountain pine beetles.

Table 3A. Trees.

Plot[a]	Est BA[b] ft²/ac	Basal area per acre removed and lost: Thinned ft²/ac	Other[c] ft²/ac	MPB[d] ft²/ac	Total ft²/ac	2012 BA ft²/ac
EF44	44	0.0	1.2	0.9	2.1	74
EF61	61	0.5	3.1	5.8	9.4	79
EF82	82	3.9	1.2	17.0	22.1	95
EF112	112	4.4	9.9	105.7	120.0	27
EF154	154	0.0	7.8	161.6	169.3	9
BM161	61	5.6	2.6	27.7	35.9	66
BM181	81	8.7	2.8	50.0	61.4	48
BM1101	101	7.5	7.5	84.6	99.7	34
BM1155	155	0.0	7.6	138.8	146.4	28
BM2102	102	16.0	4.9	76.8	97.7	42
BM2121	121	15.1	3.1	104.1	122.3	36
BM2127	127	13.2	8.3	122.7	144.2	30
Bord60	60	5.8	8.3	19.0	33.1	79
Bord80	80	6.7	8.9	55.5	71.1	71
Bord98	98	2.4	12.3	89.9	104.7	48
Bord199	199	0.0	20.5	101.0	121.5	136
Boy68	68	18.4	3.2	3.2	24.8	77
Boy79	79	14.0	1.1	43.9	59.0	56
Boy87	87	2.8	2.6	69.0	74.3	41
Boy168	168	11.7	12.7	100.0	124.4	59
Brn61	61	3.7	1.6	13.1	18.5	79
Brn81	81	2.3	1.9	49.1	53.3	64
Brn101	101	3.2	0.8	69.6	73.6	61
Brn146	146	0.4	5.7	160.8	166.9	8
CP83	83	0.7	3.0	54.2	57.8	47
CP107	107	0.0	1.7	85.7	87.4	42
CP169	169	0.0	2.2	122.1	124.3	71
CC83	83	0.3	1.9	41.9	44.0	72
MMt77	77	6.2	4.6	59.9	70.7	24
MMt92	92	10.5	2.3	99.8	112.7	1
MMt108	108	2.1	0.3	126.4	128.9	0
WHG59	59	3.3	2.1	43.4	48.8	44
WHG80	80	4.0	21.8	58.3	84.0	32
WHG118	118	12.2	6.7	97.6	116.4	34
WHG128	128	0.0	13.0	120.1	133.1	23
CMt84	84	10.5	7.3	4.7	22.5	103
CMt104	104	4.0	9.1	7.6	20.6	126
CMt119	119	15.4	5.9	4.1	25.4	139
CMt158	158	0.0	15.5	3.0	18.4	176

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est BA = basal area (feet² per acre) when plot established. See table 3A for dates when trees were removed in a thinning after the plot was established.

[c] Other = basal area (feet² per acre) killed by weather and Ips.

[d] MPB = basal area (feet² per acre) killed by mountain pine beetles.

Table 3B. Basal area.

Plot[a]	Est BA[b] ft²/ac	Basal area per acre removed and lost: Thinned ft²/ac	Other[c] ft²/ac	MPB[d] ft²/ac	Total ft²/ac	2012 BA ft²/ac
EF44	44	0.0	1.2	0.9	2.1	74
EF61	61	0.5	3.1	5.8	9.4	79
EF82	82	3.9	1.2	17.0	22.1	95
EF112	112	4.4	9.9	105.7	120.0	27
EF154	154	0.0	7.8	161.6	169.3	9
BM161	61	5.6	2.6	27.7	35.9	66
BM181	81	8.7	2.8	50.0	61.4	48
BM1101	101	7.5	7.5	84.6	99.7	34
BM1155	155	0.0	7.6	138.8	146.4	28
BM2102	102	16.0	4.9	76.8	97.7	42
BM2121	121	15.1	3.1	104.1	122.3	36
BM2127	127	13.2	8.3	122.7	144.2	30
Bord60	60	5.8	8.3	19.0	33.1	79
Bord80	80	6.7	8.9	55.5	71.1	71
Bord98	98	2.4	12.3	89.9	104.7	48
Bord199	199	0.0	20.5	101.0	121.5	136
Boy68	68	18.4	3.2	3.2	24.8	77
Boy79	79	14.0	1.1	43.9	59.0	56
Boy87	87	2.8	2.6	69.0	74.3	41
Boy168	168	11.7	12.7	100.0	124.4	59
Brn61	61	3.7	1.6	13.1	18.5	79
Brn81	81	2.3	1.9	49.1	53.3	64
Brn101	101	3.2	0.8	69.6	73.6	61
Brn146	146	0.4	5.7	160.8	166.9	8
CP83	83	0.7	3.0	54.2	57.8	47
CP107	107	0.0	1.7	85.7	87.4	42
CP169	169	0.0	2.2	122.1	124.3	71
CC83	83	0.3	1.9	41.9	44.0	72
MMt77	77	6.2	4.6	59.9	70.7	24
MMt92	92	10.5	2.3	99.8	112.7	1
MMt108	108	2.1	0.3	126.4	128.9	0
WHG59	59	3.3	2.1	43.4	48.8	44
WHG80	80	4.0	21.8	58.3	84.0	32
WHG118	118	12.2	6.7	97.6	116.4	34
WHG128	128	0.0	13.0	120.1	133.1	23
CMt84	84	10.5	7.3	4.7	22.5	103
CMt104	104	4.0	9.1	7.6	20.6	126
CMt119	119	15.4	5.9	4.1	25.4	139
CMt158	158	0.0	15.5	3.0	18.4	176

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est BA = basal area (feet^2 per acre) when plot established. See table 3A for dates when trees were removed in a thinning after the plot was established.

[c] Other = basal area (feet^2 per acre) killed by weather and Ips.

[d] MPB = basal area (feet^2 per acre) killed by mountain pine beetles.

Table 3C. Cubic volume.

Plot[a]	Est volume[b] ft³/ac	Volume per acre removed and lost: Thinned ft³/ac	Other[c] ft³/ac	MPB[d] ft³/ac	Total ft³/ac	2012 Volume ft³/ac
EF44	916	0	26	23	48	1,913
EF61	1,359	11	75	138	224	2,087
EF82	1,711	93	24	387	504	2,334
EF112	2,086	72	195	2,316	2,583	1,527
EF154	2,775	0	153	3,338	3,490	288
BM161	1,377	136	57	817	1,009	2,454
BM181	1,671	197	65	1,251	1,514	1,284
BM1101	2,161	183	203	2,323	2,708	1,534
BM1155	3,204	0	164	3,644	3,807	741
BM2102	1,974	305	132	1,778	2,215	1,129
BM2121	2,207	260	51	2,249	2,560	1,060
BM2127	2,062	197	141	2,368	2,707	889
Bord60	1,334	142	189	562	894	2,747
Bord80	1,773	158	190	1,594	1,942	3,590
Bord98	2,180	72	240	2,505	2,817	3,430
Bord199	3,902	0	361	2,469	2,830	3,468
Boy68	1,461	409	51	84	543	2,001
Boy79	1,621	291	16	1,084	1,392	2,155
Boy87	2,031	54	59	1,878	1,991	2,577
Boy168	3,219	340	194	2,322	2,856	1,372
Brn61	1,439	91	35	363	489	2,540
Brn81	1,811	51	46	1,263	1,359	2,041
Brn101	2,424	68	21	1,889	1,978	2,240
Brn146	3,543	8	135	4,371	4,514	566
CP83	2,391	17	85	1,508	1,610	2,714
CP107	2,785	0	45	2,225	2,270	2,685
CP169	4,388	0	55	2,948	3,003	4,229
CC83	1,985	5	46	1,135	1,186	2,236
MMt77	2,064	153	115	1,818	2,086	951
MMt92	2,361	282	48	2,897	3,227	104
MMt108	2,752	53	3	3,583	3,639	0
WHG59	1,423	78	60	1,276	1,413	1,993
WHG80	1,771	82	565	1,540	2,188	1,864
WHG118	2,670	278	164	2,471	2,913	1,655
WHG128	2,766	0	312	2,845	3,157	826
CMt84	2,228	277	222	132	631	3,211
CMt104	2,543	80	221	220	521	3,525
CMt119	3,162	423	154	116	693	4,276
CMt158	4,116	0	434	84	518	5,056

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est Volume = volume in feet^3 per acre when the plot was established. See table 3A for dates when trees were removed in a thinning after the plot was established.

[c] Other = cubic volume (feet^3) killed by weather and Ips.

[d] MPB = cubic volume (feet^3) killed by mountain pine beetles.

Table 3D. Scribner board foot volume.

		Volume per acre removed and lost				
Plot[a]	Est volume[b] bd ft/ac	Thinned bd ft/ac	Other[c] bd ft/ac	MPB[d] bd ft/ac	Total bd ft/ac	2012 Volume bd ft/ac
EF44	3,173	0	105	89	194	8,288
EF61	5,310	41	308	583	931	9,147
EF82	6,046	372	57	1,522	1,951	9,818
EF112	5,383	81	534	8,442	9,057	1,684
EF154	7,026	0	340	10,538	10,878	89
BM161	5,115	461	186	3,796	4,443	8,142
BM181	5,374	688	259	4,969	5,916	5,285
BM1101	7,268	590	825	10,044	11,461	3,497
BM1155	9,964	0	404	14,140	14,544	2,501
BM2102	5,358	599	469	6,928	7,996	3,424
BM2121	5,107	364	24	8,070	8,458	2,704
BM2127	2,380	73	178	6,759	7,009	1,554
Bord60	4,881	558	744	2,654	3,958	11,024
Bord80	6,443	631	582	7,511	8,725	9,632
Bord98	7,754	307	590	11,339	12,238	5,974
Bord199	10,676	0	510	9,543	10,053	10,725
Boy68	5,067	1,262	49	364	1,675	8,822
Boy79	5,415	882	24	4,589	5,495	5,787
Boy87	8,070	154	186	8,482	8,822	4,484
Boy168	9,292	1287	162	8,417	9,867	2,890
Brn61	5,763	372	130	1,611	2,113	10,725
Brn81	6,912	194	178	5,472	5,844	7,600
Brn101	10,012	259	89	8,636	8,984	7,536
Brn146	14,861	24	534	19,579	20,138	809
CP83	10,943	57	413	6,912	7,382	5,941
CP107	11,777	0	210	9,794	10,004	4,792
CP169	17,977	0	227	12,101	12,327	7,090
CC83	8,160	20	192	5,172	5,384	9,224
MMt77	9,179	623	437	8,749	9,810	3,343
MMt92	10,158	1,247	162	13,453	14,861	105
MMt108	11,825	210	0	16,398	16,608	0
WHG59	5,828	210	300	6,168	6,767	5,982
WHG80	6,589	235	2428	6,750	9,413	3,570
WHG118	10,319	1,056	654	10,478	12,189	4,001
WHG128	10,028	0	1255	11,154	12,408	2,323
CMt84	9,915	1,206	1068	591	2,865	15,686
CMt104	10,174	186	858	963	2,007	16,374
CMt119	14,116	1,821	664	550	3,035	20,785
CMt158	17,969	0	1781	380	2,161	23,610

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est Volume = equals the volume in Scribner board feet per acre when plot established. See table 3A for dates when trees were removed in a thinning after the plot was established.

[c] Other = board foot (bd ft) volume killed by weather and Ips.

[d] MPB = board foot (bd ft) volume killed by mountain pine beetles.

Figure 77—When Bear Mountain One plot-BM1155 was visited in 2012, 40 trees per acre and 28 feet^2 of basal area per acre remained. Photograph shows the center of the plot taken from the plot border.

EF154—On the Black Hills Experimental Forest, an untreated plot was established (figs. 47, 50, 56). The trees were approximately 95 years old, the site index was 61, the SDI 299, and the habitat type was kinnikinnick (table 1). The plot contained 154 feet^2 of basal area per acre, distributed over 375 trees per acre and their mean DBH was 8.7 inches with a moderate amount of variation (1.91 inch standard deviation). The tree density peaked in 1994 at 162 feet^2 per acre of basal area and MPB-caused tree mortality began around 1996 as the tree density decreased slowly as it reached 155 feet^2 of basal area per acre in 2004 as a result of losing 30 trees per acre (fig. 76). After 2004, MPB-caused mortality greatly increased and in 2008 the tree density was 89 feet^2 of basal area per acre; in 2010, 18 feet^2 of basal area per acre; and in 2012, 9 feet^2 of basal area per acre. From 2004 through 2012, 302 trees and 10,425 board feet per acre were lost to MPBs. As a result of MPBs on the untreated plot located on the Experimental Forest, 162 feet^2 of basal area, 309 trees, and 10,538 board feet per acre were lost from 1988 through 2012, with the greatest losses occurring after 2004 (table 3, fig. 78).

Boy168—Just north of the Medicine Mountain Boy Scout Camp on a kinnikinnick habitat in a stand with 120-year-old trees, an untreated plot was established (figs. 47, 57, 59). The stand had a site index of 73, an SDI of 326, 168 feet^2 per acre of basal area, and 417 trees per acre that had a mean DBH of 8.6 inches with considerable variation (standard deviation of 2.97 inches) (table 1). With the exposure to MPBs around 1995, 12 trees per acre were killed by the year 2000 and the tree density dropped to 153 feet^2 of basal area per acre (fig. 76). From 2000 to 2004 MPBs killed another 129 trees per acre and the basal area decreased to 67 feet^2 per acre. Tree mortality was light the next 6 years as only 3 trees per

Figure 78—The untreated plot (EF154) located on the Black Hills Experimental Forest experienced a large amount of mortality caused by MPBs as only 34 trees per acre were alive in 2012 covering 9 feet^2 of basal area per acre. Photograph shows the center of the plot taken from the plot border.

acre were killed by MPBs and the basal area per acre slightly increased. However, MPB attacks increased, and 28 trees per acre were killed by 2012 and when the plot was visited in 2013 the majority, if not all of the remaining trees, were showing signs of MPB attacks. As a result of MPBs from 1991 through 2012, 172 trees per acre, 100 feet^2 of basal area per acre, and 8,417 board feet of timber per acre were lost (table 3, fig. 79).

CP169—West of Highway 385 near the junction of the Custer Peak Road (316) an untreated plot was established (figs. 47, 50, 54). The 112-year-old stand was located on a common juniper habitat type, the site index was 64, the SDI was 293, it had a tree density of 169 feet^2 of basal area and 234 trees per acre with the trees having a mean DBH of 11.5 inches with a 1.61 inch standard deviation (table 1). Ten years later in 2004 the basal area per acre on the plot peaked at 181 feet^2 and MPBs were infesting a few trees (fig. 76). The basal area per acre decreased slightly by 2006 and rose slightly by 2010 before plummeting to 71 feet^2 of basal area per acre in 2012. In these 2 years, 128 trees, 114 feet^2 of basal area, and 11,324 board feet of volume per acre were lost to MPBs. Because of MPBs in the untreated plot at Custer Peak from 1994 through 2012, 150 trees, 122 feet^2 of basal area, and 12,101 board feet of timber per acre were lost (table 3, fig. 80).

Bord199—Just west of the Wyoming border along Wagon Canyon Road (105), the untreated plot with the highest tree density of all of the plots was established in an 87-year-old stand (figs. 47, 50, 52). Located on a common juniper habitat type with a site index of 65 and SDI of 382, the plot had 199 feet^2 of basal area, 462 trees, and 10,676 board feet of timber per acre (table 1). The trees had a mean diameter of 8.9 inches with a standard deviation of 2.02 inches and the area was first exposed to MPBs circa 1990. MPBs killed 15 trees per acre and another 43 trees per acre were killed by weather and the pine engraver Ips by 1997.

Figure 79—The untreated plot (Boy168) located on the northern border of the Medicine Mountain Boy Scout Camp lost 172 trees and 100 feet^2 of basal area per acre to MPBs from 1991 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 80—The untreated plot (CP169) located at Custer Peak lost 150 trees and 122 feet^2 of basal area per acre to MPS from 1994 through 2012. Photograph shows the center of the plot taken from the plot border.

Nevertheless, because of more growing space created by the tree mortality, stand density increased to 202 feet^2 of basal area per acre (fig. 76). This trend continued through 2004 when the basal area per acre peaked on the plot at 217 feet^2 per acre even though another 25 trees per acre were killed by weather, MPBs, and Ips. From 2004 through 2012 the mortality caused by MPBs was rather constant at 10 feet^2/acre/year of basal area. As a result of MPBs from 1987 through 2012, 147 trees, 101 feet^2 of basal area, and 9,543 board feet of timber per acre were lost. Similar to the other high density untreated plots the remaining trees in the border plot were heavily infested by MPBs in 2013 indicating that more loss was going to occur (table 3, fig. 81).

All of the plots having tree densities ranging from 150 to 220 feet^2 of basal area per acre and exposed to MPBs from 1987 through 2012 experienced high tree mortality. This impact was exemplified by the untreated plot located on the Black Hills Experimental Forest as in 8 years from 2004 through 2012, 99 percent of its peak basal area per acre (162 feet^2) per acre and 78 percent of its peak board foot volume (13,344) per acre were lost to MPBs. Also, the Bear Mountain One plot BM1155 shows that in some areas in the Hills, considerable MPB-caused tree mortality in dense stands was occurring in the mid-1990s as nearly 14,000 board feet per acre of timber were lost from 1987 through 1995. These MPB impacts to dense stands were distributed throughout the central Hills and across a variety of biophysical settings and stand conditions (fig. 76).

Figure 81—The untreated plot (Bord199) located on the Wyoming border lost 147 trees and 101 feet^2 of basal area per acre to MPBs from 1987 through 2012. Photograph shows the center of the plot taken from the plot border.

Plots With Establishment and Maximum Densities Ranging From 120 to 150 Feet^2 of Basal Area Per Acre

Brn146—In 1985, the tree density of a stand located east of Highway 385 along Halso Road, just south of the junction of 385 and the Custer Peak Road, was 146 feet^2 of basal area per acre (figs. 47, 50, 55). This untreated 110-year-old stand was located at Brownsville on a common juniper habitat type with a site index of 74 and an SDI of 243. The plot had 167 trees per acre and they had a mean DBH of 12.7 inches, which had a standard deviation of 1.92 inches (table 1). A low level of MPB activity was occurring in the area when the plot was established and through 1990, when 3 trees per acre were killed by MPBs, the basal area per acre increased to 148 feet^2 per acre (fig. 82). From this peak basal area density in 1990, the tree mortality caused by MPBs and expressed by basal area was quite linear at 6.4 feet^2/acre/year, arriving at 8 feet^2 per acre in 2012. During this period the majority of the 148 trees, 161 feet^2 of basal area, and the 19,579 board feet per acre that were lost on the plot to MPBs occurred (table 3, fig. 83).

BM2127 and **BM2121**—In proximity of the Bear Mountain One plots, a treated plot with 127 feet^2 of basal area and a treated plot with 121 feet^2 of basal area per acre were established (figs. 47, 57, 62). Both Bear Mountain Two plots were located on a common juniper habitat type with a site index of 64 and contained 87-year-old trees (table 1). The denser of the two plots (BM2127) contained 381 trees per acre that had a mean DBH of 7.8 inches (1.26 inch standard deviation) and an SDI of 257. The second plot (BM2121) had an SDI of 232 created by 282 trees per acre with a mean DBH of 8.9 inches that had a 1.67 inch standard deviation. In contrast to other plots, both of these plots were thinned in 1997, further reducing their density. BM2121 had 42 trees and 15 feet^2 of basal area per acre removed and BM2127 had 49 trees and 13 feet^2 of basal area per acre removed (fig. 82). In 1997 there were MPBs in the area and by 2004, 102 trees per acre were killed by MPBs in the plot that started with 127 feet^2 of basal area per acre and 137 trees per acre were killed in the plot that started with 121 feet^2 of basal area per acre. As both plots had approximately 120 feet^2

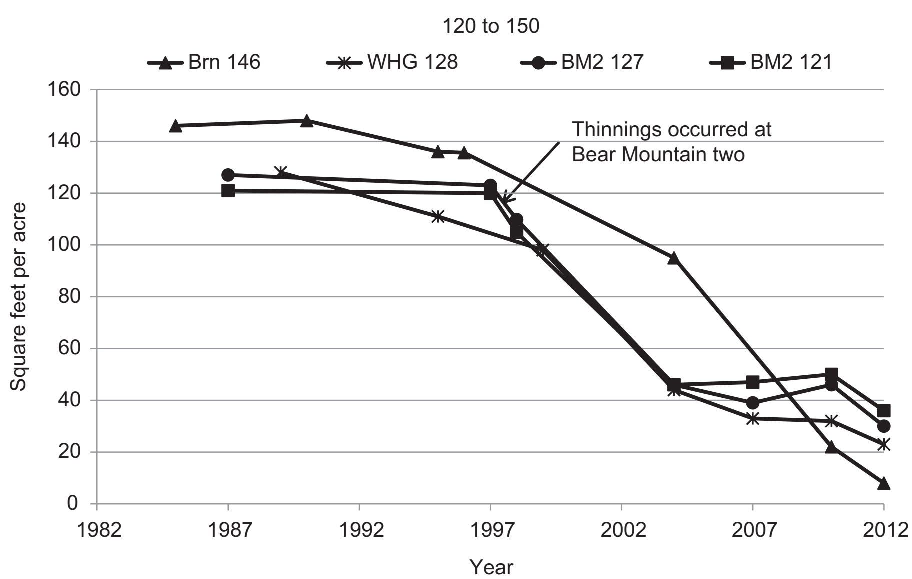

Figure 82—These plots contained tree densities ranging from 120 to a maximum of 150 feet^2 of basal area per acre. They were located at Brownsville (Brn146), White House Gulch (WHG128), and Bear Mountain Two (BM2127 and BM2121).

Figure 83–The untreated plot (Brn146) located off of Highway 385 just south of the Custer Peak Road lost 148 trees and 161 feet^2 of basal area per acre to MPBs from 1985 through 2012. Photograph shows the center of the plot taken from the plot border.

of basal area per acre in 1997, the tree mortality in both plots expressed as basal area per acre was nearly identical at 4.1 feet^2/acre/ year (fig. 82). The mortality in both plots caused by MPBs continued to be similar through 2012 when the plot that started with 127 feet^2 of basal area per acre had 30 feet^2 of basal area per acre and had lost since establishment 252 trees, 123 feet^2 of basal area, and 6,759 board feet of timber per acre to MPBs. Similarly, the less dense plot lost 169 trees, 104 feet^2 of basal area, and 8,070 board feet per acre to MPBs through 2012, which resulted in a residual density of 36 feet^2 of basal area per acre (table 3, figs. 84, 85).

WHG128—The White House Gulch plots are situated south of the Medicine Mountain Boy Scout Camp (figs. 47, 57, 60). They were established in an 89-year-old stand located on a kinnikinnick habitat type with a stand site index of 73 (table 1). The untreated plot had a density of 128 feet^2 of basal area and 202 trees per acre, which had a mean DBH of 10.8 inches (1.33 inch standard deviation) that resulted in an SDI of 228. The stand had a low level of MPB activity in 1989 and by 1995, 32 trees per acre were killed by MPBs (fig. 82). This trend continued through 1999 when the tree density decreased to 98 feet^2 of basal area per acre because of MPBs. This rather linear loss in basal area of about 4.4 feet^2/acre/year continued through 2012 in the untreated plot at White House Gulch, with 23 feet^2 of basal area per acre remaining. From its establishment in 1989 the plot lost 160 trees, 120 feet^2 of basal area, and 11,154 board feet of timber per acre to MPBs (table 3, fig. 86).

MPBs were present in the plots that had tree densities ranging from 120 to 150 feet^2 of basal area per acre when they were established. The tree mortality caused by MPBs was rather constant after 1990 at Brownsville and White House Gulch and after 1997 at Bear Mountain Two. The White House Gulch area, as exemplified by the untreated plot, had considerable mortality caused by the MPB starting in 1989 and continuing through 2012.

Figure 84—The plot thinned (BM2127) to 127 feet^2 of basal area per acre located at Bear Mountain Two lost 252 trees and 123 feet^2 of basal area per acre to MPBs from 1987 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 85—The plot thinned (BM2121) to 121 feet^2 of basal area per acre located at Bear Mountain Two lost 169 trees and 104 feet^2 of basal area per acre to MPBs from 1987 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 86—The untreated plot (WHG128) located at White House Gulch lost 160 trees and 120 feet^2 of basal area per acre from 1989 through 2012 to MPBs. Photograph shows the center of the plot taken from the plot border.

All of the plots lost over 85 percent of their maximum basal area per acre by 2012. The Brownsville plot lost 109 percent of its maximum basal area per acre because basal area and volume continued to accumulate on residual trees as trees were killed. Thus, the amount lost could exceed the maximum amount that occurred on the plot. Also, the 19,579 board feet per acre (113 percent of maximum) lost to MPBs on the Brownsville plot was the most volume lost on any of the plots that Schmid and Mata established. These results indicate that the threshold for minimizing MPB mortality is less than the 125 feet^2 of basal area that Sartwell and Stevens (1975) suggested and Schmid and Mata (1992) set out to test.

Plots With Establishment and Maximum Densities Ranging From 80 to 125 Feet^2 of Basal Area Per Acre

EF112—The tree density of 8 plots ranged from 80 at establishment to a maximum of 125 feet^2 of basal area per acre. Of these plots, four had dramatic drops in tree density as the result of MPBs and four others had mixed and more gradual basal area losses because of MPBs. Beginning with the plots with the sudden and intense MPB-caused tree mortality, a plot located on the Black Hills Experimental Forest that started with 112 feet^2 of basal area per acre typifies this MPB-caused tree mortality trend (figs. 47, 50, 56). The plot was located on a kinnikinnick habitat type in a 95-year-old stand that had a site index of 61. After treatment the plot contained 246 trees per acre that had a mean diameter of 9.1 inches (1.97 inch standard deviation) and the stand SDI was 213 (table 1). Minimal MPB activity occurred in the plot through 1994 and the basal area peaked at 122 feet^2 per acre (fig. 87). The plot was thinned in 1998, with 14 trees per acre removed and 2 additional trees killed by Ips. Even with these trees removed and an additional 11 trees per acre killed by MPBs, the plot still contained 122 feet^2 of basal area per acre in 2008 indicating that stand growth was

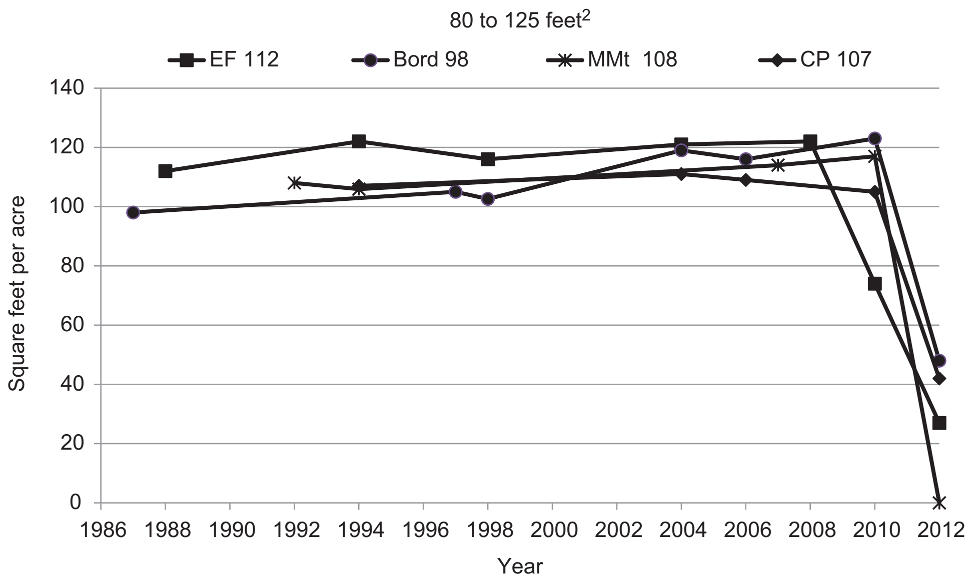

Figure 87—Eight plots contained tree densities ranging from 80 to a maximum of 125 feet^2 of basal area per acre. The four illustrated were located at Black Hills Experimental Forest (EF112), on the Wyoming Border (Bord98), Medicine Mountain (MMt108), and Custer Peak (CP107).

not readily impacted by tree mortality (fig. 87). However, from 2008 through 2012 a loss of 24 feet^2 of basal area/acre/year resulted in a residual of 27 feet^2 of basal area per acre. As a result, 164 trees, 106 feet^2 of basal area, and 8,442 board feet of timber per acre were lost to MPBs on the plot located on the Black Hills Experimental Forest (table 3). As in other locations a visual inspection of the plot in 2013 revealed that the majority of the remaining trees located on the plot were heavily infested with MPBs (table 3, fig. 88).

Figure 88—At the Black Hills Experimental Forest on plot EF112, 164 trees and 106 feet^2 of basal area per acre were lost to MPBs from 1988 through 2012. Photograph shows the center of the plot taken from the plot border.

MMt108—On the ridge west of the Medicine Mountain Road, a short distance from the Medicine Mountain and Reno Gulch Road intersection, an unthinned 104-year-old stand located on a kinnikinnick habitat type with a site index of 73 was selected for plot establishment (figs. 47, 57, 58). The untreated plot had 108 feet^2 of basal area per acre and 118 trees per acre with a mean diameter of 12.9 inches (2.23 inch standard deviation) that resulted in an SDI of 179 (table 1). Even though 14 trees per acre were killed by MPBs and 2.4 trees per acre were removed for unknown reasons, by 2010 the plot had 117 feet^2 of basal area per acre (fig. 87). Within 2 years (2012) all of the remaining trees on the plot were killed by MPBs. As a result, 112 trees, 126 feet^2 of basal area, and 16,398 board feet of timber per acre were lost to MPBs in the untreated plot at Medicine Mountain (table 3, fig. 89).

CP107—At Custer Peak a stand was thinned resulting in a residual density of 107 feet^2 of basal area per acre and an SDI of 179 (figs. 47, 50, 54). The plot was located on a common juniper habitat type that had 112-year-old trees and the site index was 64 (table 1). There were 122 trees per acre on the plot and they had a mean DBH of 12.7 inches and the DBH standard deviation was 1.42 inches. Even though 6 trees per acre were killed by MPBs at the time the plot was established in 1994, the tree density of the plot peaked at 111 feet^2 of basal area per acre in 2004 and decreased minimally to 105 feet^2 of basal area per acre by 2010 (fig. 87). By 2012 another 62 trees per acre died because of MPBs and the basal area per acre decreased to 42 feet^2. A visual inspection of the plot in 2013 indicated that the majority of the trees were infested with MPBs and would likely die in the coming year. As caused by MPBs, 81 trees, 86 feet^2 of basal area, and 9,794 board feet per acre were lost on plot CP107 (table 3, fig. 90).

Figure 89—On the untreated plot at Medicine Mountain (MMtn108), all of the 118 trees per acre were killed by MPBs from 1992 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 90—At Custer Peak on plot CP107, 81 trees and 9,794 board feet per acre were lost to MPBs from 1994 through 2012. Photograph shows the center of the plot taken from the plot border.

Bord98—The Bord98 plot was located in a stand just west of the Wyoming border on a common juniper habitat type with a site index of 65 that contained 87-year-old trees (figs. 47, 50, 52). After thinning, the plot contained 159 trees and 98 feet^2 of basal area per acre. The trees had a mean diameter of 10.7 inches (1.84 inch standard deviation) and the SDI was 176 (table 1). Tree mortality caused by Ips and weather started in the early 1990s as 23 trees per acre were killed by 1997 and 11 trees per acre were killed by MPBs in 2010 (fig. 87). The basal area peaked on the plot at 123 feet^2 per acre in 2010 and sharply decreased by 2012 to 48 feet^2 of basal area per acre as a result of 67 trees per acre being killed by MPBs. From 1987 through 2012, 83 trees, 90 feet^2 of basal area, and 11,339 board feet per acre were killed by MPBs on plot Bord98 (table 3). Again, through a visual inspection in 2013, the majority of the remaining trees were infested with MPBs (table 3, fig. 91).

Bord80—The Bord80 plot was located in 1987 just west of the Wyoming border in a stand with a common juniper habitat type, a site index of 65, and 87-year-old trees (figs. 47, 50, 52). After thinning, the plot had 80 feet^2 of basal area and 125 trees per acre that had a mean DBH of 10.8 inches (1.46 inch standard deviation) that resulted in an SDI of 142 (table 1). By 1997, 9 trees were thinned and 16 trees per acre were lost to weather and Ips (fig. 92). The thinning and tree mortality did not affect stand growth on the plot as 1.8 feet^2 of basal area/acre/year accumulated through 2010, resulting in a tree density of 122 feet^2 of basal area per acre (fig. 92). However, this endemic level of MPB mortality turned epidemic, killing 41 trees per acre and in 2 years through 2012 the tree density was 71 feet^2 of basal area per acre. Also, when inspected in 2013 the majority of the remaining trees were infested with MPBs, indicating more MPB-caused tree mortality was likely. From 1987 through 2012, 45 trees, 56 feet^2 of basal area, and 7,511 board feet of volume per acre were killed by MPBs on the plot and more loss was imminent (table 3, fig. 93).

Figure 91—At the Wyoming border, on plot Bord98 from 1987 through 2012, 83 trees and 11,339 board feet per acre were lost to MPBs. Photograph shows the center of the plot taken from the plot border.

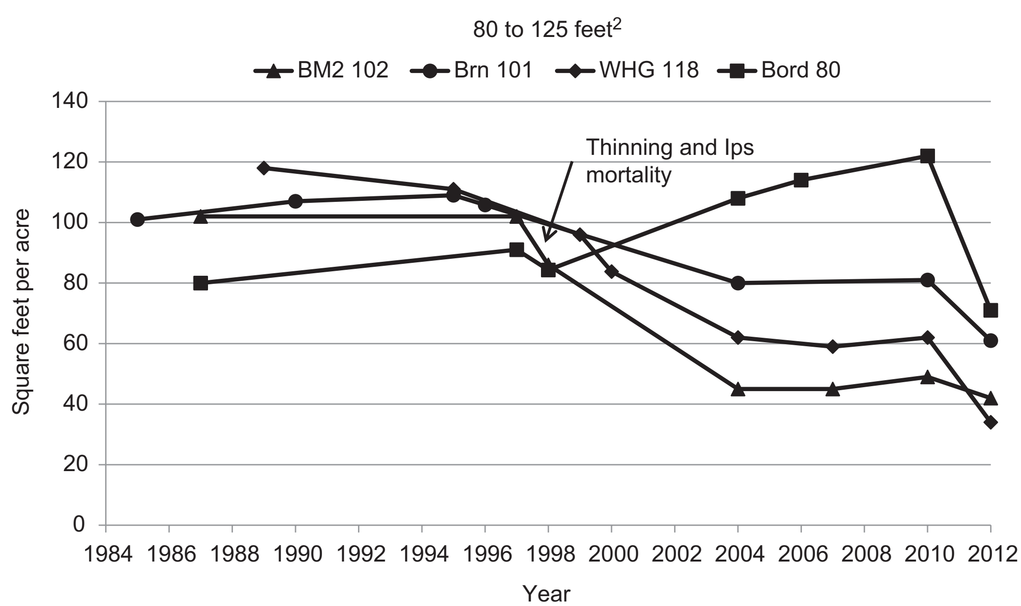

Figure 92—Eight plots contained tree densities ranging from 80 to a maximum of 125 feet^2 of basal area per acre. The four illustrated were located at Bear Mountain Two (BM2102), Brownsville (Brn101), White House Gulch (WHG118), and on the Wyoming border (Bord80).

Figure 93—On a well-represented common juniper habitat type, the Bord80 plot located on the Wyoming border lost 45 trees and 7,511 board feet per acre to MPBs from 1987 through 2012. Photograph shows the center of the plot taken from the plot border.

WHG118—At White House Gulch a thinned plot was established in 1989 that contained 118 feet^2 of basal area per acre (figs. 47, 57, 60). The stand was 89 years old growing on a kinnikinnick habitat type that had a site index of 73. After thinning, the plot contained 160 trees per acre that averaged 11.6 inches DBH (1.11 inch standard deviation) that resulted in an SDI of 203. MPBs were active in the area in the early 1990s as 19 trees per acre were killed by 1995 and in 1999, 16 trees per acre were removed through thinning; however, the basal area per acre only decreased to 111 feet^2 (fig. 92). MPB-caused tree mortality was rather constant through 2007 with 56 trees per acre killed by MPBs, as the basal area per acre reached 59 feet^2. Since no trees died through 2010, the tree density increased to 62 feet^2 of basal area per acre and subsequently plummeted to 34 feet^2 of basal area per acre in 2012, as another 28 trees per acre were killed by MPBs. As the result of MPB-caused mortality, 104 trees, 98 feet^2 of basal area, and 10,478 board feet per acre were lost on the plot even though an intermediate thinning to improve growing conditions occurred. As evident with most of the plots, the majority of the remaining trees in 2013 had high levels of MPB infestation (table 3, fig. 94).

Brn101—At Brownsville, a thinned plot was established on a common juniper habitat in a 110-year-old stand with a site index of 74 (figs. 47, 50, 55). The basal area per acre was 101 feet^2, the mean DBH of the 113 trees per acre was 12.8 inches (1.29 inch standard deviation) and the SDI was 168 (table 1). Through 2004, only 6 trees per acre were removed, 5 by thinning and 1 was killed by Ips, and the tree density increased to 109 feet^2 of basal area per acre (fig. 92). By 2010, 40 trees per acre were killed by MPBs and through 2012 another 18 trees per acre succumbed to MPBs. The result was 61 feet^2 of basal area per acre remained on the plot in 2012 and the majority if not all of the remaining 49 trees per acre had signs of MPB attacks in 2013 (fig. 91). From 1985 through 2012, 58 trees, 70 feet^2 of basal area, and 8,636 board feet per acre were lost to MPBs (table 3, fig. 95).

Figure 94—At White House Gulch on plot WHG118, 104 trees per acre and 10,478 board feet per acre were lost to MPBs from 1989 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 95—At Brownsville on plot Brn101, 58 trees and 8,636 board feet per acre were lost to MPBs from 1985 through 2012. Photograph shows the center of the plot taken from the plot border.

BM2102— A thinned plot was established at Bear Mountain Two, on a common juniper habitat type in an 87-year-old stand with a site index of 64 (figs. 47, 57, 62). After thinning, it contained 102 feet^2 of basal area and 230 trees per acre that had a mean DBH of 9.0 inches (2.45 inch standard deviation) that resulted in an SDI of 195 (table 1). In 1997, 48 trees per acre were removed by thinning and through 2007 another 97 trees per acre were killed by MPBs and the tree density decreased to 45 feet^2 of basal area per acre (fig. 92). From 2007 through 2010 no trees died and the tree density increased to 49 feet^2 of basal area per acre. Subsequently MPB infestations increased and another 15 trees per acre were killed by MPBs resulting in a stand density of 42 feet^2 of basal area per acre. As with the other plots located at Bear Mountain Two, in 2013 when the plot was visited the remaining 60 trees per acre were heavily infested with MPBs. From 1987 through 2012, 112 trees, 77 feet^2 of basal area, and 6,928 board feet per acre were killed by MPBs (table 3, fig. 96).

The 8 plots that had establishment and maximum densities ranging from 80 to 125 feet^2 of basal area per acre all had major mortality caused by MPBs. The four plots (EF112, Bord98, MMt108, and CP107) all had minimal tree mortality through 2008. Then major MPB-caused tree mortality occurred through 2012 with all 118 trees per acre (112 to MPBs) lost on plot MMt108 (table 3). Similar results occurred on plots BM2102, Brn101, and WHG118, but the MPB-caused tree mortality often started in the late 1990s and was less intense but by 2012 major tree losses had occurred. The growth dynamics of trees growing on plot Bord80 were rather unique, as the plot was thinned in 1997 and the residual trees responded with rapid growth, but in 2010 at a tree density of 122 feet^2 per acre of basal area,

Figure 96—At Bear Mountain Two on plot BM2102 from 1987 through 2012, 112 trees and 6,928 board feet per acre were lost to MPBs. Photograph shows the center of the plot taken from the plot border.

major MPB-caused tree mortality occurred. Also, these plots show how MPB-thinned stands and tree density measured by basal area actually would remain constant or increase as the residual trees had more growing space. Most importantly, these plots illustrate that as the MPB population increased in the Black Hills, stand densities as low as 100 feet^2 of basal area per acre were very susceptible to being infested and killed by MPBs.

Plots With Establishment and Maximum Densities Ranging From 80 to 100 Feet^2 of Basal Area Per Acre

MMt92—Seven plots had stand densities established and maximum densities ranging from 80 to 100 feet^2 of basal area per acre in the years 1985 through 2010. Among these seven plots, the impact MPBs had on stand dynamics was not fully consistent as trees in three plots showed some resistance to MPBs and four plots had major tree mortality caused by MPBs (fig. 97). The thinned plot containing 92 feet^2 of basal area per acre located at Medicine Mountain typifies a stand that was severely impacted by MPBs yet had a relatively low tree density (figs. 47, 57, 58, 97). The plot was established in 1992 in a 104-year-old stand growing on kinnikinnick habitat type that had a site index of 73. The mean DBH of the 95 trees per acre was 13.3 inches (1.90 inch standard deviation) and the SDI was 150 (table 1). MPBs were active in the area in the early 1990s and seven trees per acre were removed circa 1994 by thinning and two trees per acre were killed by MPBs. By 2007, eight more trees per acre were killed by MPBs and two trees per acre succumbed to other causes, as the basal area decreased to 82 feet^2 per acre. Major MPB-caused tree mortality occurred in the area and another 66 trees per acre were killed on the plot by 2010 and by 2012 only three trees and 1 foot^2 of basal area per acre remained (table 3, fig. 97). As the result of MPBs in plot MMt92, 79 trees, 100 feet^2 of basal area, and 13,453 board feet of volume per acre were lost (table 3). When visited in 2013 the remaining three trees on the plot were highly stressed and were likely to die (fig. 98).

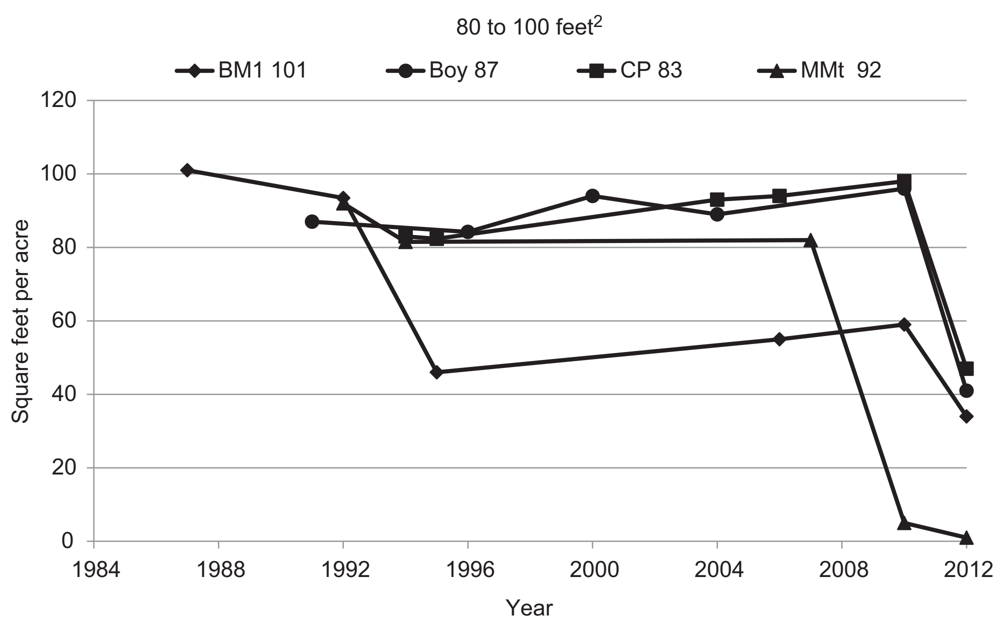

Figure 97—Seven plots contained tree densities ranging from 80 to a maximum of 100 feet^2 of basal area per acre. The four illustrated were located at Bear Mountain One (BM1101), Boy Scout Camp (Boy87), Custer Peak (CP83), and at Medicine Mountain (MMt92).

Figure 98—At Medicine Mountain, 79 trees, 100 feet^2 of basal area, and 13,453 board feet per acre were killed by MPBs on plot MMtn92. In 2012 only 3 trees and 1 foot^2 of basal are per acre remained on the plot. Photograph shows the center of the plot taken from the plot border.

BM1101—At Bear Mountain One, a 92-year-old stand, growing on a common juniper habitat type, was thinned in 1987 and again in the early-1990s when another 15 trees per acre were removed (figs. 47, 57, 61, 97). The stand had a site index of 70 and after thinning in 1987 the plot contained 170 trees per acre that had a mean DBH of 10.5 inches and a standard deviation of 1.54 inches and the stand density was 101 feet^2 of basal area per acre (table 1). Inclusive of 1987 through 1995, 78 trees per acre were killed by MPBs resulting in tree density of 46 feet^2 of basal area per acre (fig. 97). After that dramatic loss, only four trees (one by MPBs and three by other causes) per acre were killed on the plot through 2010 and the basal area per acre increased to 59 feet^2. In the next 2 years 28 trees per acre were killed by MPBs and the tree density decreased to 34 feet^2 of basal area per acre in 2012. A visual inspection in 2013 revealed that the majority, if not all, of the 38 trees per acre remaining on the plot were infested with MPBs. From 1987 through 2012, 107 trees, 85 feet^2 of basal area, and 10,044 board feet per acre were killed by MPBs (table 3, fig. 99).

Boy87—In 1991, just north of the Medicine Mountain Boy Scout Camp, a 120-year-old stand growing on a kinnikinnick habitat type was thinned (figs. 47, 57, 59). The stand had a site index of 73 and after treatment it contained 115 trees and 87 feet^2 of basal area per acre (table 1). Trees had a mean DBH of 11.8 inches (2.99 inch standard deviation) that resulted in an SDI of 150. Through 2010, 17 trees per acre were killed by MPBs and the tree density increased to 98 feet^2 of basal area per acre, then subsequently dropped to 41 feet^2 of basal area per acre in 2012, when 31 trees per acre were killed by MPBs (fig. 97). From 1991 through 2012, 62 trees, 69 feet^2 of basal area, and 8,482 board feet per acre were killed by MPBs on plot Boy87 (table 3). As was the case with most of the plots, the remaining 41 trees per acre were heavily infested by MPBs when visited in 2013 (table 3, fig. 100).

Figure 99—At Bear Mountain One, on plot BM1101, 107 trees and 10,044 board feet per acre were killed by MPBs. Photograph shows the center of the plot taken from the plot border.

Figure 100—North of the Medicine Mountain Boy Scout Camp on plot Boy87 from 1991 through 2012, 62 trees and 8,482 board feet per acre were lost to MPBs. Photograph shows the center of the plot taken from the plot border.

CP83—At Custer Peak, a 112-year-old stand growing on a common juniper habitat type was thinned to a residual tree density of 83 feet^2 of basal area per acre (figs. 47, 50, 54). The remaining 83 trees per acre had a mean DBH of 13.6 inches (1.40 inch standard deviation) and the SDI was 136 (table 1). The development of the trees on this plot in the face of MPBs was uncommonly similar in intensity and timing to how Boy87 developed (fig. 97). With minimal (2 per acre) trees killed by MPBs through 2010, the stand density increased to 98 feet^2 of basal area per acre before plummeting to 47 feet^2 of basal area per acre in 2012, as 41 trees per acre were killed by MPBs (fig. 97). From plot establishment in 1994 through 2012, 44 trees, 54 feet^2 of basal area, and 6,912 board feet per acre were killed by MPBs and the remaining 36 trees per acre were heavily infested by MPBs when visited in 2013 (table 3, fig. 101).

Brn81—Three of the seven plots that had establishment densities of 80 to a maximum of 100 feet^2 showed some resistance to MPBs. Exemplifying this trend was plot Brn81. The plot was established at Brownsville on a common juniper habitat type in a 110-year-old stand with a site index of 74 (figs. 47, 50, 55). After thinning, the plot had 81 feet^2 of basal area and 112 trees per acre that had a mean DBH of 11.5 inches (1.54 inch standard deviation) that resulted in an SDI of 140 (table 1). Even though MPBs were active in the area, it wasn’t until 2004 that two trees per acre were killed by MPBs and prior to then, three trees per acre were removed by thinning and two trees per acre were killed by other causes, as the tree density increased to 95 feet^2 of basal area per acre (fig. 102). An additional 47 trees per acre were killed by MPBs through 2012 and the stand density decreased to 64 feet^2 of basal area per acre. MPBs were very active in the Brownsville area and the majority, if not all, of

Figure 101—At Custer Peak on plot CP83 from 1994 through 2012, 44 trees, 54 feet2 of basal area, and 6,912 board feet per acre were lost to MPBs. Photograph shows the center of the plot taken from the plot border.

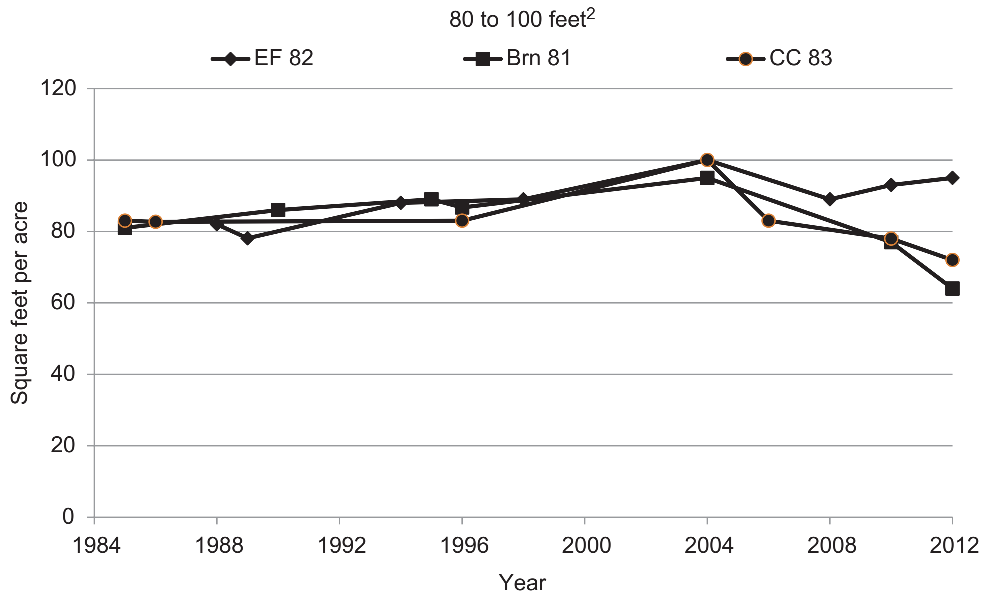

Figure 102—Seven plots contained tree densities ranging from 80 to a maximum of 100 feet^2 of basal area per acre. The three illustrated were located at the Black Hills Experimental Forest (EF82), Brownsville (Brn81), and at Custer Crossing (CC83).

the 58 trees per acre on the plot in 2013 were infested with MPBs. From 1985 through 2012, 49 feet^2 of basal area, 49 trees, and 5,472 board feet per acre were killed by MPBs on plot Brn81 (table 3, fig. 103).

CC83—A single thinned plot was established at Custer Crossing. The plot was located on the west side of Highway 385, south of the Nemo Road, and just north of where Road 539 and Highway 385 intersect (figs. 47, 50, 53). The 99-year-old stand was growing on a common juniper habitat type that had a site index of 61. After thinning, the plot had 83 feet^2 of basal area and 92 trees per acre that had a mean DBH of 12.8 inches (1.51 inch standard deviation) and an SDI of 137 (table 1). Only 35 trees per acre were killed by MPBs at Custer Crossing from 1985 through 2012 (fig. 102). With this moderate amount of tree mortality, the tree density on the plot peaked in 2004 when the basal area per acre was 100 feet^2. On plot CC83 by 2012, 42 feet^2 of basal area and 5,172 board feet per acre were killed by MPBs. At Custer Crossing through 2012, MPBs had mixed effects as they did on many of the stands in the area. When visited in 2013 a large number of the remaining 54 trees per acre on the plot were infested with MPBs, making the likelihood that a large amount of tree mortality would occur in the future (fig. 104). However, if the MPB populations would have not been so high in the area, the 83 to 103 feet^2 of basal area per acre that occurred on the plot might have been more resistant to MPBs (table 3, fig. 102).

EF82—On the Black Hills Experimental Forest a 95-year-old stand was thinned to 82 feet^2 of basal area per acre (figs. 47, 50, 56). The plot was established on a kinnikinnick habitat type with a site index of 61. After thinning, the plot had 128 trees per acre that had a mean DBH of 10.8 inches (1.91 inch standard deviation) that resulted in an SDI of 145 (table 1). The trees in this plot were showing some resistance to attack by MPBs. From establishment through 2012, only 22 trees per acre were killed by MPBs and the basal area of the plot peaked at 101 feet^2 per acre in 2004 (fig. 102). During this period, three trees per acre were killed by Ips and weather and six trees per acre were removed by thinning.

Figure 103—At Brownsville, on plot Brn81, 58 trees per acre remained in 2012 of the 112 per acre that the plot started with. However nearly all of these remaining trees were infested with MPBs when the plot was visited in 2013. Photograph shows the center of the plot taken from the plot border.

Figure 104—At Custer Crossing on plot CC83, 35 trees per acre and 5,172 board feet per acre were killed by MPBs from 1985 and 2012. Photograph shows the center of the plot taken from the plot border.

Also, after reaching a low in 2008 of 89 feet^2 of basal area per acre, tree density increased and in 2012 it was 95 feet^2 of basal area per acre, greater than the tree density at establishment. Again, the stand structures exemplified by EF82 showed some resistance to MPBs, as through 2012 only 17 feet^2 of basal area and 1,522 board feet per acre were killed by MPBs. Nevertheless the stand and plot were overwhelmed by the high population of MPBs in the area and in 2013 the majority of the trees on the plot were infested with MPBs (table 3, fig. 105).

Two contrasting outcomes of MPBs attacking stands with tree densities ranging from 80 to 100 feet^2 of basal area per acre occurred within the Black Hills. The plots at the Black Hills Experimental Forest, Brownsville and Custer Crossing, showed some resistance to MPBs as their tree densities ranged from 80 to 100 feet^2 of basal area per acre. Plots with the same range of densities located at Custer Peak, Medicine Mountain, and near the Boy Scout Camp experienced high levels of mortality from 2007 through 2012 after a couple of decades of minimal tree kill by MPBs. The plot with the same tree density range that had the most unique outcome over the years due to MPBs was BM1101 located at Bear Mountain One. Upon establishment in 1987, MPBs killed many trees through 1995, decreasing the tree density to 46 feet^2 of basal area per acre even though it had a second thinning. Subsequently, there was no appreciable mortality for the next 15 years, indicating the structure had some resistance to MPBs. However, after 2010 the trees on this plot experienced a major infestation of MPBs.

Figure 105—On the Black Hills Experimental Forest, plot EF82 was thinned to 82 feet^2 per acre. The trees on the plot showed some resistance to MPBs as only 17 feet^2 of basal area and 1,522 board feet were lost from 1988 through 2012. Photograph shows the center of the plot taken from the plot border.

Plots With Establishment and Maximum Densities Ranging From 80 to 90 Feet^2 of Basal Area Per Acre

WHG80—Four plots had tree densities ranging from 80 feet^2 of basal area per acre at establishment to a maximum of 90 feet^2 of basal area per acre (figs. 47, 57, 60). At White House Gulch a thinned plot was established that contained 80 feet^2 of basal area per acre. The stand was 89 years old growing on a kinnikinnick habitat type that had a site index of 73. After thinning, the plot contained 119 trees per acre that had a mean DBH of 11.1 inches (1.42 inch standard deviation) that resulted in an SDI of 141 (table 1). Tree mortality caused by MPBs was light, as three trees per acre were killed by MPBs through 2004 and seven trees per acre were removed by a thinning (fig. 106). Another 15 trees per acre were killed by MPBs by 2007 and the tree density decreased to 72 feet^2 of basal area per acre. By 2010, 3 more trees per acre were killed and through 2012, 37 more trees per acre were killed by MPBs and the tree density decreased to 32 feet^2 of basal area per acre. In 2013 when the plot was visited the remaining 32 trees per acre were highly infested with MPBs indicating that more trees were likely to die. From 1989 through 2012, 58 feet^2 of basal area, 58 trees, and 6,750 board feet per acre were killed by MPBs (table 3, fig. 107).

Boy79—Just north of the Medicine Mountain Boy Scout Camp, a 120-year-old stand growing on a kinnikinnick habitat type was thinned (figs. 47, 57, 59). The stand had a site index of 73 and after treatment it contained 139 trees and 79 feet^2 of basal area per acre. Trees on the plot had a mean DBH of 10.2 inches (2.42 inch standard deviation) that resulted in an SDI of 143 (table 1). Circa 1996, 29 trees and 14 feet^2 of basal area per acre were removed in a thinning (fig. 106). Tree growth on the plot responded to the thinning and only 1 tree per acre was killed by MPBs through 2000, as the tree density increased to 80 feet^2 of basal area per acre. The basal area per acre on the plot increased to 85 feet^2 in 2004 and

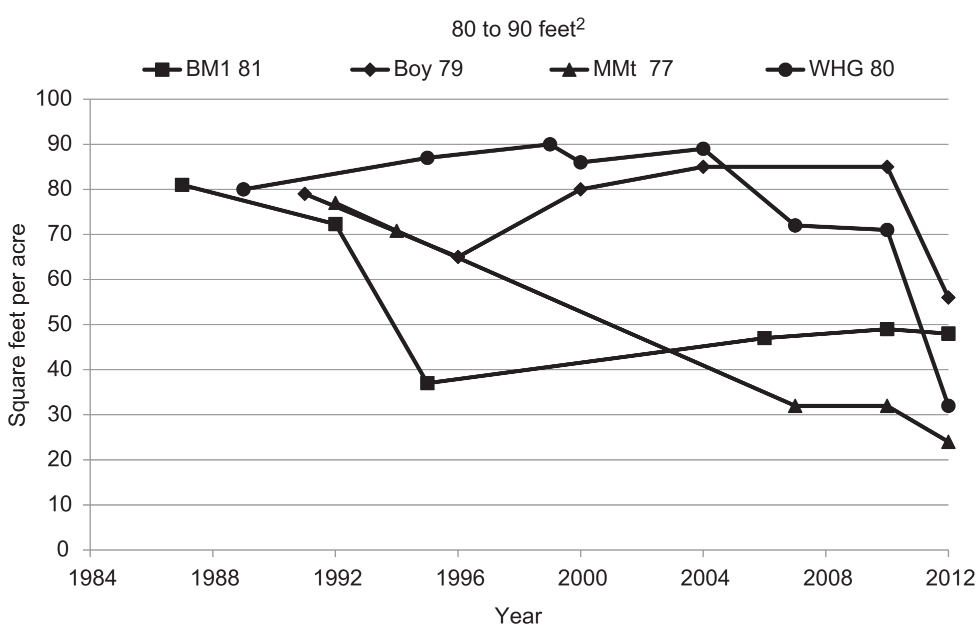

Figure 106—Four plots contained tree densities ranging from 80 to a maximum of 90 feet^2 of basal area per acre. The plots were located at Bear Mountain One (BM181), Boy Scout Camp (Boy79), Medicine Mountain (MMt77), and White House Gulch (WHG80).

Figure 107—At White House Gulch, the trees on WHG80 showed some resistance to MPBs but by 2013 only 32 trees per acre remained and they were heavily infested with MPBs. Photograph shows the center of the plot taken from the plot border.

remained there through 2010 as many trees were likely infested with MPBs. Immediately, 15 trees per acre were killed by MPBs and through 2012, 31 more trees per acre were killed by MPBs and the tree density decreased to 56 feet^2 of basal area per acre. When visited in 2013, the majority of the remaining 59 trees per acre were heavily infested with MPBs. From 1991 through 2012, 44 feet^2 of basal area, 47 trees, and 4,589 board feet per acre were killed by MPBs even though two thinnings occurred to modify the impacts of MPBs (table 3, fig. 108).

MMt77—In 1992, a 104-year-old stand at Medicine Mountain was thinned (figs. 47, 57, 58). Located on a kinnikinnick habitat type with a site index of 73, after treatment the plot had 77 feet^2 of basal area per acre and 74 trees per acre that had a mean diameter of 13.8 inches (2.36 inch standard deviation), which resulted in a stand SDI of 125 (table 1). In the early to mid-1990s, seven trees per acre were removed in a thinning, one tree per acre was lost to MPBs, and five trees per acre were killed by weather and Ips (fig. 106). By 2007 another 34 trees per acre were killed by MPBs and the tree density decreased to 32 feet^2 of basal area per acre and remained at that level through 2010. In 2012 the density decreased to 24 feet^2 of basal area per acre as seven more trees per acre were killed by MPBs. Through 2012, and by that time, 60 feet^2 of basal area, 43 trees, and 8,749 board feet per acre were killed by MPBs (table 3, fig. 109). As at many of the other plots, MPBs had infested nearly all of the 17 trees per acre remaining on the plot in 2013.

Figure 108—North of the Medicine Mountain Boy Scout Camp on plot Boy79, 47 trees and 4,589 board feet per acre were lost to MPBs from 1991 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 109—At Medicine Mountain on plot MMt77, 43 trees and 8,749 board feet per acre were killed by MPBs from 1992 through 2012. Photograph shows the center of the plot taken from the plot border.

BM181—The Bear Mountain One plots were located on a site with a common juniper habitat type and 92-year-old trees (figs. 47, 57, 61). The site index was estimated at 70 and the trees were exposed to MPBs circa 1990. A plot was thinned to a residual tree density of 81 feet^2 of basal area and 146 trees per acre. The SDI was 148, mean DBH was 10.1, and standard deviation of the DBH mean was 1.52 inches. As with the other treated plots located at Bear Mountain One, BM181 was thinned circa 1992, removing 16 trees per acre and also during this period 3 trees per acre were killed by Ips (fig. 106). Through 1995, 71 trees per acre were killed by MPBs and the basal area decreased to 37 feet^2 per acre. Only two trees per acre were killed by MPBs through 2010 on the plot as the basal area increased to 49 feet^2 per acre and subsequently began decreasing to 48 feet^2 of basal area per acre in 2012 as two more trees per acre were killed by MPBs. Many of the 49 remaining trees per acre were infested with MPBs when the plot was visited in 2013. Nevertheless, the remaining 48 feet^2 per acre of basal area remaining in 2012 showed some resistance to MPB attack. From 1987 through 2012, 50 feet^2 of basal area, 77 trees, and 4,969 board feet per acre were killed by MPBs (table 3, fig. 110).

Plots with establishment and maximum tree densities ranging from 80 to 90 feet^2 of basal area tended to have three different trajectories in how they were impacted by MPBs. The plots at White House Gulch and near the Boy Scout camp had minimal tree mortality until 2005 and then large amounts of trees were killed by MPBs and the tree densities decreased rapidly. At Medicine Mountain, tree mortality was more constant from the time the plot was established in 1992 through 2012, with 2.7 feet^2 of basal area/acre/year killed. In contrast, the plot located at Bear Mountain One had a high number of trees killed by MPBs in the

Figure 110—At Bear Mountain One, on plot BM181, 77 trees and 4,969 board feet per acre were lost but the remaining trees, even though several showed signs of MPB infestation, the plot showed some resistance to MPB attacks. Photograph shows the center of the plot taken from the plot border.

mid-1990s and minimal tree mortality through 2012 as did both plots BM1155 and BM1101 located nearby. Even though the initial tree densities expressed as basal area per acre were similar among the plots, board foot volumes lost to MPBs ranged from 4,589 on the plot located near the Boy Scout Camp to over 8,700 on the plot located at Medicine Mountain. These plots with tree densities of 80 feet^2 of basal area per acre showed little resistance to attack by mountain pine beetles. But when the tree density at Bear Mountain One decreased to 37 feet^2 of basal area per acre because of MPBs and thinning, few trees were lost or infested until 2013.

Plots With Establishment and Maximum Densities Ranging From 60 to 90 Feet^2 of Basal Area Per Acre

Bord60—Four plots had establishment and maximum tree densities ranging from 60 to 90 feet^2 of basal area per acre. In general, tree densities increased on all four plots and then from 2004 through 2012 large amounts of trees and volume were lost to MPBs (fig. 111). The Bord60 plot was located just west of the Wyoming border on a common juniper habitat type with a site index of 65 that contained 87-year-old trees (figs. 47, 50, 52). After thinning, the plot had 60 feet^2 of basal area and 93 trees per acre. The trees had a mean DBH of 10.9 inches (1.40 inch standard deviation) that resulted in an SDI of 107 (table 1). MPBs were active in the area and one tree per acre was killed on the plot in the early 2000s and another two trees per acre were killed in 2010 (fig. 111). Even with these trees killed the tree density measured as basal area per acre increased to 90 feet^2 by 2010 indicating that trees on the plot were showing some resistance to attack by MPBs. However, by 2012, MPB-caused mortality and infestations increased and 11 trees per acre were lost. A visual inspection in 2013 revealed that many of the remaining 59 trees per acre were infested and they too would likely succumb to MPBs. From 1987 through 2012, 19 feet^2 of basal area, 14 trees, and 2,654 board feet per acre were killed by MPBs (table 3, fig. 112).

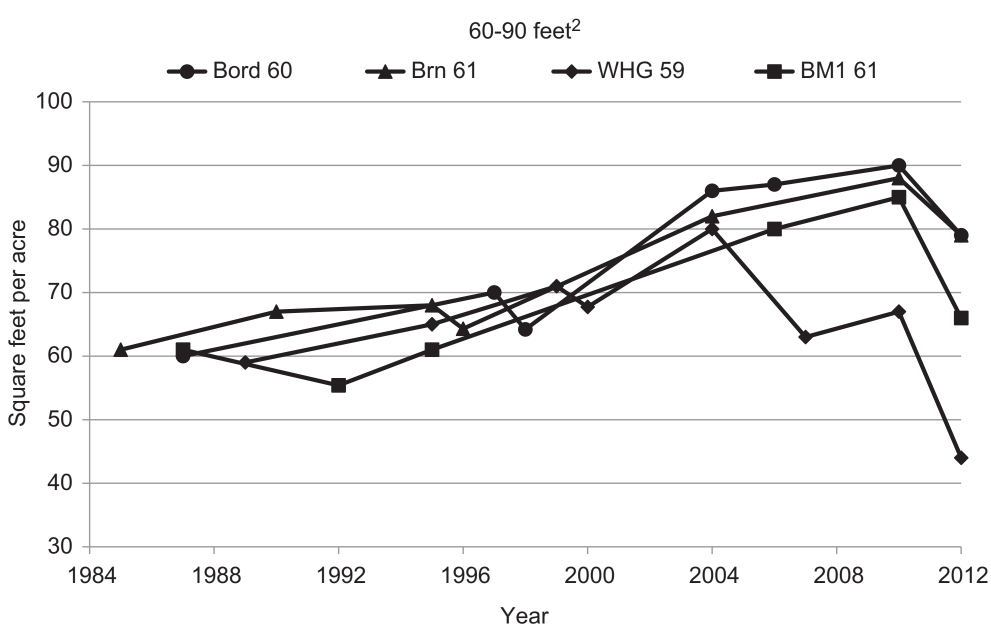

Figure 111—Four plots contained tree densities ranging from 60 to a maximum of 90 feet^2 of basal area per acre. The plots were located on the Wyoming border (Bord60), at Brownsville (Brn61), White House Gulch (WHG59), and Bear Mountain One (BM161).

Figure 112—On the Wyoming Border, on plot Bord60, 14 trees and 2,654 board feet per acre were killed by MPBs by 2012. In addition, as this tree illustrates, many were infested by MPBs when the plot was visited in 2013. Photograph shows the center of the plot taken from the plot border.

Brn61—At Brownsville, a plot was thinned on a common juniper habitat in a 110-year-old stand with a site index of 74 (figs. 47, 50, 55). After treatment, the plot had 61 feet^2 of basal area and 73 trees per acre that had a mean DBH of 12.4 inches (1.05 inch standard deviation) that resulted in an SDI of 103 (table 1). From 1985 through 2010, nine trees per acre were killed on plot Brn61 by MPBs as the tree density steadily increased to 88 feet^2 of basal area per acre (fig. 111). MPBs were very active in the area and by 2012 the basal area per acre on the plot decreased to 79 feet^2 and a visual inspection in 2013 showed the majority if not all of the remaining 56 trees per acre were infested with MPBs. From 1985 through 2012, 13 feet^2 of basal area, 11 trees, and 1,611 board feet per acre were killed by MPBs (table 3). Possibly if the MPB population was not so high near Brownsville from 2008 through 2012 and the adjacent landscape had been treated equally to this plot, the mortality caused by MPBs on plot Brn61 might have been less (table 3, fig. 113).

BM161—A thinned plot containing 61 feet^2 of basal area was established at Bear Mountain One (figs. 47, 57, 61). The plot was located on a site with a common juniper habitat type and 92-year-old trees. The site index was estimated at 70 and MPBs were active in the area by 1990. The plot had 93 trees per acre that had a mean DBH of 11.0 inches (2.22 inch standard deviation), which resulted in an SDI of 108 (table 1). Even though plots BM1155, BM1101, and BM181, located nearby, had large (100s of trees per acre) numbers of trees killed by MPBs right after they were established, plot BM161 only had 17 trees per acre killed by 1995, indicating that a stand density of 60 feet^2 of basal area showed some resistance to MPB attack (fig. 111). The tree density peaked at 85 feet^2 of basal area in 2010

Figure 113—At Brownsville on plot Brn61, 11 trees and 1,611 board feet per acre were killed by MPBs from 1985 through 2012. Although many trees were infested with MPBs, in 2013 when the plot was visited, the trees on the plot showed some resistance to MPBs. Probably the trees on the plot would have fared much better if the MPB population was not so high in the area. Photograph shows the center of the plot taken from the plot border.

and with the high population of MPBs in the area, 5 more trees per acre died by 2012 and in 2013 the remaining 57 trees per acre showed heavy infestations of MPBs. Also worth noting, the volume on this plot peaked at 11,299 board feet per acre even though its basal area ranged from 61 to 85 feet^2 per acre. From 1987 through 2012 on plot BM161, 28 feet^2 of basal area, 23 trees, and 3,796 board feet per acre were killed by MPBs (table 3, fig. 114).

WHG59—At White House Gulch a thinned plot was established that contained 59 feet^2 of basal area per acre (figs. 47, 57, 60). The stand was 89 years old growing on a kinnikinnick habitat type that had a site index of 73. After thinning, the 69 trees per acre on the plot had a mean DBH of 12.5 inches (1.73 inch standard deviation) that resulted in an SDI of 98. Through 2004, five trees per acre were killed by MPBs and the tree density peaked at 80 feet^2 of basal area per acre (fig. 111). By 2007 another 15 trees per acre were killed by MPBs and removed. With no tree mortality occurring on the plot through 2010 the basal area per acre increased from 2007. By 2012 another 17 trees per acre were killed by MPBs and the tree density reached 44 feet^2 per acre, the lowest of the plots in this cluster (fig. 111). From 1989 through 2012, 43 feet^2 of basal area, 31 trees, and 6,168 board feet per acre were killed by MPBs (table 3, fig. 115). Most likely this result was related to the high population of MPBs in the area and the 32 trees per acre remaining on the plot were heavily infested with MPBs in 2013.

Figure 114—At Bear Mountain One on plot BM161 from 1987 through 2012, 23 trees and 3,796 board feet per acre were lost to MPBs. However, compared to the other forest structures created at Bear Mountain One, trees on this plot did show some resistance to MPBs. Photograph shows the center of the plot taken from the plot border.

Figure 115—At White House Gulch on plot WHG59, 31 trees and 6,168 board feet per acre were killed by MPBs from 1989 through 2012. Photograph shows the center of the plot taken from the plot border.

The trees on plots Bord60, Brn61, and BM161 with establishment and maximum tree densities ranging from 60 to 90 feet^2 of basal area per acre showed some resistance to MPBs until their tree densities neared 90 feet^2 of basal area per acre (fig. 111). This 25 to 30 feet^2 increase in basal area per acre under less extreme levels of MPB populations may have not caused the trees on the plots to be susceptible to MPB attack. However, at White House Gulch when the tree density reached 80 feet^2 of basal area per acre, the plot became very susceptible to MPBs and suffered the greatest losses to MPBs of this cluster of plots with rather low tree densities. As a result, densities of 60 feet^2 to 90 feet^2 of basal area per acre showed some resistance to MPBs. However, there was a major exception at White House Gulch where plot WHG59 with tree density ranging from 59 feet^2 to 80 feet^2 of basal area per acre had major MPB-caused tree mortality (figs. 111, 115).

Plots With Establishment and Maximum Densities Ranging From 45 to 80 Feet^2 of Basal Area

Three plots (Boy68, EF44, and EF61) had establishment and maximum tree densities ranging from 45 to 80 feet^2 of basal area. The trees on all of these plots showed considerable resistance to attack by MPBs even though high populations of the insects were close to if not passing through the plot or even landing on the trees. But, surprisingly, from 1988 through 2012, only a total of 11 trees per acre were killed by MPBs on the 3 plots combined. Contributing to this outcome on Boy68, the plot was thinned circa 1996 reducing the tree density to 50 feet^2 of basal area per acre.

Boy68—Just north of the Medicine Mountain Boy Scout Camp, a 120-year-old stand growing on a kinnikinnick habitat type was thinned (figs. 47, 57, 59). The stand had a site index of 73 and after treatment it contained 123 trees and 68 feet^2 of basal area per acre. Trees had a mean DBH of 10.1 inches (3.3 inch standard deviation) that resulted in an SDI of 124 (table 1). With 68 percent of the trees on the plot having DBHs between 6.8 and 13.4 inches as indicated by the standard deviation, it and Boy79 were the two most diverse plots that Schmid and Mata established. Upon establishment, two trees per acre were killed by MPBs on the plot and one tree per acre was removed for unknown reasons (fig. 116). About 1996, 36 trees per acre were removed from the plot in a thinning, increasing the mean DBH to 12.1 inches. From 1996 through 2012, the plot had basal area growth of 1.7 feet^2/acre/year, resulting in a tree density of 77 feet^2 of basal area per acre. During these 16 years only one tree per acre was killed by MPBs. As a result of MPBs from 1991 through 2012 on plot Boy68, three trees, 3 feet^2 of basal area, and 364 board feet per acre were lost to MPBs (table 3, fig. 117).

EF61—On the Black Hills Experimental Forest, a 95-year-old stand was thinned to a tree density of 61 feet^2 of basal area per acre (figs. 47, 50, 56). The plot was established on a kinnikinnick habitat type with a site index of 61. After treatment the plot had 79 trees per acre that had a mean DBH of 10.9 inches (1.67 inch standard deviation) that resulted in an SDI of 104 (table 1). Immediately after establishment, four trees per acre were killed by MPBs; by 1994, one tree per acre was killed by weather; and in 1998, one tree per acre was removed for unknown reasons (fig. 116). Basal area growth from 1989 through 2012 was very constant on plot EF61, as 0.81 feet^2/acre/year as two trees per acre were killed during this period by MPBs. Most likely influenced by the relatively low density occurring on the plot, only seven trees, 6 feet^2 of basal area, and 583 board feet per acre were killed by MPBs on plot EF61 from 1988 through 2012. As a result, 68 trees, 79 feet^2 of basal area, and 9,147 board feet per acre remained on the plot in 2012 (table 3, fig. 118).

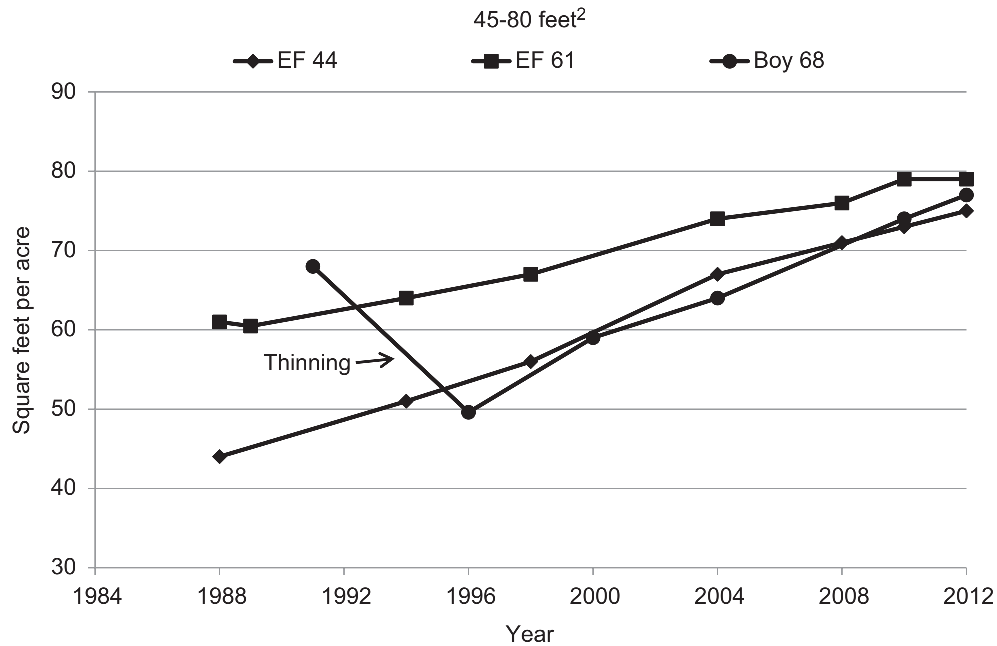

Figure 116—Three plots contained tree densities ranging from 45 to a maximum of 80 feet^2 of basal area per acre. The plots were located on the Black Hill Experimental Forest (EF44 and EF61) and near the Medicine Mountain Boy Scout Camp (Boy68). Of all of the plots Schmid and Mata established on the Black Hills that were exposed to MPBs, the trees on these three plots showed the most resistance to MPB attack.

Figure 117—North of the Medicine Mountain Boy Scout Camp on plot Boy68, 3 trees and 364 board feet per acre were lost to MPBs from 1991 through 2012. Photograph shows the center of the plot taken from the plot border.

Figure 118—The trees on plot EF61, located on the Black Hills Experimental Forest, showed considerable resistance to attack by MPBs as only 7 trees and 583 board feet per acre were lost to MPBs from 1988 through 2012. Photograph shows the center of the plot taken from the plot border.

EF44—Near plot EF61 on the Black Hills Experimental Forest, a stand was thinned to a tree density of 44 feet^2 of basal area per acre (figs. 47, 50, 56). After treatment, the plot had 71 trees per acre that had a mean DBH of 10.6 inches (1.99 inch standard deviation) that resulted in an SDI of 79 (table 1). Similar to plot EF61, basal area growth from 1988 through 2012 was very constant on plot EF44, at 1.30 feet^2/acre/year, as only one tree per acre succumbed to MPBs in 2012 and two trees per acre were killed by weather (table 3, fig. 116). As a result of these minor losses in 2012, 69 trees, 74 feet^2 of basal area, and 8,288 board feet per acre remained on plot EF44 (fig. 119).

It was remarkable that the trees in these three plots withstood the enormous number of MPBs that were attacking trees nearby. The Experimental Forest plots and the Boy Scout plot both had MPB activity in their vicinity by 2000 and high numbers of trees killed by 2006 as indicated by MPB surveys (fig. 68). At the Experimental Forest plots, MPB-caused tree mortality became noticeable in 2004, increased in 2008, and was epidemic by 2010 (figs. 69, 120). The number of trees killed in the area decreased by 2012, most likely not from the lack of MPBs but rather the lack of suitable host trees and suitable forest conditions. For example, both plot EF44 and EF61 were within 750 feet of plot EF154 that had over 300 trees per acre killed by MPBs (figs. 56, 120). The population of MPBs that attacked and killed trees in plot EF154 also tested the veracity of the EF44 and EF61 stand structures as being resistant to MPBs. In addition, freshly hatched vigorous and fit MPBs exiting from trees in plot EF154 could have easily attacked trees in plots EF44 and EF61, but did not (Amman and Logan 1998; Byers 2000; Negrón and Fettig 2014; Progar et al. 2014).

Figure 119—The trees on plot EF 44, located on the Black Hills Experimental Forest, showed excellent resistance to MPBs as only one tree per acre was killed by MPBs from 1988 through 2012. Photograph shows the center of the plot taken from the plot border.

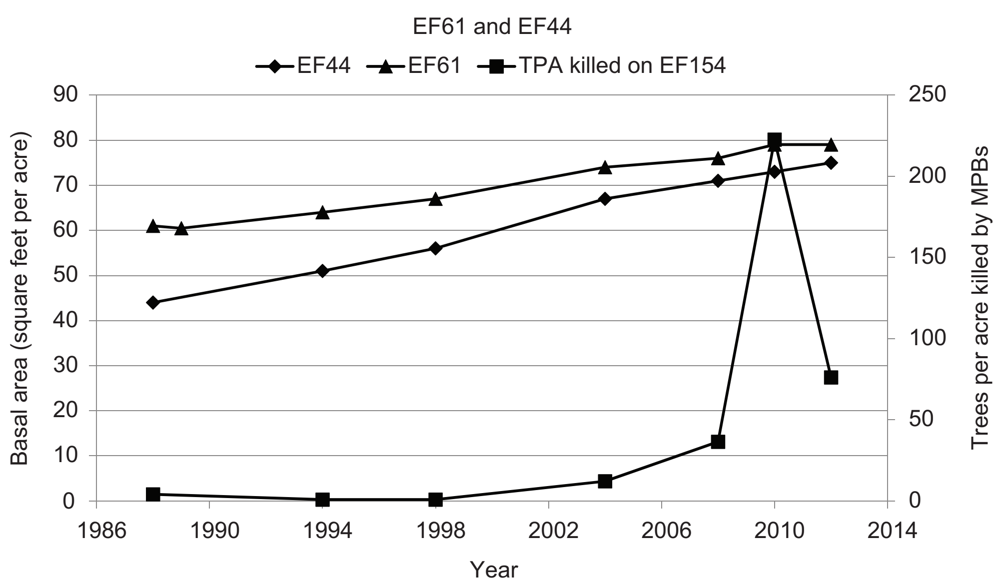

Figure 120—The trees on plots EF44 and EF61 located on the Black Hills Experimental Forest, showed outstanding MPB resistance. Within approximately 750 feet of both of these plots, intense MPB attacks occurred on plot EF154 where over 300 trees per acre (TPA) were killed in 2010 (see fig. 56).

Similarly, the trees in plot Boy68 were minimally impacted by MPBs (fig. 121). This plot had a common border with plot Boy168, which had 172 trees per acre killed by MPBs, and the remaining 157 trees per acre were heavily infested with insects when they were visited in 2013 (fig. 59). Very likely the thinning that occurred after the plot was established, reducing the tree density to 50 feet^2 of basal area per acre, contributed to this positive outcome. Plot Boy79 was also thinned but its density quickly exceeded 80 feet^2 of basal area per acre and subsequently in 2010 major tree mortality caused by MPBs occurred.

It is uncertain why tree density measured by basal area per acre has such a good relationship when defining risk and hazard of MPBs attacking trees. Sartwell and Stevens, Miller and Keen, Amman and Cole, Schmid and Mata, and numerous others have used this metric in describing bark beetle dynamics. Wind, air temperature, humidity, bark temperature, and other unknown variables are constrained by stand density and will be discussed later. The MPB epidemic occurring in the Black Hills beginning in earnest in 2000 has been one of the largest and most severe since 1900 and provided a large and intense MPB population to attack trees on the 35 plots. As a result, it appears that tree densities below 80 feet^2 of basal area per acre are resistant to attack by MPBs. Higher densities did show some resistant to attack but trees on plots Boy68, EF44, and EF61 showed remarkable resistance to MPBs when trees on plots nearby were nearly or totally killed by MPBs (figs. 120, 121).

Crook Mountain Plots With Establishment and Maximum Densities Ranging From 84 to 176 Feet^2 of Basal Area

In natural systems there is invariably an outcome that is contrary to the expected or not readily related to outcomes of similar conditions. This was the case of how MPBs impacted the forests located north and east of Deadwood and in particular by those represented by the Crook Mountain plots (figs. 47, 50, 51). These plots were established in 1986 and located on a site with a bur oak habitat type and a site index of 66. In the 100-year-old stand, 3 thinned

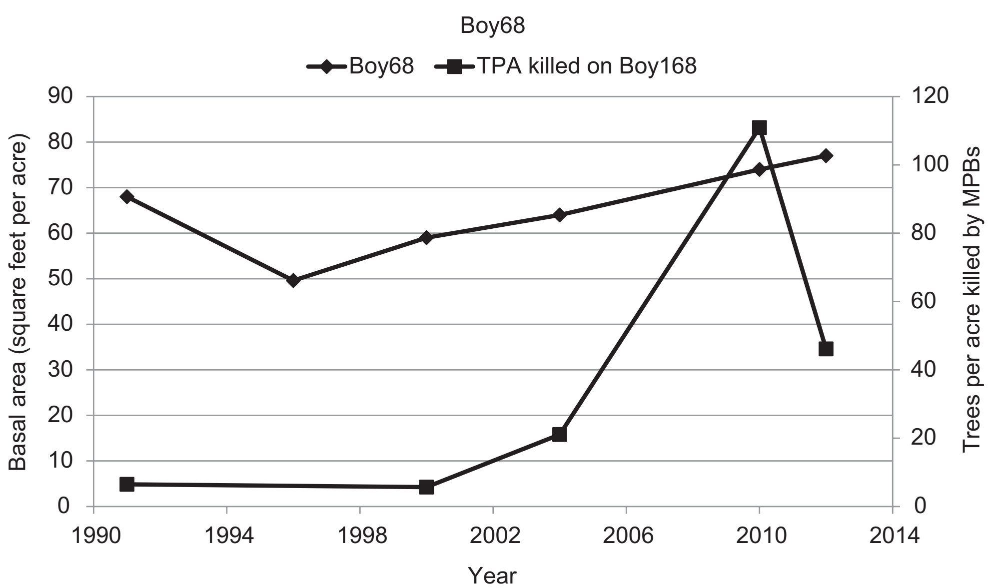

Figure 121—The trees on plot Boy68 showed outstanding resistance to MPB attack. This resistance was extraordinary as plot Boy168, which has a common border with Boy68, had over 110 trees per acre (TPA) killed in 2010 (see fig. 59).

plots were established at 84, 104, and 119 feet^2 of basal area per acre and an untreated plot was established that had a tree density of 158 feet^2 of basal area per acre. Being a bur oak habitat type, the site had abundant ground-level vegetation, which was indicative of a site having a moister microclimate than most of the stands where the other plots were located.

CMt84—Plot CMt84 was thinned to a residual basal area of 84 feet^2 of basal area per acre. The mean DBH of the trees on the plot was 13.7 inches, which had a standard deviation of 1.83 inches, and the SDI was 136 (table 1). Immediately after establishment in 1986, two trees were killed by MPBs and another tree was removed for unknown reasons. The tree density on the plot steadily increased to 89 feet^2 per acre by 1996 and 11 trees per acre were removed in a thinning, reducing the tree density to 79 feet^2 of basal area per acre (fig. 122). Through 2012, four trees per acre were killed by MPBs and six trees were killed by wind and/or snow as the tree density reached 103 feet^2 of basal area per acre. As a result of the thinning and light mortality in 2012, plot CMT84 contained 61 trees and 15,686 board feet per acre (table 3, fig. 123).

CMt104—Plot CMt104 after thinning contained 104 feet^2 of basal area per acre consisting of trees with a mean DBH of 11.9 inches (2.38 inch standard deviation) that resulted in an SDI of 179 (table 1). Similar to the trees on plot CMt84, four trees were killed by MPBs on plot CMt104 right after the plot was established. Through 1996, one tree per acre was lost to weather, one to Ips, and eight trees per acre were removed in a thinning, decreasing the density to 98 feet^2 of basal area per acre (fig. 122). From 1996 through 2012 the tree density increased to 126 feet^2 of basal area per acre, even though 13 trees per acre were lost to snow and/or wind and 7 trees per acre were killed by MPBs (table 3). At Crook Mountain, on plot CMt104, the MPBs caused minimal tree mortality and in 2012, 107 trees and 16,374 board feet per acre remained on the plot (fig. 124).

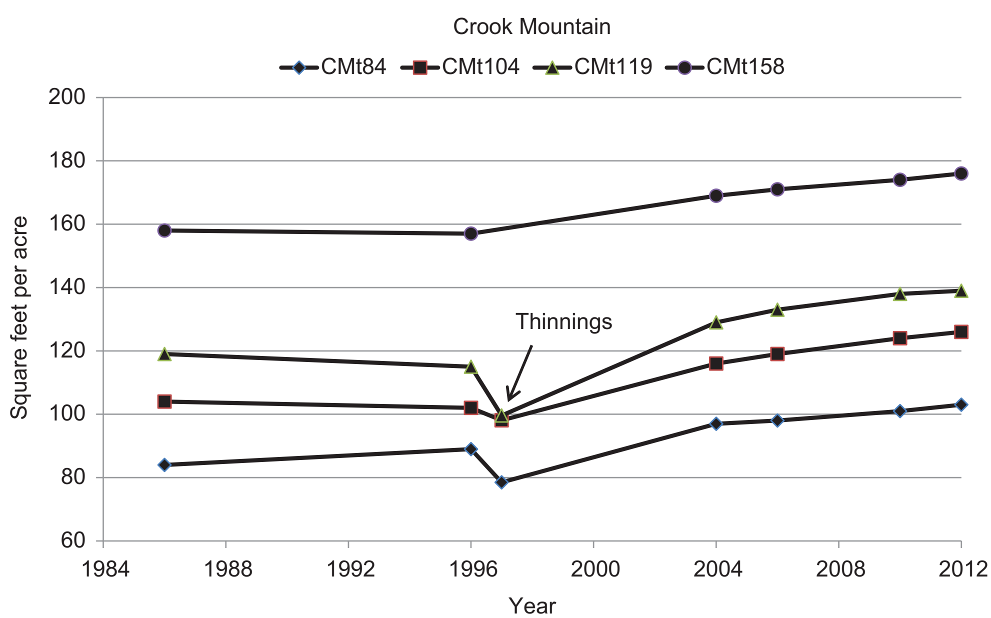

Figure 122—At Crook Mountain, four plots were established in 1986 with tree densities ranging from 84 to 154 feet^2 per acre of basal area. Contrary to the other 35 plots located in the Black Hills, these plots did not experience appreciable tree mortality caused by MPBs.

Figure 123—At Crook Mountain on plot Cmt84, 61 trees and 15,686 board feet per acre occurred on the plot in 2012, as MPBs minimally impacted the trees. Photograph shows the center of the plot taken from the plot border.

Figure 124—In 2012, plot CMt104 contained 107 trees and 16,374 board feet per acre as MPBs killed few trees. Photograph shows the center of the plot taken from the plot border.

CMt119—Plot CMt119 was thinned to a density of 119 feet^2 per acre of basal area in 1986. The trees on the plot had a mean DBH of 13.7 inches and the standard deviation was 1.89 inches (table 1). The plot contained 116 trees per acre and the SDI of the plot was 193. Similar to the other plots located at Crook Mountain, MPBs were in the area when the plot was established and they killed one tree per acre on plot CMt119. In 1996, 17 trees per acre were removed from the plot in a thinning and one tree per acre was killed by weather as the tree density on the plot decreased to 100 feet^2 of basal area per acre by 1997 (fig. 122). Through 2012, three trees per acre were killed by MPBs on plot CMt119 and seven trees per acre were killed by weather and the basal area per acre increased to 139 feet^2 (table 3). With the minimal tree mortality caused by MPBs, plot CMt119 contained 89 trees and 20,785 board feet per acre in 2012 (fig. 125).

CMt158—The untreated plot established at Crook Mountain contained 158 feet^2 of basal area and 181 trees per acre and the SDI was 264. The mean DBH of the trees was 12.6 inches and its standard deviation was 2.88 inches (table 1). By 1996, three trees per acre were killed by weather and one tree per acre was killed by MPBs as the tree density decreased to 157 feet^2 of basal area per acre (fig. 122). From 1996 through 2012 the basal area per acre on the plot steadily increased to 176 feet^2 per acre even though 26 trees per acre succumbed to weather, 4 trees per acre were killed by Ips, and 2 trees per acre were killed by MPBs (table 3, fig. 122). In 2012, plot CMt158 contained 148 trees and 23,610 board feet per acre (fig. 126).

Even though MPBs did not impact the Crook Mountain plots to any degree, they were present on the plots beginning in 1986 when the plots were established and MPBs were killing trees as recently as 2010. Also, in 2013 when the plots were visited, there was evidence

Figure 125—At Crook Mountain, plot CMt119 contained 89 trees, 139 feet^2 of basal area and 20,785 board feet per acre in 2012. Photograph shows the center of the plot taken from the plot border.

Figure 126—In 2012 at Crook Mountain on plot CMt158, 148 trees per acre and 23,610 board feet per acre occurred. Photograph shows the center of the plot taken from the plot border.

of additional trees being attacked by MPBs, but there was no indication that a major infestation of MPBs on the plots was imminent. Compared to the impact MPBs had on the other 32 plots that had major tree mortality caused by the MPBs, their impact at Crook Mountain was an anomaly. This outcome was even more extraordinary as the tree densities on all 4 of these plots exceeded the densities of the other 32 plots that had major tree mortality. It could be argued that the MPB populations had not reached the Crook Mountain area but as the MPB surveys showed there were major MPB populations in the area (fig. 69). Although compared to other portions of the Black Hills, the continuity of the infestation was lower.

Forest Impacts by Mountain Pine Beetles in the Black Hills From 1985 Through 2012

It was very fortunate that the MPB study plots were established in the Black Hills and revisited several times prior to the occurrence of this latest MPB epidemic (fig. 31). Seldom is there such good pre-disturbance (e.g., wildfire, hurricane, insect, disease) data available to use in chronicling, describing, and showing the impact of such a major disturbance that has hit Black Hills' forests since 1899 (figs. 65–69). The 39 useable plots were distributed from near the northern border of the Black Hills National Forest next to Deadwood to the southern portion of the Forest just north and west of Custer (fig. 47). As a result, when the MPB populations increased across the South Dakota share of the Forest, all of the plots were readily exposed to MPBs and all of the plot locations except Crook Mountain had major tree mortality caused by MPBs but not necessarily on every plot (fig. 69).

Mountain Pine Beetle Impacts by Plot

Based on how the forests represented by the plots responded to the intense attack by MPBs, they were placed into one of seven clusters (using establishment and maximum tree density expressed as basal area per acre that occurred on the plot) that were exposed to MPBs (table 2). The Crook Mountain plots, although exposed for some unknown reason, had minimal MPB-caused tree mortality and were placed into a separate cluster (table 2). Within the plots, the first trees killed by MPBs were at Custer Crossing in 1985 and in the same vicinity MPBs first killed trees at Custer Peak in 2004 (fig. 63). Between these two dates, trees growing at all 11 areas where plots were established had some trees killed by MPBs (fig. 63). Beginning in 1987, at Bear Mountain within plot BM1155, the first major tree mortality caused by MPBs among the study plots established by Schmid and Mata commenced (fig. 127). Five plots had major tree mortality starting in 1995, 6 plots in 2004, and 11 plots in 2010.

As Schmid and Mata established the thinned and untreated plots across the Black Hills, a wide variety of tree densities expressed by basal area per acre were represented (table 1, fig. 48). At the Black Hills Experimental Forest, a plot (EF44) was established with 44 feet^2 of basal area and 71 trees per acre and an untreated plot (Bord199) on the Wyoming border contained 199 feet^2 of basal area and 462 trees per acre that characterized the density extremes. In general, as the tree density of the forest increased, more trees were killed by MPBs. The plots that contained 45 to 80 feet^2 of basal area per acre over the years they were monitored had the fewest trees killed by MPBs while those with basal areas ranging from 120 to 220 feet^2 per acre had the most trees killed (fig. 128, table 4). Some of the plots had trees removed through thinnings—which changed their structure—weather, Ips, and other agents, but these losses were inconsequential compared to those caused by MPBs.

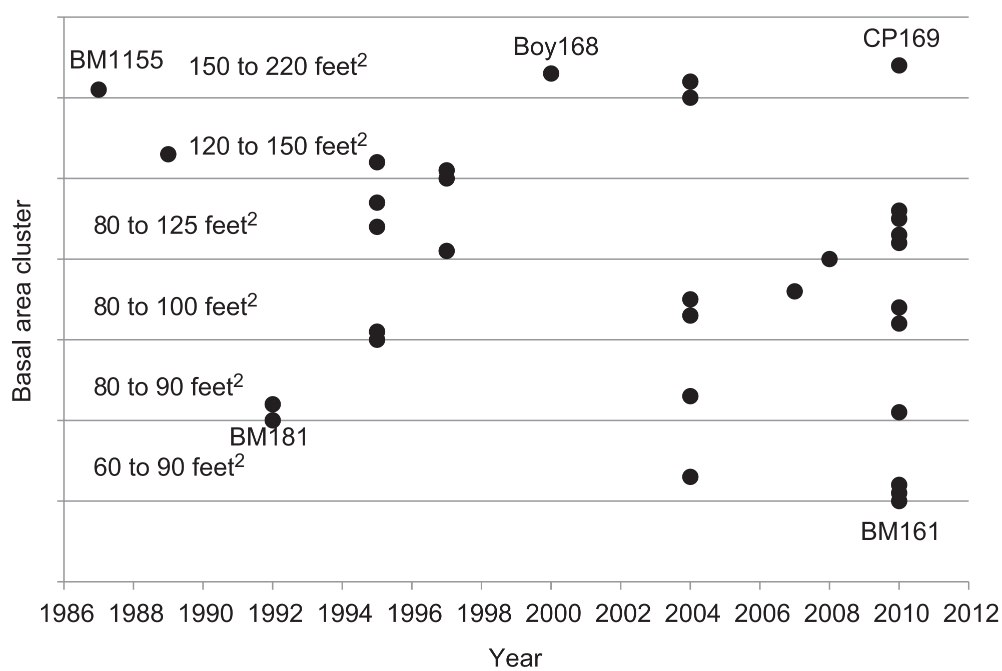

Figure 127—The date at which major tree mortality caused by MPBs began for each of the plots and the basal area cluster to which the plot belonged are shown. Plots BM1155, Boy168, CP169, BM181, and BM161 are highlighted illustrating the diversity of where and when major MPB-caused tree mortality commenced. Plots Boy68, EF44, EF61, and the Crook Mountain plots are not included as they had no major tree mortality caused by MPBs.

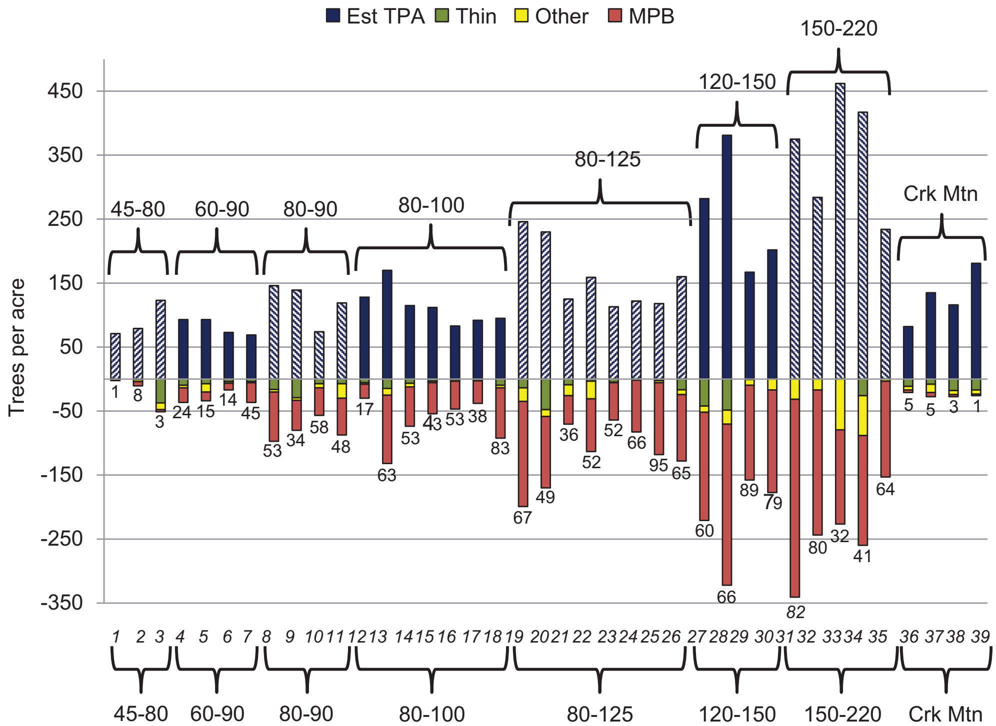

Figure 128—Shown are the trees per acre on the plots at the time they were established (positive values) and the number of trees removed in thinnings, trees per acre killed by weather, Ips, and other causes, and trees killed by MPBs after the plots were established (negative values). The plots are clustered by their density at establishment and the maximum tree density that occurred on the plot as measured in square feet of basal area per acre. The last 4 bars on the right of the graph show the minimal loss and removals that occurred at Crook Mountain. The values below the bars are the percentage of the trees per acre at establishment that were killed by MPBs and the italicized numbers below the graph indicate which plot they represent as defined in table 4.

Table 4—The basal area cluster, plot name, and the number of the plot displayed on figures 128 through 131 and figure 133.

Cluster	No.	Plot	Group	No.	Plot	Group	No.	Plot
45-80	1	EF44	80-125	19	EF112	Crk Mtn	36	CMt84
45-80	2	EF61	80-125	20	BM2102	Crk Mtn	37	CMt104
45-80	3	Boy68	80-125	21	Bord80	Crk Mtn	38	CMt119
60-90	4	BM161	80-125	22	Bord98	Crk Mtn	39	CMt158
60-90	5	Bord60	80-125	23	Brn101			
60-90	6	Brn61	80-125	24	CP107			
60-90	7	WHG59	80-125	25	MMT108			
80-90	8	BM181	80-125	26	WHG118			
80-90	9	Boy79	120-150	27	BM2121			
80-90	10	MMt77	120-150	28	BM2127			
80-90	11	WHG80	120-150	29	Brn146			
80-100	12	EF82	120-150	30	WHG128			
80-100	13	BM1101	150-220	31	EF154			
80-100	14	Boy87	150-220	32	BM1155			
80-100	15	Brn81	150-220	33	Bord199			
80-100	16	CP83	150-220	34	Boy168			
80-100	17	CC83	150-220	35	CP169			
80-100	18	MMt92						

The fewest trees killed by MPBs were at the Experimental Forest on plot EF44 (table 4, fig. 128-plot 1) where one tree per acre was killed; within 750 feet of this plot, on plot EF154 (fig. 128-plot 31), 309 trees per acre were killed (figs. 56, 76, 116, 128). Another noteworthy loss of trees from MPBs occurred at Bear Mountain (BM2127, fig. 128-plot 28) where 251 out of 381 trees per acre were killed and also on this plot, 49 trees per acre were removed in a thinning (figs. 62, 82, 128-plot 28). How MPBs impacted the trees on plot EF82 (fig. 128-plot 12) is also notable as only 22 trees per acre were killed by MPBs while in the same basal area cluster 106 trees per acre were killed on plot BM101 (fig. 128-plot 13) and 77 trees per acre were killed on plot BM181 (fig. 128-plot 8). Not only were the numbers of trees per acre killed by MPBs greater on the plots with the high tree densities, the proportion (percentage) of trees killed by MPBs was also greater on the plots with higher tree densities compared to plots with the low tree densities (fig. 128). However, 83 percent of the trees were killed at Medicine Mountain by MPBs on plot MMt92 (fig. 128-plot 18) when the basal area per acre never exceeded 92 feet^2 per acre and the majority of this mortality occurred when the tree density was 82 feet^2 per acre of basal area (figs. 97, 128). Also, at Medicine Mountain, 95 percent of the trees on plot MMt108 (fig. 128-plot 25) were killed by MPBs but the mortality occurred when the basal area was 117 feet^2 per acre; and at the Experimental Forest on plot EF154 (fig. 128-plot 31), 82 percent of the 375 trees per acre occurring on the plot were killed by MPBs (figs. 76, 128). Both in magnitude and proportion of the plots readily exposed to MPBs, only 1 percent of the trees were killed by MPBs on plot EF44 (plot 1) located on the Experimental Forest (fig. 128). The plots (36-39) located at Crook Mountain (Crk Mtn) had the fewest trees and proportions of trees killed by MPBs, which is a common thread of these data and the reason behind these outcomes is far from being understood (fig. 128).

The tree losses caused by MPBs expressed as square feet of basal area per acre had a similar trend to that of trees lost (expressed by trees per acre) to MPBs with some notable exceptions (fig. 129). Ips, weather, and thinnings reduced the basal area of the plots but MPBs accounted for the greatest losses. The basal area per acre of the plots when they were established ranged from 44 to 199 feet^2 per acre and the maximum tree densities they reached during the 28-years study ranged from 75 to 217 feet^2 of basal area per acre (table 1, figs. 48, 75). Two plots (fig. 129-plots 1, 2) located on the Black Hills Experimental Forest and one located near the Medicine Mountain Boy Scout Camp (fig. 129-plot 3) had minimum and maximum basal areas between 45 and 80 feet^2 per acre and had the least amount basal area killed by MPBs of all of the plots exposed to MPBs. Also on the Experimental Forest, plot EF154 (fig. 129-plot 31) lost 162 feet^2 of basal area, the largest amount of basal area lost to MPBs of all 35 plots experiencing tree mortality. These results were similar the losses caused by MPBs based on trees per acre, but the proportional losses differed (figs. 128, 129).

Over the 28 years the plots were monitored, trees were lost and the residual trees continued to grow and accumulate wood. As a result, the losses caused by MPBs expressed by basal area could exceed the maximum amount that ever occurred on the plot. For example, Medicine Mountain plot MMt108 (fig. 129-plot 25) lost approximately 20 trees and 18 feet^2 of basal area per acre between 1992 through 2007. Even with these losses, basal area accumulated on the remaining trees and the basal area increased to 114 feet^2 by 2007, peaked at 117 feet^2 per acre in 2010, and declined to zero in 2012 (fig. 87). As a result, 126 feet^2 of basal area were lost to MPBs on plot MMt108 or 108 percent of the maximum occurred

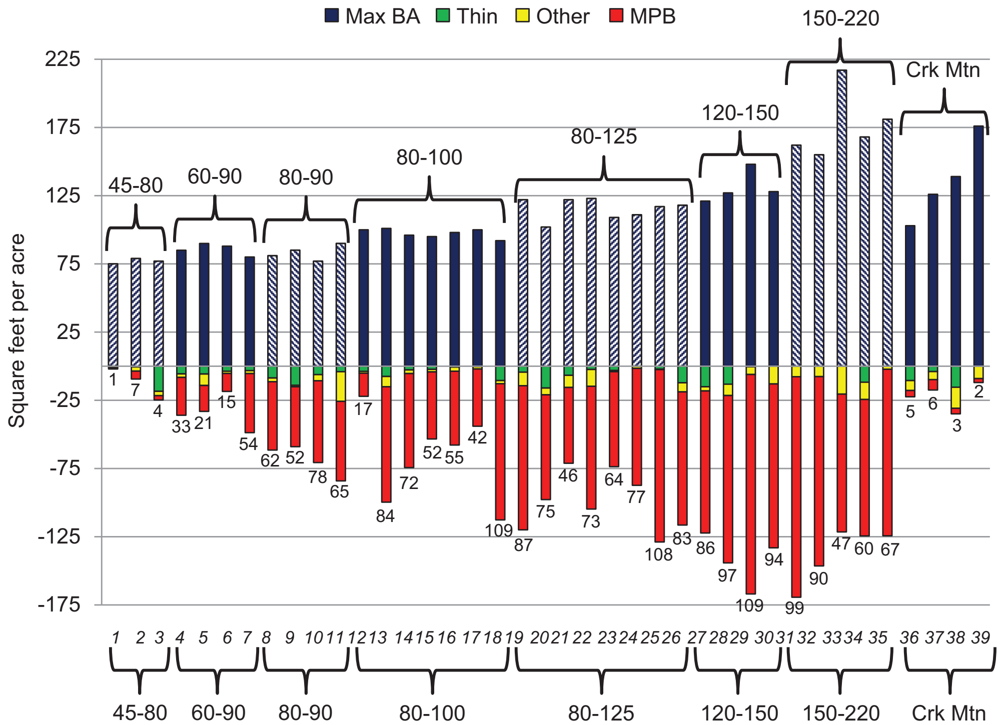

Figure 129—Shown are the maximum basal area (square feet) per acre that occurred on the plots and the square feet per acre removed in thinnings as well as square feet per acre killed by weather, Ips, and other causes; and square feet per acre killed by MPBs after the plots were established (negative values). The plots are clustered by their starting and maximum tree densities expressed by square feet of basal area per acre. The numbers below the negative bars indicate the percentage of the maximum basal area that occurred on a plot that was killed by MPBs. Because basal area continued to accumulate on the plots, the amount killed could exceed the total amount that ever occurred on the plot. These results are similar to the total yield of a stand over time when intermediate harvests are included in the estimates. The italicized numbers below the graph indicate which plot they represent as defined in table 4.

in 2010 (fig. 129-plot 25). Three additional plots had the proportion of the basal area killed by MPBs equal or exceed 100 percent of the maximum basal area that occurred on the plot. These outcomes are similar to the total volume yield of a stand when thinnings and other intermediate treatments are included so the total yield will exceed the maximum that may occur within a stand (Davis 1966). Also, at the Experimental Forest only 1 percent of the maximum basal area of plot EF44 (fig. 129-plot 1) was killed and again only 17 percent of the maximum basal area was killed by MPBs on plot EF82 (fig. 129-plot 12) indicating that the location and/or surrounding forest conditions may be influencing how MPBs have affected trees on this plot (fig. 129).

The trends of both cubic and board foot (Scribner) volume losses caused by MPBs were very similar to those of basal area among the plots and will not be further described. However, by including these data, the magnitude of the losses—especially economically—becomes abundantly clear (figs. 130, 131). At Brownsville on plot Brn146 (figs. 130, 131-plot 29), 4,371 cubic feet or 19,579 board feet per acre were lost because of MPBs. In both cases these losses exceeded the maximum that ever occurred on the plots. Also, it is worth noting that even though MPBs have not impacted the Crook Mountain plots as of yet, 23,610 board feet or 5,056 cubic feet per acre are at risk to being killed by MPBs (figs. 130, 131-plot 39).

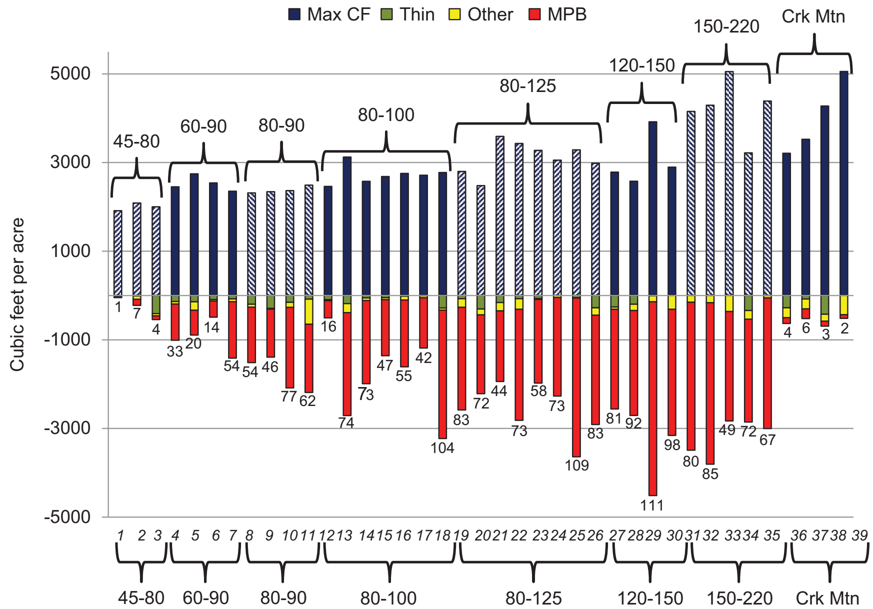

Figure 130—Shown are the maximum cubic foot volume per acre that occurred on the plots and the cubic volume per acre removed in thinnings. It also shows the volume per acre killed by weather, Ips, and other causes; and the cubic foot volume per acre killed by MPBs after the plots were established (negative values). The plots are clustered by their starting and maximum tree densities expressed by basal area per acre. The numbers below the negative bars indicate the percentage of the maximum volume that occurred on a plot that was killed by MPBs. Because volume continued to accumulate on the plots, the amount killed could exceed the total amount that ever occurred on the plot. The italicized numbers below the graph indicate which plot they represent as defined in table 4.

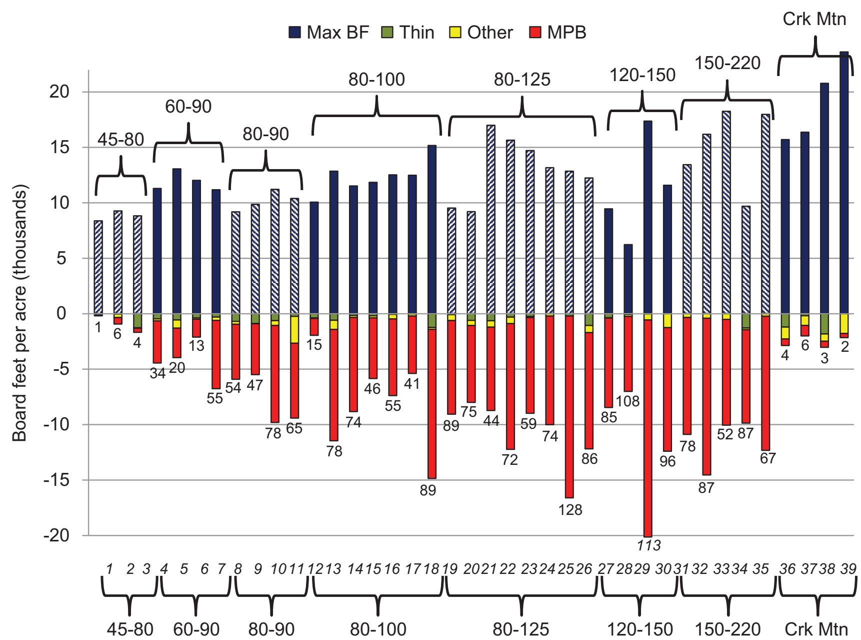

Figure 131—The maximum board foot volume per acre that occurred on the plots and the board foot volume per acre removed in thinnings; volume per acre killed by weather, Ips, and other causes; and board foot volume per acre killed by MPBs after the plots were established (negative values). The plots are clustered by their starting and maximum tree densities expressed by basal area per acre. The numbers below the negative bars indicate the percentage of the maximum volume that occurred on a plot that was killed by MPBs. Because volume continued to accumulate on the plots, the amount killed could exceed the total amount that ever occurred on the plot. The italicized numbers below the graph indicate which plot they represent as defined in table 4.

Stand Density Index and Mountain Pine Beetle Losses

The tree density measured both by SDI and square feet of basal per acre varied widely among the different plots when major MPB-caused tree mortality began. For example, at White House Gulch in 2004, major tree mortality started when the tree basal area per acre was 80 feet^2 and the SDI was 124. In contrast, in the same year, major tree mortality started on the Wyoming border when the SDI was 393 and the basal area was 220 feet^2 per acre (table 4, fig. 132). These contrasting outcomes were most likely related to the MPB populations in the area and MPB abundance (figs. 69, 132).

Plots EF44, EF61, and Boy68 had few trees killed (1 to 6 trees per acre) by MPBs as their tree densities ranged from 45 to 80 feet^2 of basal area per acre and their SDI maximums (2012) ranged from 119 to 125 (fig. 133-plots 1-3). The next cluster of plots had tree densities ranging from 60 to 90 feet^2 of basal area and their maximum SDIs ranged from 124 to 139 (fig. 133-plots 4-7). Most notably was plot WHG59, which lost 31 trees per acre or 45 percent of the trees the plot started with to MPBs and the SDI was 124 (figs. 132, 133-plot 7), less than the SDI 125 observed on plot EF61, which lost only 6 trees per acre or 8 percent of the number the plot started with. Similarly, the SDI on plot Boy68 peaked in 2012 at 123 and only 3 trees per acre were lost to MPBs or 3 percent of the trees that occurred when it was established in 1991 (fig. 133-plot 3).

The relationship between SDI and MPB-caused tree mortality was more definitive, with a notable exception, in the next cluster of plots with tree densities ranging from 80 to 90 feet^2 of basal area per acre (fig. 133-plots 8-11). Plots BM181, WHG80, and Boy79 had

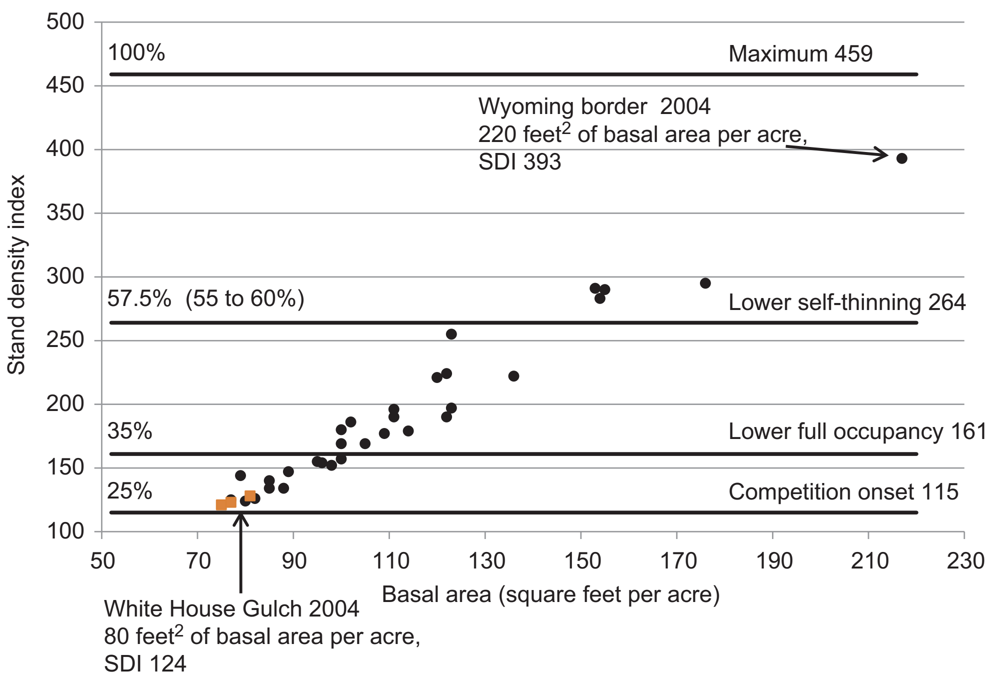

Figure 132—Stand density index (SDI) and associated stand density expressed as basal area per acre at which major tree mortality caused by MPBs are illustrated. (Crook Mountain plots are excluded as they did not experience much mortality). Yellow squares are the peak SDI and associated basal area per acre for the three plots that were subjected to MPBs but had minimal tree mortality. The maximum SDI for Black Hills ponderosa pine (459) was modified from Long and Shaw's (2005) estimate of 450. Also shown are the SDIs for onset of competition (25% max SDI), lower limit of full site occupancy (35% max SDI), and lower limit of self-thinning (57.5%—the center of the 55 to 60% max SDI).

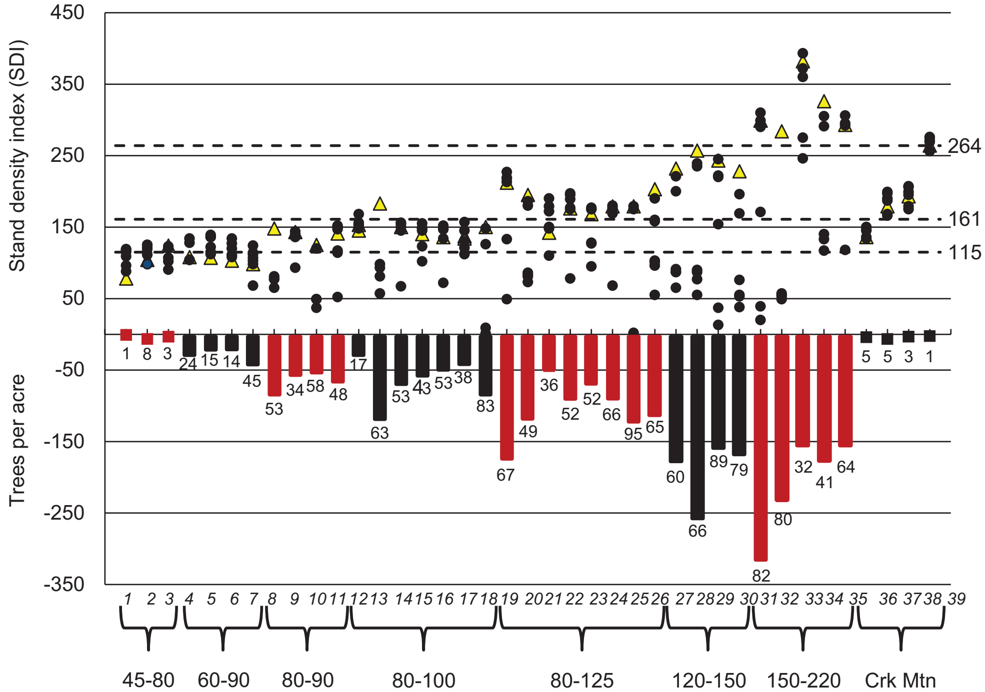

Figure 133—The stand density indices (SDI) that occurred on each of the plots from the time they were established through 2012 varied considerably. The yellow triangles indicate the SDI on each plot when they were established and the negative bars show the number of trees per acre that were killed by MPBs on each plot. The plots are clustered by their starting and maximum tree densities expressed by square feet of basal area per acre. The last four plots on the right of the graph show the minimal loss that occurred at Crook Mountain. The values below the bars are the percentage of the trees that were killed by MPBs and the italicized numbers below the graph indicate which plot they represent as defined in table 4. The three horizontal dashed lines show the SDI thresholds for onset of competition (115), lower limit of full site occupancy (161), and lower limit of self-thinning (264).

peak SDIs ranging from 143 to 152 and all had major MPB-caused mortality, giving rise to the suggestion that SDIs within this range were susceptible to MPB attack. However, within this cluster of plots, MMt77 had MPB-caused mortality commencing when the SDI was 125—very similar to the SDIs occurring on plots EF44, EF61, and Boy68, which had few trees killed by MPBs. Stand densities ranging from 45 to 80 feet^2 of basal area per acre were resistant to MPB attack and having SDIs ranging from 119 to 125, giving rise to the suggestion that SDIs in the range of 119 to 125 were also resistant to attack. As discussed above, plots with SDIs of 124 (WHG59) and 125 (MMt77) had a large number of trees killed by MPBs with WHG59 loosing 31 trees per acre (45 percent) and MMt77 loosing 45 trees per acre (58 percent), reinforcing the notion that basal area is more telling than SDI of describing MPB risk and establishing target stand conditions. Nevertheless, a possible generality revealed in these SDI data is that the onset of competition (SDI 115) threshold also would be a target for MPB resistance (fig. 133). (See Appendix A for how SDI reflected the MPB-caused mortality on each of the plots.) As illustrated by the impacts the MPBs made on individual plots, similar trends were evident among the plot density clusters.

Mountain Pine Beetle Impacts by Density Cluster (Feet^2 of Basal Area Per Acre Cluster)

Minimal changes in stand density measured by basal area per acre resulted in striking differences in the number of trees killed by MPBs. The cluster of plots with densities ranging from 45 to 80 feet^2 of basal area per acre had a mean of 4 trees killed per acre while a 15 feet^2 minimum increase and a 10 feet^2 change in maximum basal area, resulted in over a fourfold increase in the mean number of trees killed to 19 trees per acre in the cluster of plots that had densities ranging from 60 to 90 feet^2 of basal area per acre (fig. 134). Similarly, a 20 feet^2 change in minimum basal area densities per acre resulted in over a mean of 56 trees killed per acre while the maximum density stayed the same at 90 feet^2 of basal area per acre between the cluster with densities of 60 to 90 feet^2 of basal area per acre and those with densities ranging from 80 to 90 feet^2 of basal area per acre (fig. 134). The clusters with the highest density (120 to 220 feet^2 of basal area per acre) had a mean of over 180 trees per acre killed by MPBs. Although the cluster of plots with densities ranging from 150 to 220 feet^2 of basal area per acre had a mean of over 200 trees killed per acre by MPBs, the proportion killed was less than the proportion killed in the plots that had densities of 120 to 150 feet^2 of basal area per acre (fig. 134). Even though the differences in stand densities among the plot clusters were minimal, the changes in number of trees killed per acre were rather striking.

In 2012, a mean of 77 feet^2 per acre of basal area was alive on the plots that had densities ranging from 45 to 80 feet^2 per acre of basal area, which was only exceeded by the amount of basal area alive on the plots at Crook Mountain that were minimally impacted by MPBs (fig. 135). These results suggest that stands with densities ranging from 45 to 80 feet^2 of basal area per acre show considerable resistance to attack by MPBs (fig. 135). The plots

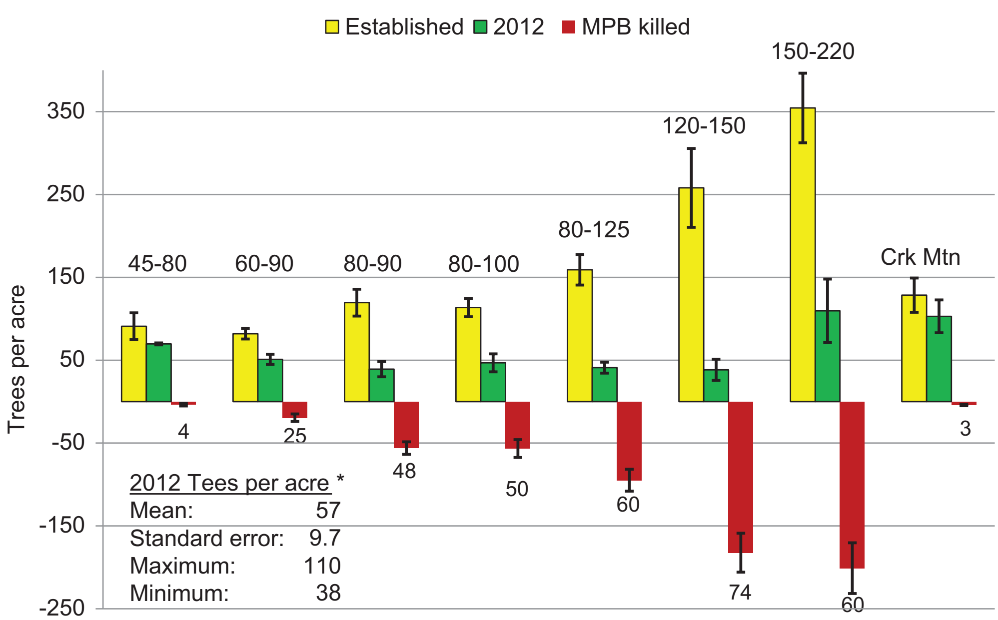

Figure 134—Shown are the mean trees per acre for each basal area cluster (e.g., 45–80, 80–100, 150–220) at the time they were established in 2012 and the trees per acre killed by MPBs (negative values) from the time the plots were established (1985–1991) through 2012. The bars are the standard errors of the means and the values below the bars are the percentage of the trees killed by MPBs. *2012 trees per acre summary does not include Crook Mountain.

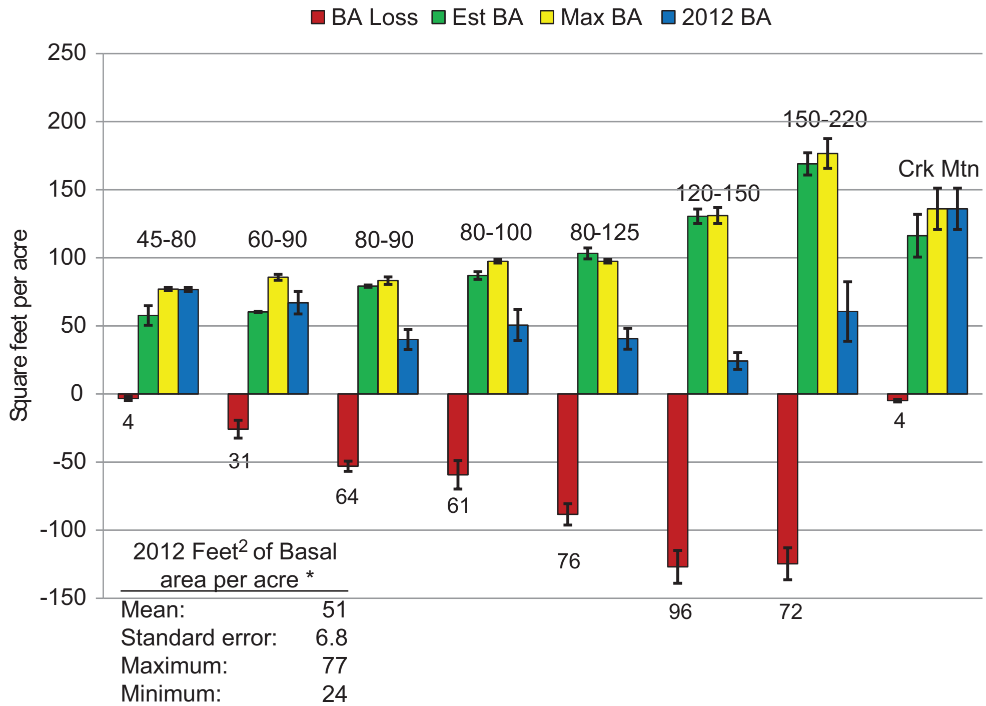

Figure 135—Shown are the mean basal area per acre in square feet for each basal area cluster when established, maximum, in 2012, and the basal area killed by MPBs (negative values) from the time the plots were established (1985–1991) through 2012. The bars are the standard errors of the means and the numbers below the bars indicate the mean proportion of the maximum basal area per acre that occurred on the plot that was killed by MPBs. *2012 feet^2 of basal area per acre summary does not include Crook Mountain.

with tree densities ranging from 120 to 150 feet^2 per acre of basal area had the least amount of basal area alive in 2012 (mean of 24 feet^2 of basal area per acre), the most killed (mean of 127 feet^2 of basal area per acre), and the largest proportion killed (96 percent). Notable about this finding was that the plots with higher densities had less basal area killed both proportionally and in magnitude (fig. 135).

The mean peak SDI of the plots (i.e., basal area cluster 45–80) with the least MPB-caused mortality was 123. Just an increase of 10 SDI points to 133 resulted in the 60–90 basal area cluster's mean of 20 trees per acre killed by MPBs or 25 percent of the amount the plot had when established (fig. 136). Another increase of just over 10 SDI points to 142 (basal area cluster 80–90) resulted in a mean of 56 trees per acre killed by MPBs or 48 percent of those that occurred on the plot when it was established (fig. 136). These data give rise to the suggestion that stands with SDIs ranging from 102 to 122 show considerable resistance to MPB attack and those with SDIs ranging from 104 to 133 showed some resistance. These SDI values were much lower than the 230 to 270 SDI ranges Cochran et al. (1993) and the 245 to 365 SDI ranges Oliver (1995) suggested were the upper limits for reducing ponderosa pine losses to bark beetles. As data reported here when the SDI increased from 139 to 324, MPB-caused mortality also increased and plots with a mean SDI of 240 were highly susceptible to attack by MPBs, below where self-thinning (264) occurs and above the SDI where a stand is fully occupied (161) (fig. 136).

With the exception of the Crook Mountain plots, the most volume expressed by both cubic feet and board feet alive in 2012 occurred on plots with basal areas ranging from 60

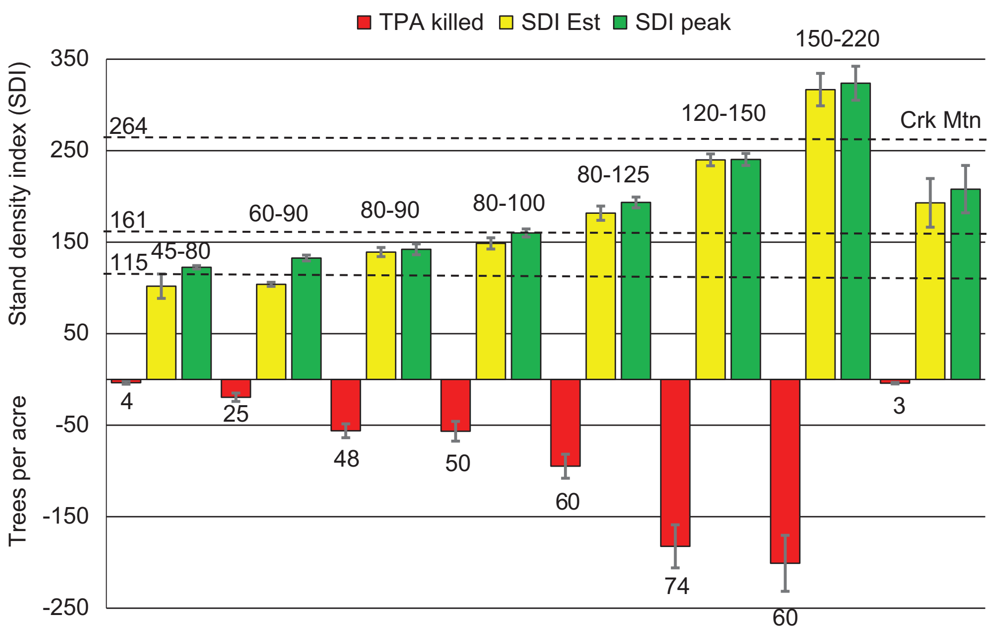

Figure 136—Shown are the mean stand density indices (SDI) for each basal area cluster (e.g., 45–80, 80–100, 150–220) at the time they were established (Est) and the mean peak SDI that occurred in each cluster. Also shown are the trees per acre (TPA) killed by MPBs (negative values) from the time the plots were established (1985–1991) through 2012. The bars are the standard errors of the means and the values below the bars are the mean percentage of trees killed by MPBs in each cluster. The horizontal dotted lines indicate the SDI thresholds for lower self-thinning (264), lower full occupancy (161), and competition onset (115).

to 90 feet^2 of basal area per acre (means of 2,434 feet^3 and 8,968 board feet per acre). The plots with tree densities of 120 to 150 feet^2 of basal area per acre lost the most volume to MPBs and the board foot losses exceeded 100 percent of the maximum that occurred on the plots (figs. 137, 138). A subtle trend noticeable among the different basal area clusters was that the impact MPBs had on the plots with 150 to 220 feet^2 of basal area per acre was less than the cluster of plots that had densities ranging from 120 to 150 feet^2 of basal area per acre. The standard errors of the loss means overlapped between the two high density clusters indicating the means were not statistically different (figs. 137, 138).

A relatively strong relationship (unadjusted R^2 of 0.77) occurred between the midpoint of each basal area cluster and the mean trees per acre killed by MPBs within each cluster (fig. 139). The relationship tended to be rather linear from 60 through 110 feet^2 of basal area per acre and reinforced the notion that tree densities from 40 to 90 feet^2 of basal area per acre were somewhat resistant to attack by MPBs. Also, this relationship shows how dramatic the number of trees killed by MPBs increased as stand density increased from 60 to 100 feet^2 per acre of basal area. Stand densities in the range of 100 feet^2 of basal area were usually considered resistant to attack by MPBs (Alexander 1987; Sartwell and Stevens 1975; Schmid and Mata 1992; Schmid et al. 1994). Using mean basal area per acre killed by MPBs as the dependent variable, the decrease in MPB impacts at the highest density was more pronounced than using trees per acre (fig. 140). Also, these data show that within stand densities from 60 to 100 feet^2 of basal area per acre, for every square foot increase in stand density approximately an additional 1 square foot of basal area was killed by MPBs (fig. 140).

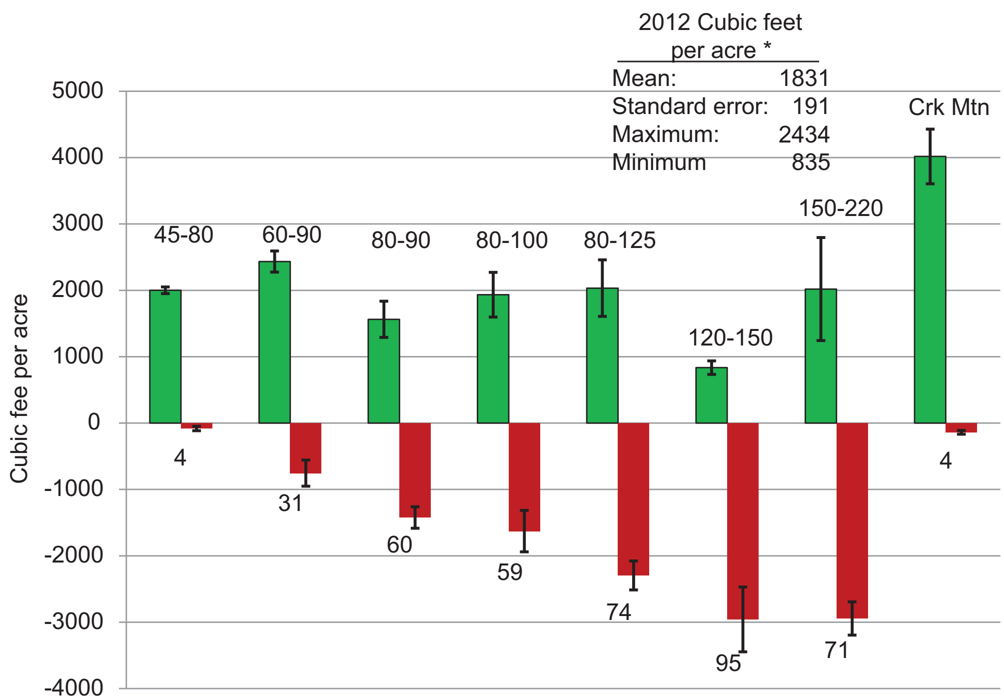

Figure 137—Shown are the mean volume in cubic feet for each basal area cluster (e.g., 45–80, 80–100, 150–220) in 2012 and the volume killed by MPBs (negative values) from the time the plots were established (1985–1991) through 2012. The bars are the standard errors of the means and the numbers below the bars indicate the mean proportion of the maximum cubic feet per acre that occurred on the plot that was killed by MPBs. *2012 cubic feet per acre summary does not include Crook Mountain.

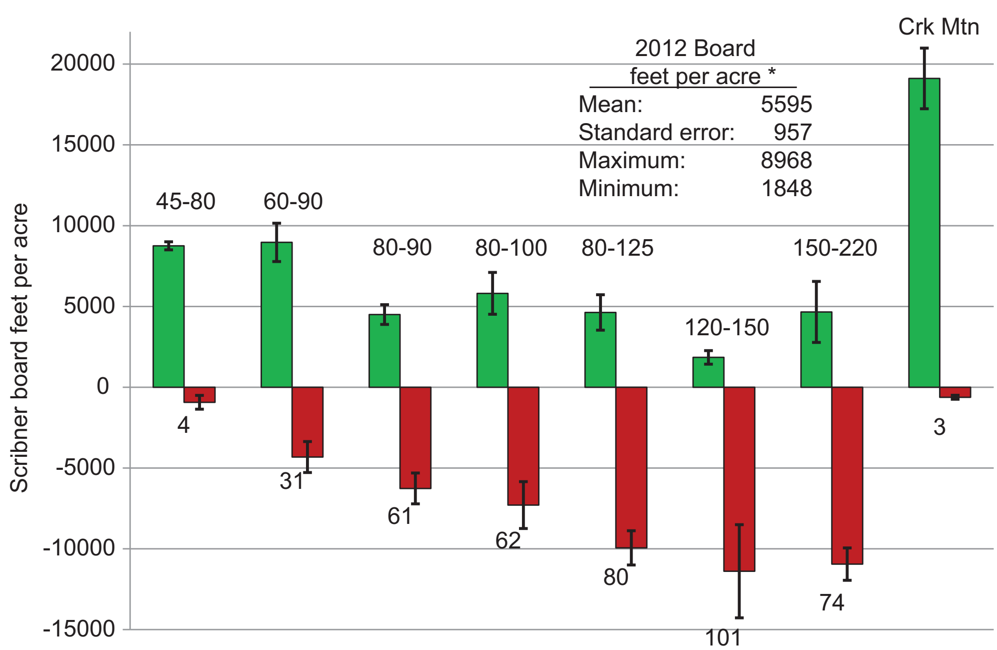

Figure 138—Mean volume in Scribner board feet for each basal area cluster in 2012 and the volume killed by MPBs (negative values) from the time the plots were established (1985–1991) through 2012. The bars are the standard errors of the means and the numbers below the bars indicate the mean proportion of the maximum board feet per acre that occurred on the plot that was killed by MPBs. *2012 board feet area per acre summary does not include Crook Mountain.

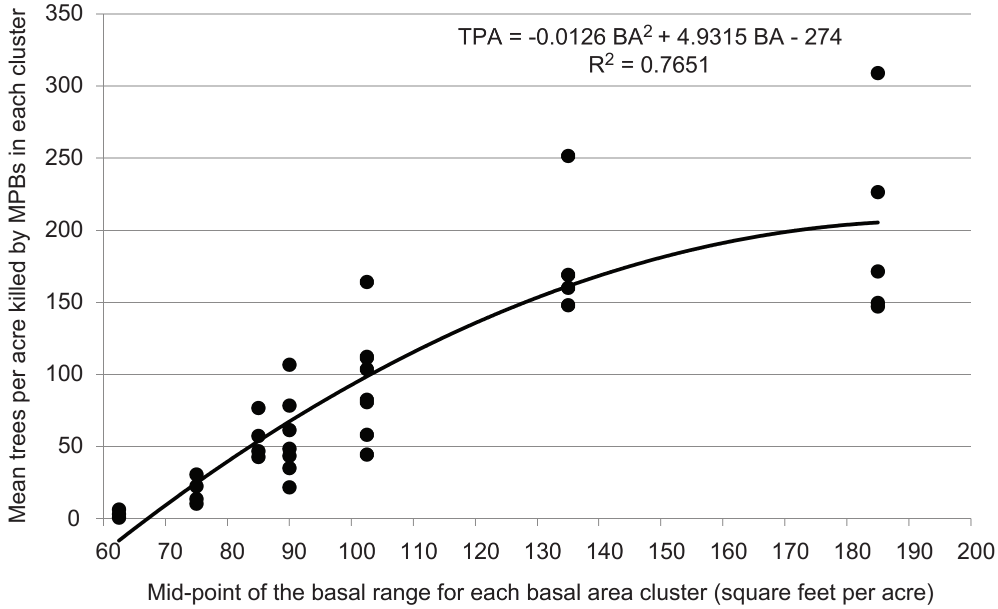

Figure 139—Relationship between tree density estimated by square feet of basal area per acre and mean number of trees killed per acre by MPBs within each basal area cluster.

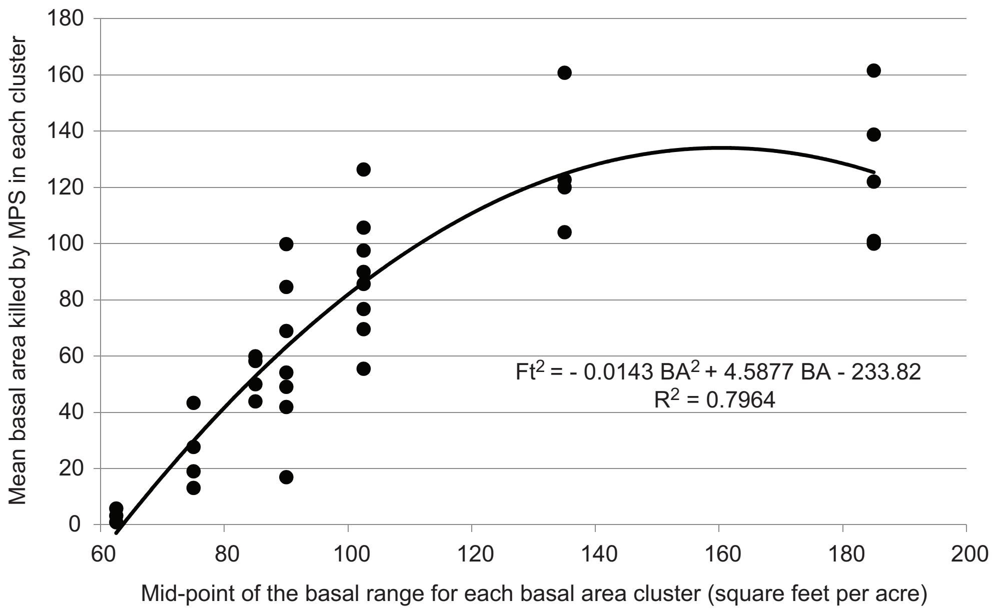

Figure 140—Relationship between tree density estimated by square feet of basal area per acre and the mean amount of basal area per acre killed by MPBs within each basal area cluster.

Also, these relationships measured by proportion or amount revealed the MPB-caused losses at tree densities over 150 feet^2 of basal area per acre and were less severe, although still very high, than those of forests with tree densities ranging from 120 to 150 feet^2 of basal area per acre (fig. 141). Figure 141 again shows the impact that MPBs had on the volume lost in the Black Hills even at densities near 100 feet^2 of basal area per acre, where 16,398 board feet or 128 percent of the maximum volume that ever existed on plot MMt108 at Medicine Mountain was killed (figs. 131, 138).

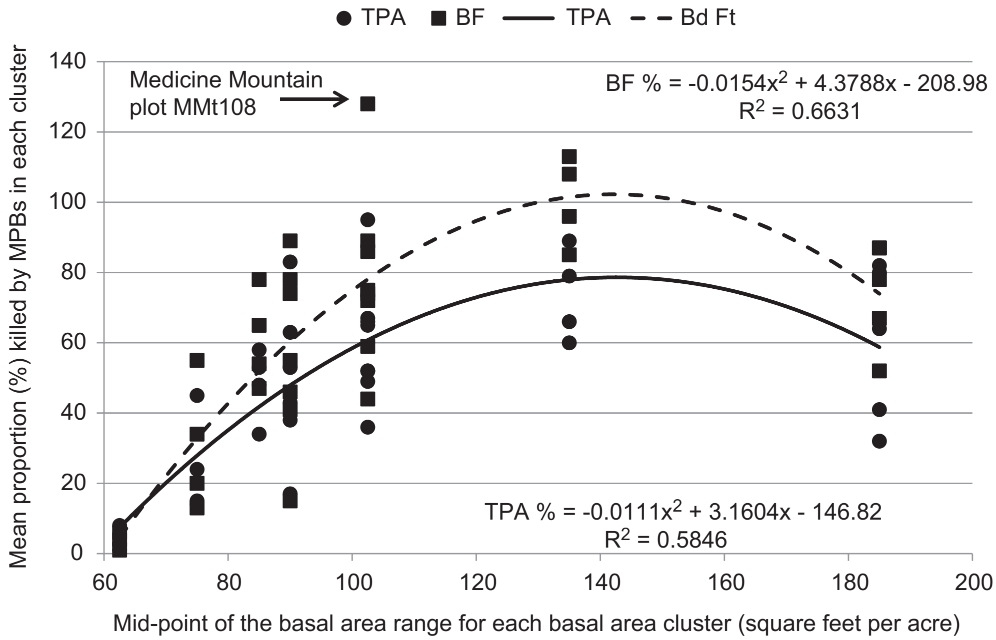

Figure 141—Relationship between tree density estimated by square feet of basal area per acre and the mean proportion of both trees and board feet per acre killed by MPBs within each basal area cluster.

These downward trends in MPB-caused losses at the higher tree densities could be related to trees being differentially selected by MPBs to attack because of their DBH or by wide differences in the DBHs of the trees available to the MPBs. However, as figure 74 showed, there was nearly a one to one relationship between the DBHs of the trees alive on the plots and the DBHs of trees killed on the plots by MPBs. Similarly, within each cluster of trees described by basal area, the standard error of the DBH in 2012 and the mean DBH of the trees killed by MPBs overlap (fig. 142). As a result, a differential between mean DBH of trees killed and living on the plots could not be influencing how MPB impacts tended to decrease as tree density increased. As would be expected, as stand density increased the mean DBH of both trees killed and trees remaining on the plots decreased to around 10 inches from those approaching 16 inches that grew on plots with 60 to 90 feet^2 of basal area per acre (fig. 142).

Major losses caused by MPBs began over an extreme range of stand densities. Major mortality commenced at densities of 77 feet^2 of basal area per acre to those with densities nearing 220 feet^2 of basal area per acre (fig. 127). When Schmid and Mata established this series of plots in the Black Hills, the understanding at that time was that stand densities below 120 to 125 feet^2 of basal area per acre were relatively resistant to attack by MPBs (Sartwell and Stevens 1975; Schmid et al. 1994). However, major tree mortality occurred on the majority of the plots at densities below these thresholds and at densities below 80 feet^2 of basal area per acre (fig. 127). These findings indicate that at high population levels of MPBs a wide range of ponderosa pine forest structures can be attacked and killed and the losses can be severe. MPBs killed over 19,500 board feet per acre at Brownsville on plot Brn146 that was in basal area cluster 120–150 feet^2 of basal area per acre and the mean board feet per acre killed in that cluster was 11,390 board feet. In contrast, 89 board feet per acre were killed at the Experimental Forest on plot EF44 and the mean board foot killed within basal area cluster 45–80 was 933 board feet per acre (figs. 131, 138).

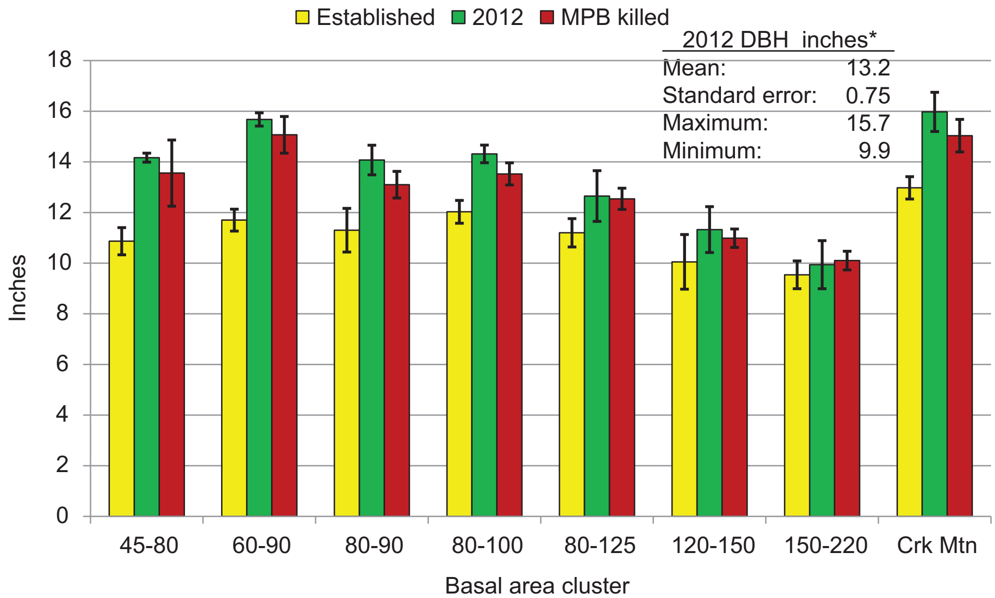

Figure 142—Mean tree DBH (estimated from the tree of average basal area or quadratic mean diameter-QMD) for each basal area cluster (e.g., 45–80, 80–100, 150–220) when they were established, the 2012 means, and the mean DBH of the trees killed by MPBs. The bars represent the standard error of the means. *2012 DBH summary does not include Crook Mountain.

A very interesting result was the losses caused by MPBs measured by amount or proportion that linearly increased as stand densities approached 150 feet^2 per acre and then decreased (figs. 139–141). This trend was most notable in that 34 percent of the trees were killed by MPBs when the tree density was 85 feet^2 of basal area per acre and 32 percent of them were killed when the tree density was 185 feet^2 of basal area per acre (fig. 141). Even though the loses caused by MPBs among the plots (with some exceptions) was dramatic, as it has been across the northern portion of the South Dakota Black Hills, means of 57 trees and 51 feet^2 of basal area per acre still occupy the plots and these residual trees have a mean DBH of 13.2 inches (figs. 134, 135, 142). Keen (1950) postulated that bark beetles were silvicultural agents as they regenerated, thinned, and modified forest succession. Although it appears the epidemic of MPBs attacking the pines in the Hills is waning, the fate of these remaining trees is far from certain.

Mountain Pine Beetles, Climate, and Microclimate

Climate expressed by elevation and habitat type appears to influence how MPBs impact lodgepole pine forests (Amman and Baker 1972). For example, in Wyoming, Amman and Baker (1972) found a higher proportion of lodgepole pine trees surviving attacks by MPBs within similar forest conditions at elevations exceeding 8,500 feet compared to those at 7,000 feet. Roe and Amman (1970) found similar trends of MPBs killing more lodgepole pine trees in Montana at an elevation of 6,400 feet compared to those growing at 7,000 feet. Roe and Amman (1970) found that lodgepole pines growing on a subalpine fir (*Abies lasiocarpa*)/*Clintonia uniflora* habitat type were at a higher risk to attack by MPBs than those growing on a subalpine fir/dwarf huckleberry (*Vaccinium scoparium*) or Douglas-fir/pine grass (*Calamagrostis rubescens*) habitat types. Amman and Baker (1972) showed similar results for the lodgepole pines growing on the *Clintonia* and dwarf huckleberry habitat types. As mentioned before, in the Black Hills neither elevation nor habitat type (indicators of climate) appeared related to MPB dynamics but stand density, which likely influences microclimate, was.

Microclimate

Tree density affects light intensity, wind movement, insolation, and air temperatures within forest stands that either separately or in various combinations appears to affect MPB activity (Bartos and Amman 1989). Lethal temperatures to bark beetle eggs and larvae that exceed 115 to 120 °F below tree bark would not occur in standing trees, but more subtle changes in bark temperatures related to different stand densities may affect bark beetle activity (Bartos and Amman 1989; Miller and Keen 1960). MPBs usually do not fly when air temperatures are below 60 °F and will land and burrow under bark scales or within bark crevices of live trees when air temperatures drop below 63 °F, which they often encounter in the evenings. When air temperatures increase the next day they will begin burrowing or fly to another tree (Rasmussen 1974). Gray et al. (1972) showed that the optimum temperature for MPB flight was 77 to 86 °F with flying decreasing at temperatures exceeding 86 °F. MPBs' behavior may have evolved to avoid situations where their broods are not likely to survive. In open stands, where tree temperatures are a few degrees above those of more closed stands, MPBs' development may proceed too far before winter, thus entering the winter in the pupal stage rather than in the larval stage. MPB pupae are more susceptible to cold injury than MPB larvae (Amman 1973; Bartos and Amman 1989; Reid 1963).

Wind speed and its direction influences the timing and direction that bark beetles fly, and stand density, canopy height, and tree crown architecture all impact winds within a stand. In general, MPBs do not fly when wind speeds exceed 6.8 miles per hour and they show a preference for flying when wind speeds are less than 2 miles per hour (Gray et al. 1972). Also, these authors showed that twice as many males as females flew when wind speeds exceeded 3.6 miles per hour and most flying occurred below 20 feet above ground level. MPBs usually fly with the wind, but ambrosia bark beetles (*Trypodendron lineatum*) most often fly against the wind and their activity dropped off markedly when winds exceeded 3.4 miles per hour and when winds were very light (Chapman 1962; Gray et al. 1972). Salom and McClean (1991) showed that the ambrosia beetle preferred little or no wind when it was within 3 to 6 feet of a tree before landing. The ambrosia beetle has a maximum flight speed of 4 miles per hour in still air and the large *Ips typographus* bark beetle can fly for several hours at 4.5 miles per hour. In still air MPB flight speed is most likely in the same range (Byers 2000; Chapman 1962; Gray et al. 1972). Pheromone concentrations and distribution also are influenced by winds and in general wind speeds are greater in open than dense stands, further complicating MPB dynamics.

Communication through pheromones is essential for MPB populations to thrive. Bark beetle semiochemical communication systems are complex involving insect physiology, pheromone chemistry, and microclimate processes within forest stands and operate on a timescale that is on the order of seconds or smaller (Thistle et al. 2004). Pioneering females, after initiating gallery excavation, release the aggregating pheromone trans-verbenol that serves as a signal for MPBs to mass attack the tree (Pitman et al. 1968; Progar et al. 2015; Vité and Pitman 1968). Schlyter (1992) gave an approximate pheromone attraction range for moths and butterflies (*Lepidoptera*) of 650 to 1,300 feet, but indicated bark beetles being attracted by pheromones usually occurred at less than 325 feet, depending on the species.

Elkinton et al. (1984) showed that pheromone plumes most often exist below the canopy where the winds are light and stable. Such conditions are highly dependent on over all wind speed in the area and the atmospheric stability within the canopy. Stable atmospheric layers typically occur at predawn on clear nights, which in turn can generate local air flows that will transport plumes in a relatively concentrated fashion (Thistle et al. 2004). Also, stable air under dense canopies can be facilitated by sunlight warming the upper canopy, which in turn heats the surrounding air, creating air instability above the tree canopies. These conditions tend to create inversions that trap stable air below dense tree canopies (Chapman 1967; Fares et al. 1980; Fritschen 1984). As a result, a pheromone cloud within a dense stand on a sunny day would be trapped beneath the canopy until it flowed to a point where the canopy was less dense or where there was a canopy opening (Fares et al. 1980; Farrell et al. 2002). Such horizontal movement of pheromone plumes near and around tree boles would facilitate excellent MPB communication and tree infestation (Bartos and Amman 1989).

Heterogeneous stands with numerous canopy openings allow sunlight to penetrate and differentially heat the forest floor, resulting in convection air currents and turbulence that would disrupt pheromone plumes, making them travel vertically rather than horizontally (Bartos and Amman 1989; Rosenberg et al. 1983). The presence of ground level vegetation and its canopy roughness can also contribute to plume disruption (Strand et al. 2009). As the pheromone plumes rise above tree canopies they will be torn apart by the more turbulent air (Fares et al. 1980). As a result of the unsettled air currents that occur in open stands, MPB pheromone communication would be disrupted near tree boles and MPB infestations would likely be impeded (Schmitz et al. 1989).

Because pheromone plume movement and dispersion are dependent on air movement and mixing, tree thinning would result in increases in wind speed and turbulence within canopies. For example, in Louisiana, a loblolly pine (*Pinus taeda*) forest was progressively thinned from 140, to 100, and then to 70 feet^2 of basal area per acre. With each reduction in tree canopy the amount that the gas plume's meander decreased and plume dilution increased. As a result, the mean concentrations of the tracer gas within the tree canopies subsequently decreased with each reduction in tree density, showing how thinning would disrupt pheromone plumes produced by bark beetles (Edburg et al. 2010). Stand density influences air temperature, vegetation temperature, wind speed, wind turbulence, and their interactions, which in turn affect MPB activity. And as with other aspects of Schmid and Mata's work, they also observed weather in several of the MPB plots they established in the Black Hills.

Weather Among Differing Stand Structures in the Black Hills

The plots that Schmid and Mata established in the Black Hills extended throughout the South Dakota portion of the Black Hills and contained a wide range of tree densities that potentially could affect the local weather, which in turn, as the previous discussion indicated, could influence MPB dynamics. The minimal variation in topography that occurs in the Black Hills has little effect on prevailing winds as to their speed and direction. As shown in figure 143, a modeled 12 miles per hour wind blowing from the southwest generally remained so as it blew over the Black Hills Experimental Forest (Butler et al. 2006; Forthofer et al. 2014). Even though these winds were modelled 20 feet above the tree canopy, those under the tree canopy could be influenced by canopy density, canopy gaps, and differential forest floor heating.

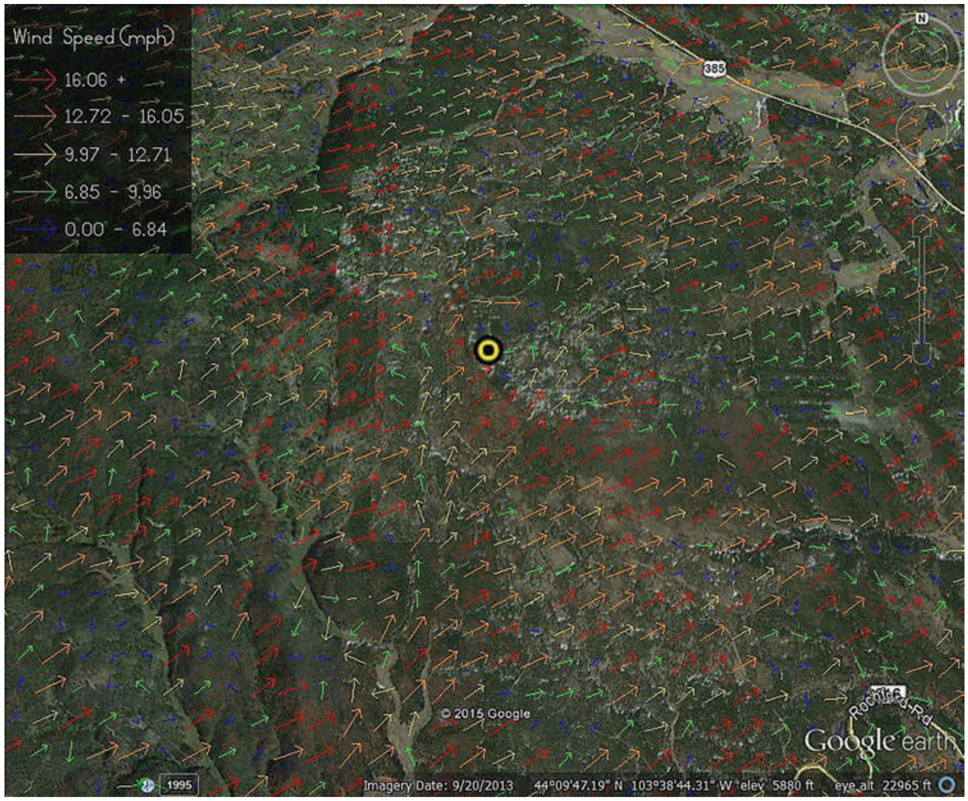

Figure 143—The gentle topography of the Black Hills minimally influences the direction or speed of prevailing winds. Using WindWizard, a "snapshot" of a single point in time is shown here, for 12 miles per hour winds blowing from the southwest (azimuth 240 degrees). When they blew over the Black Hills Experimental Forest their speed or direction was minimally affected by topography. Yellow dot in the center of the photo is the location of the Experimental Forest MPB plots and the arrows are spaced 590 feet apart (Butler et al. 2006).

Schmid et al. (1992) in 1988, at Brownsville, measured both horizontal and vertical winds blowing in plots Brn67 and Brn148 in late July and early August that would correspond to the time that MPBs would be flying to attack new trees. Schmid et al. (1995) measured horizontal wind speeds at White House Gulch in plots WHG80 and WHG128 during similar weeks in 1992. At both locations, although not statistically different, the mean wind speeds in the plots with the higher tree densities were slower than the winds blowing in the plots with the lower tree density (fig. 144). These wind speeds would not impede MPB flight but in combination with the wind, changing direction 37 times a day at Brownsville (mean 3.13 miles per hour winds), might have been sufficient to disrupt pheromone plume movement and dissuade MPBs from attacking trees when the stand density was 67 feet^2 of basal area per acre (fig. 144). Vertical winds were measured at Brownsville and both upward and downward winds within and between the plots were similar at ≈0.5 miles per hour (fig. 144). Most likely the vertical winds alone would not have influenced MPB dynamics but combined with wind changes and horizontal winds they could have contributed to air turbulence that would disrupt pheromone plumes (fig. 144). Over 35 percent of the time at White House Gulch in late July and early August 1992, 2 to 3 miles per hour winds blew in the plot with 80 feet^2 of basal area per acre and also in the plot with 128 feet^2 of basal

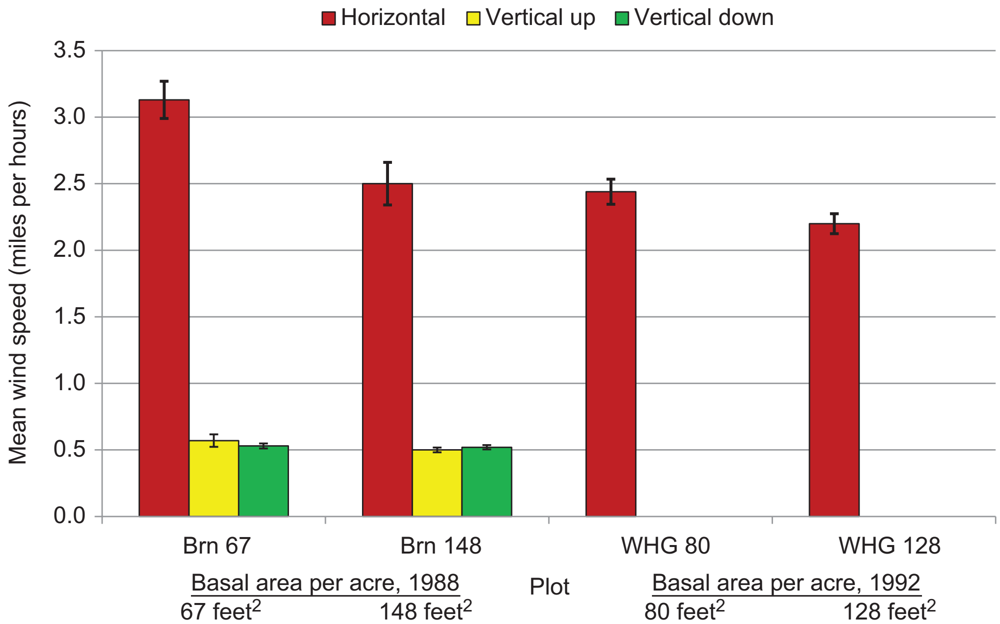

Figure 144—At Brownsville, in plots Brn67 and Brn148, wind speed was measured for both horizontal and vertical winds from July 20 through 27 and from July 31 through August 2, 1988. At White House Gulch in plots WHG80 and WHG128, horizontal winds were measured from July 21 through August 15, 1992. White House Gulch wind data were adapted from Schmid et al. (1995). Hourly wind speeds and Brownsville data were adapted from the wind speed frequencies for 15 minute intervals from 0600 to 1900 on those dates presented by Schmid et al. (1992).

area per acre (Schmid et al. 1995). Also at White House Gulch, 11 percent of the winds did exceed 4 miles per hour and that would be sufficient to interfere with MPB flight along with being disruptive to pheromone plumes (fig. 145).

Air and bark temperatures were observed at White House Gulch from July 21 through August 16, 1992 (Schmid et al. 1995). During both day and night there were minimal differences in the air temperatures in the plot with 80 feet^2 of basal area per acre compared to the plot with 128 feet^2 of basal area per acre (fig. 146). On August 8, 1992, a high air temperature of nearly 85 °F was reached in both plots and a low of 38 °F was recorded in plot WHG80 on August 12. Bark temperature on the north and south sides of 5 trees in each plot was also monitored from July 21 through August 16, 1992, at 4.5 feet above the forest floor. Similar to air temperatures, minimal differences in north side bark temperatures were noted between the two plots with 81 °F reached on August 8, and a low of 43 °F was recorded on July 22 (fig. 147). However, a difference in south side bark temperatures between the two plots was observed. The trend in south side bark temperature was for the plot with 80 feet^2 of basal area per acre to have lower minimums (e.g., 44 to 46 °F) and higher maximums (e.g., 91 to 96° F) than the plot with 128 feet^2 of basal area per acre (fig. 148). So when MPBs would be flying in the Black Hills, neither air nor bark temperatures would be sufficient to kill or injure a beetle (i.e., 115 to 120 °F) as south side bark temperatures only exceeded 90 °F on 3 days and the mean daily south side bark temperature was 82 °F on the plot with 80 feet^2 of basal area per acre (figs. 148, 149).

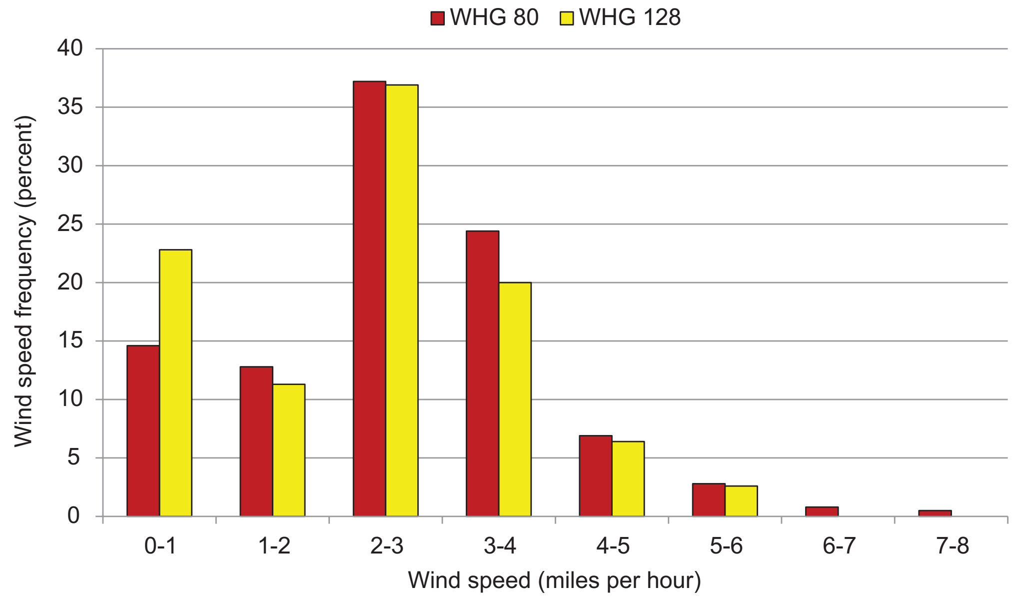

Figure 145—At White House Gulch in plots WHG80 (80 feet^2 of basal area per acre) and WHG128 (128 feet^2 of basal area per acre), horizontal winds were measured hourly from July 21 through August 15, 1992 (Schmid et al. 1995).

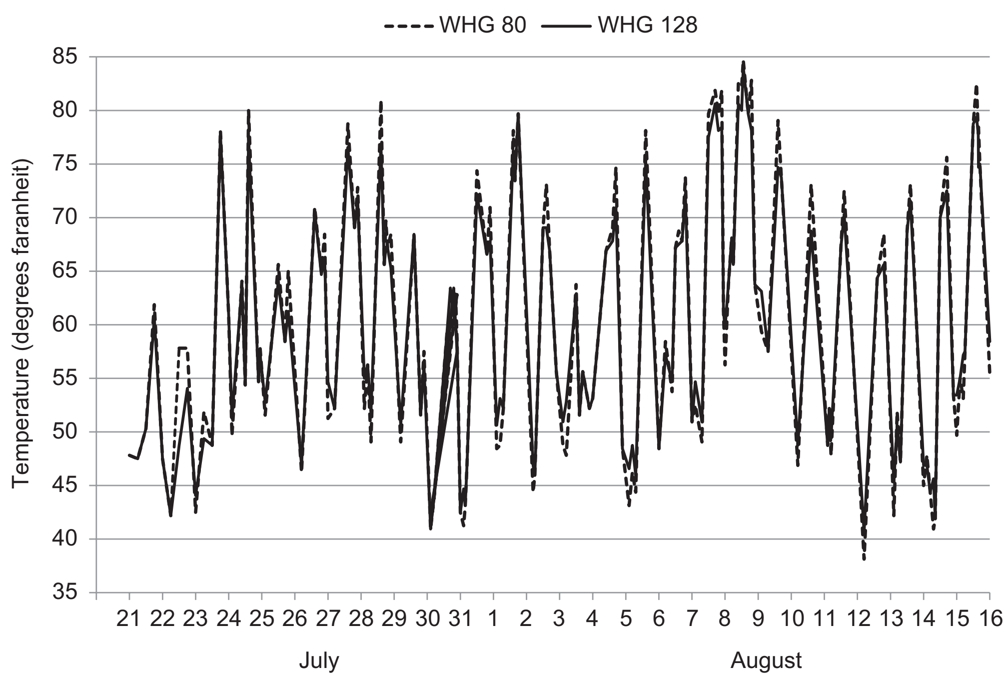

Figure 146—Air temperatures were measured at White House Gulch in plots WHG80 (80 feet^2 of basal area per acre) and WHG128 (128 feet^2 of basal area per acre) from July 21 through August 16, 1992 (adapted from Schmid et al. 1995).

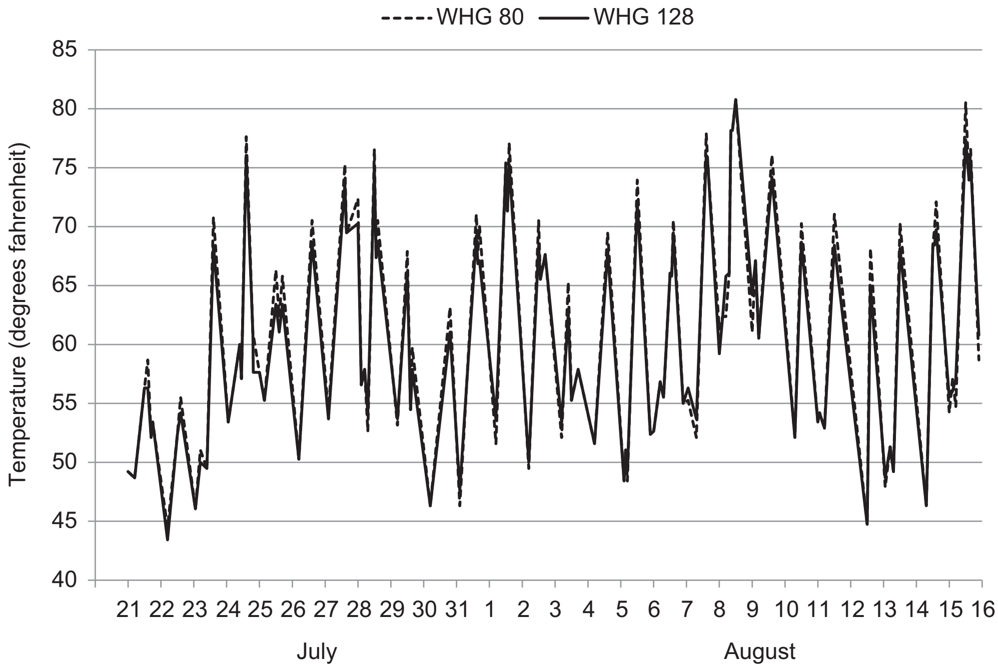

Figure 147—Mean bark temperatures at breast height on the north side of five trees located at White House Gulch in plots WHG80 (80 feet^2 of basal area per acre) and WHG128 (128 feet^2 of basal area per acre) from July 21 through August 16, 1992 (adapted from Schmid et al. 1995).

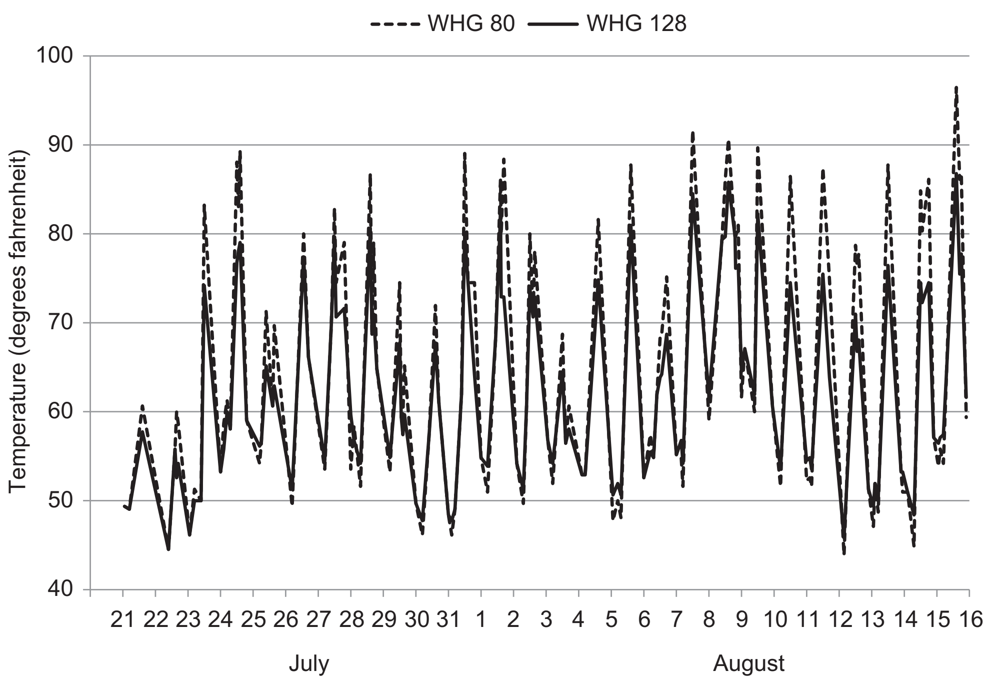

Figure 148—Mean bark temperature at breast height on the south side of five trees located at White House Gulch in plots WHG80 (80 feet^2 of basal area per acre) and WHG128 (128 feet^2 of basal area per acre) from July 21 through August 16, 1992 (adapted from Schmid et al. 1995).

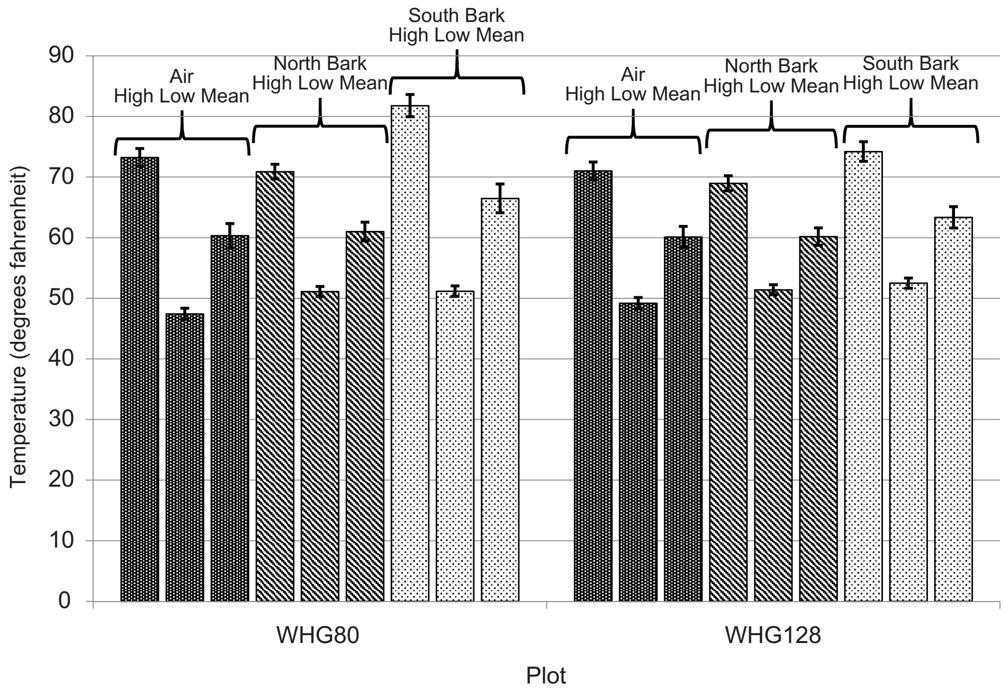

Figure 149—Mean air and bark temperatures at breast height on the south and north side of five trees located at White House Gulch in plots WHG80 and WHG128 from July 21 through August 16, 1992. These data and their standard errors were calculated from the daily high and low temperatures (adapted from Schmid et al. 1995).

However, in general the south side bark temperatures on the plot with 80 feet^2 of basal area exceeded those on the plot with 128 feet^2 of basal area per acre by about 10 °F and the difference between the means was 8 °F (figs. 148, 149). Also, as mentioned before, through evolved behavior the warmer bark on trees in the open stand may dissuade some MPBs from attacking as their broods might develop too quickly and be susceptible to cold injury during the winter. Of the weather metrics recorded at White House Gulch, solar radiation showed the most potential for modifying MPB behavior.

Schmid et al. (1995) measured solar radiation in WHG80 and WHG128 plots from July 21 through August 16, 1992. The sensors were placed in the center of the plots to capture the average canopy conditions that existed in both plots. Of the weather variables collected on the plots, incoming solar radiation differed substantially between the two plots (fig. 150). Not only was the amount of radiation filtering through the canopy much greater on the plot with 80 feet^2 of basal area per acre (173 watts per m^2 mean versus 68 watts per m^2 mean), but the variation in the daily maximum and minimum incoming solar radiation was much greater on the plot with the lower tree density compared to the one with the higher tree density (fig. 150). Although not estimated, based on crown competition factors (CCF)[6],

[6] Crown competition factor (CCF) (Krajicek et al. 1961) is a relative measurement of stand density that is also based on tree diameters. Tree values of CCF estimate the percentage of an acre that would be covered by the tree's crown if the tree were open grown. Stand CCF is the summation of individual tree CCF values. A value of 100 theoretically indicates that tree crowns will just touch in an unthinned, evenly spaced stand.

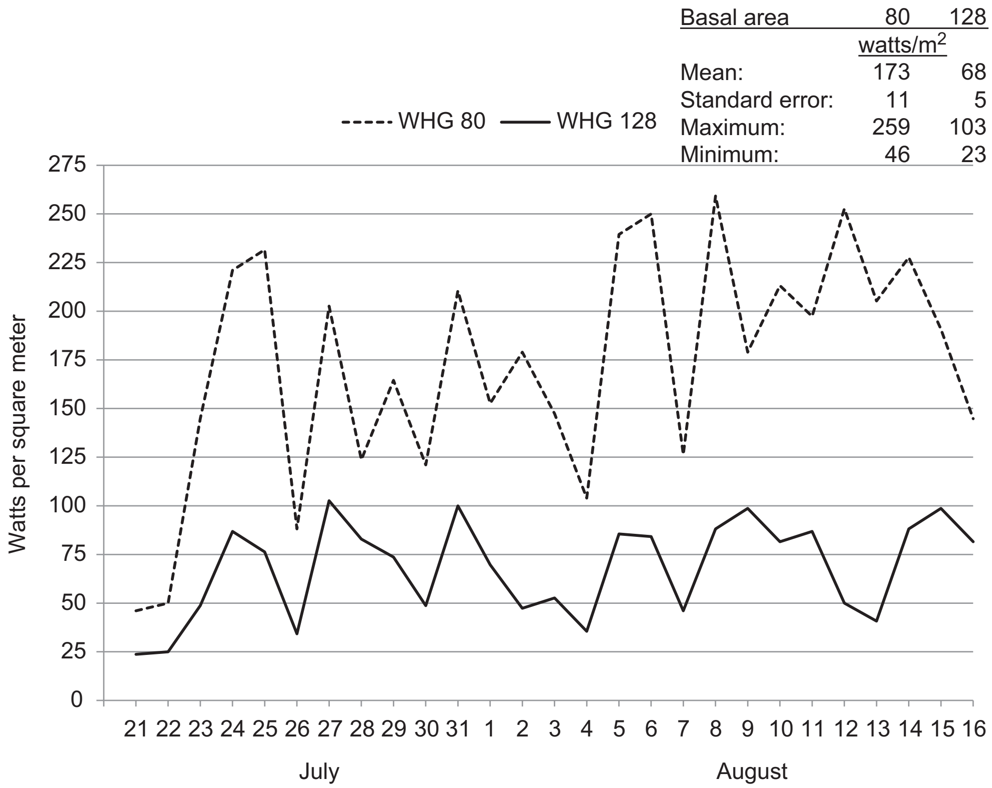

Figure 150—Mean daily incoming solar radiation at White House Gulch in plots WHG80 (80 feet^2 of basal area per acre) and WHG128 (128 feet^2 of basal area per acre) from July 21 through August 16, 1992 (adapted from Schmid et al. 1995).

plot WHG128 with a CCF of 109 most likely had continuous canopy cover while plot WHG80 with a CCF of 69 had numerous openings in the canopy (fig. 151). The amount of and differential heating to the forest floor that would occur in the two plots is dependent on the character and amount of material on the floor and in the Black Hills the abundance and amount of seedlings and saplings that dominate most stands. Nevertheless, with this contrast in solar heating potential, differences in surface winds within the two plots could occur.

Weather, as influenced by stand density, has been frequently associated with bark beetle behavior. In the Black Hills, since Sartwell and Stevens (1975) postulated that stand densities less than 125 feet^2 per acre of basal area showed resistance to attack by MPBs, such stand prescriptions have been widely applied. Schmid and Mata established the MPB plots reviewed here by using the assumption that stand density expressed as basal area per acre was the metric to use. As shown here, MPB attacks were few to none in stands with consistent densities less than 80 feet^2 of basal area per acre, nevertheless a strong microclimate rationale for this behavior is still wanting. Air and north side bark temperature showed minimal differences between the plot containing 80 feet^2 of basal area per acre compared to the plot containing 128 feet^2 of basal area per acre (figs. 146, 147). South side bark temperatures in the plot with the lower tree density were higher than those recorded in the plot that had higher tree density and more shade (figs. 148, 149). However, the temperatures reached were far from lethal to MPBs and the bark temperatures on other tree sides would be more conducive to attack. Possibly, the high temperatures on the south side bark might contribute to a MPB not attacking the tree as its brood might develop too quickly and be prone to being killed in the winter (Amman 1973; Bartos and Amman 1989; Reid 1963).

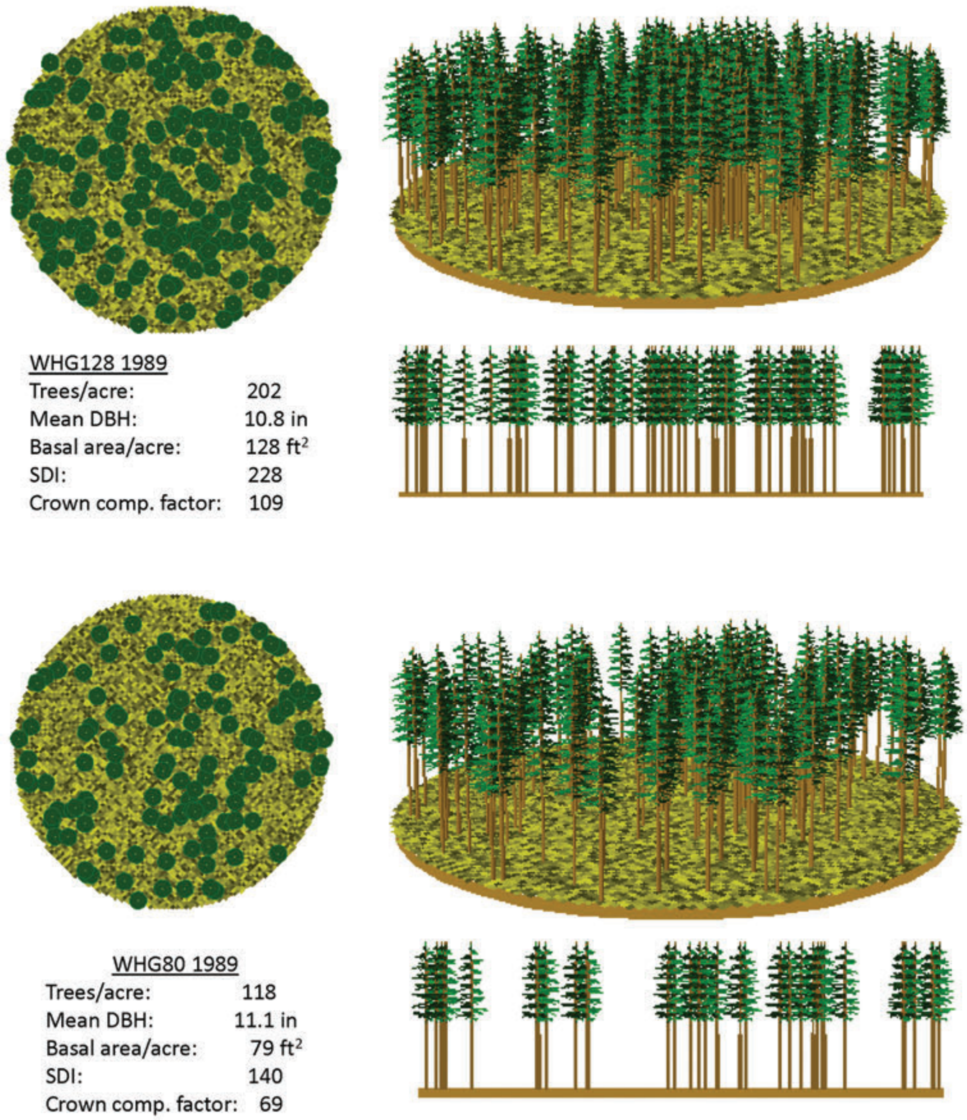

Figure 151—One acre Stand Visualization System (SVS) renderings of plots WHG128 and WHG59 in 1989 where Schmid et al. (1995) recorded air and bark temperatures along with incoming solar radiation.

Of the characteristics associated with MPB behavior that might relate to more open stands being resistant to attack is the differences in wind currents that could be associated with incoming solar radiation and pheromone plume dispersal. With air inversions capable of developing under dense tree canopies and the concept that differential heating of the forest floor can contribute to air turbulence, an argument can be formed that weather in open stands compared to closed stands can alter MPB behavior (fig. 151). Solar radiation striking the forest floor in plot WHG80 was significantly more than striking the floor in plot WHG128. It was very fortuitous that Schmid and Mata observed the solar radiation in a plot with the very density of ≈80 feet^2 of basal area that plots EF44, EF61, and Boy68 contained in 2012, which showed the most resistance to MPBs of any of the plots subjected to MPB mortality (fig. 152). These data also suggest that stands with a CCF of less than 70 shows some resistance to MPBs, which can infer, especially in the even-aged ponderosa pine stand of the Black Hills, a canopy cover in the range of 45 to 60 percent (fig. 152).

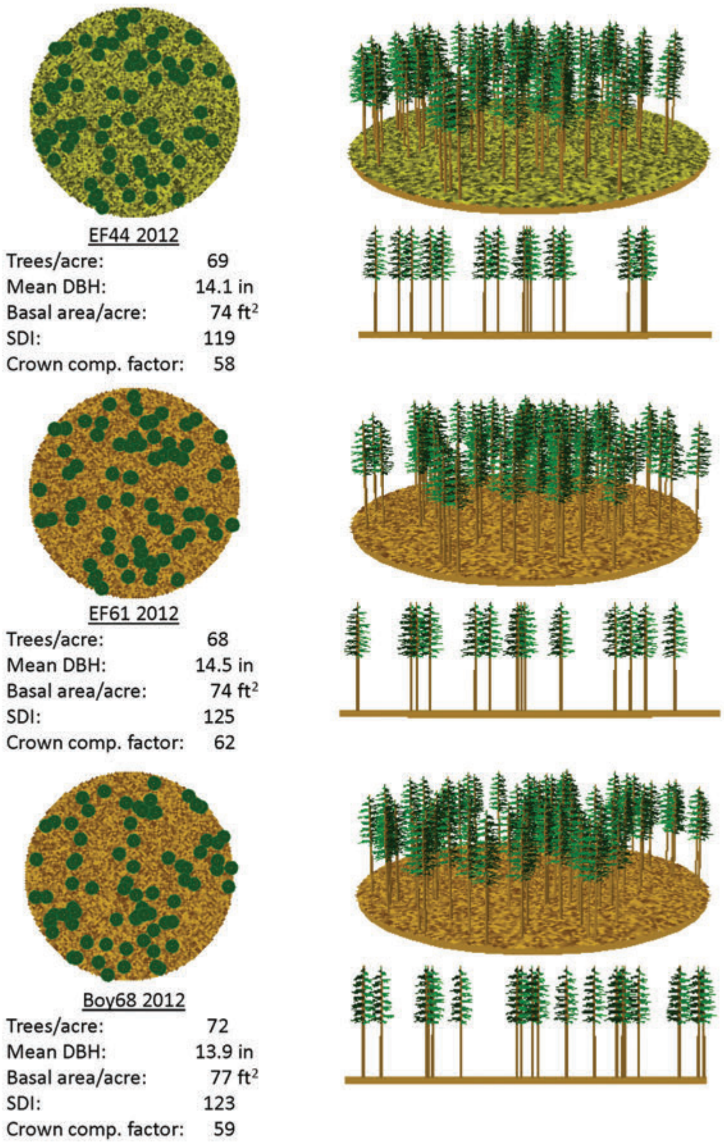

Figure 152—The stand structures displayed here using the Stand Visualization System (SVS) of plots EF44, EF61, and Boy68 in 2012. Of the 35 plots experiencing considerable pressure from MPB attacks, the trees in these three plots had few or no trees killed.

Stands and Landscapes Resistant to Mountain Pine Beetles

The stand structures of plots EF44, EF61, and Boy68 were resistant to attack by MPBs from the time they were established (1988–1991) through 2012. Moreover, all three plots were exposed to high numbers of MPBs at both locations and within a few hundred feet of these plots hundreds of trees per acre were killed by MPBs (figs. 56, 59, 120, 121). The structures of these three plots in 2012 were remarkably similar (fig. 152). DBHs ranged from 13.9 to 14.5 inches, trees per acre from 68 to 72, CCF from 58 to 62, and basal area per acre from 74 to 77 feet^2. Tree vigor and within-stand weather were both influenced by these structures, which in turn likely influenced MPB behavior. In terms of preparing a silvicultural prescription, these would be the “desired conditions” for a MPB-resistant Black Hills ponderosa pine stand (fig. 152).

Stand Treatments

Using the desired conditions for a MPB-resistant stand, a silvicultural system was developed to produce and maintain such conditions while providing habitat for the northern goshawk, a Forest Service sensitive species (Graham et al. 2015; Reynolds et al. 1992) (fig. 152). Located within the northern portion of the Black Hills Experimental Forest, a stand was harvested in the 1980s by using a two-step shelterwood silvicultural method, not far from where Schmid and Mata established the MPB plots (figs. 47, 56, 69). As a result, and similar to many stands located in the Black Hills, a few large trees overtopping an abundant amount of seedlings and saplings remained (fig. 153). After a 2013 harvest and masticating the unwanted seedlings and saplings, the stand contained 51 feet^2 of basal area and 125 trees per acre that had a mean DBH of 8.7 inches that resulted in an SDI of 99 (fig. 154, table 5).

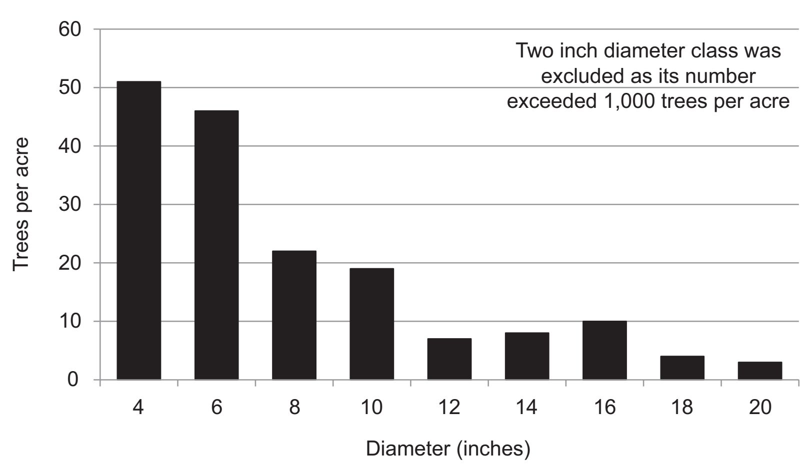

Figure 153—Picture (circa 2010) of the stand and its diameter distribution used in the MPB resistant stand simulation was typical for the Black Hills (located on the Black Hills Experimental Forest). It was harvested in the 1980s and contained abundant natural regeneration. Marked trees are to be left after a harvest.

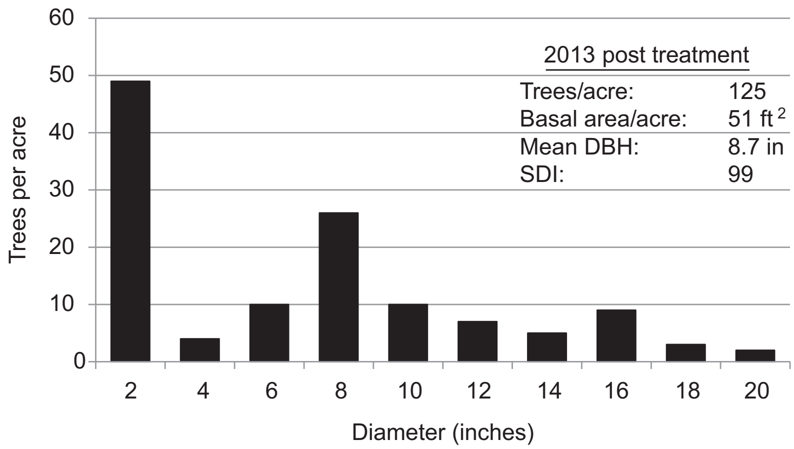

Figure 154—The diameter distribution and picture of the stand used in the MPB resistant stand simulation located on the Black Hills Experimental Forest after the first entry (2013 harvesting and masticating unwanted tree regeneration) of an irregular selection system aimed at creating and maintaining MPB resistant stands.

Using this beginning, an irregular selection system[7] that maintained high forest cover, important for northern goshawks, while incorporating the desired conditions for MPB resistance, was simulated for 100 years (table 5, fig. 155) (Graham et al. 2015; Reynolds et al. 1992).

[7] Irregular selection: meaning that the timing and intensity of tree removals and regeneration are predicated on how the stand develops and not applied on a preconceived plan or specific DBH, basal area, tree spacing or other metrics that are often used (Graham and Jain 2005). The overarching silvicultural goal was to maintain high forest cover dominated by large trees yet keep the stand densities near 70 to 80 feet^2 of basal area per acre.

Table 5—Stand characteristics of a 100-year simulation using the Forest Vegetation Simulator (FVS) for producing and maintaining MPB resistant stands and goshawk habitat on the Black Hills Experimental Forest.

	Before treatment								Removals				After treatment			
	Trees	BA[a]		Height	DBH[c]	Total	Merchantable		Trees	Total	Merchantable		BA[a]		Height	DBH[c]
Year	per/ac	ft^2/ac	SDI[b]	ft	inches	ft^3/ac	ft^3/ac	BF[d]/ac	per/ac	ft^3/ac	ft^3/ac	BF/ac	ft^2/ac	SDI[b]	ft	inches
2013	170	74	142	64	8.9	1987	1755	9300	44	1369	1210	6409	51	99	58	8.7
2023	123	65	120	59	9.9	1362	1131	5363	0	0	0	0	65	120	59	9.9
2033	121	78	139	60	10.9	1650	1388	6725	25	316	254	1111	63	111	60	11.0
2043	93	74	125	60	12.0	1579	1378	6736	0	0	0	0	74	125	60	12.0
2053	91	84	139	61	13.0	1817	1627	7838	5	116	101	486	79	130	61	12.9
2063	105	88	148	61	12.4	1926	1752	8266	2	179	175	977	81	138	61	12.0
2073	101	90	149	61	12.8	1958	1784	8228	17	338	317	1404	74	124	59	12.8
2083	82	83	134	60	13.6	1824	1663	7922	0	0	0	0	83	134	60	13.6
2093	100	90	150	61	12.9	2007	1823	9227	7	527	500	2853	67	116	60	11.5
2103	91	76	128	60	12.3	1683	1503	7795	0	0	0	0	76	128	60	12.3
2113	90	84	138	61	13.1	1872	1687	8843	0	0	0	0	84	138	61	13.1

[a] BA = Basal area

[b] SDI = Stand density index

[c] DBH = Diameter breast height (diameter of the tree with the mean basal area or quadratic mean diameter at 4.5 feet)

[d] BF = Scribner board foot

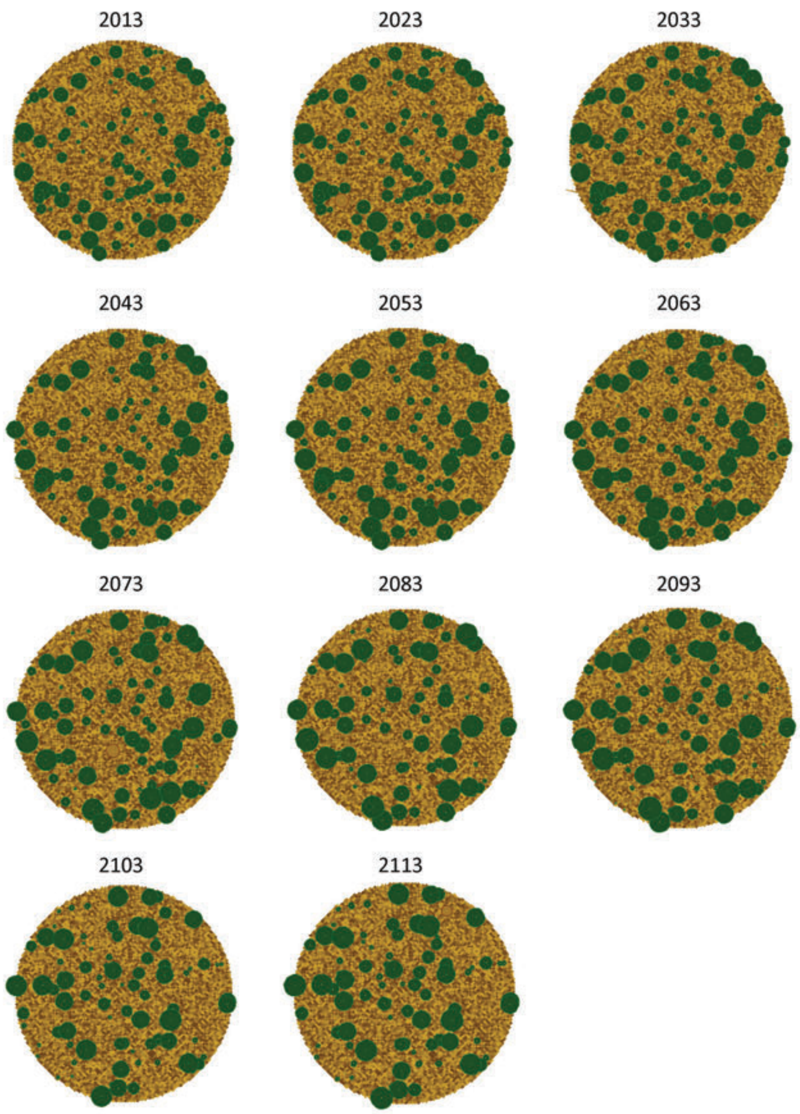

Figure 155—Overhead views for each year of the simulation after a treatment (e.g., precommercial thinning and commercial harvest).

Starting out with a tree density of 74 feet^2 of basal area per acre, the first harvest in 2013 reduced the tree density to 51 feet^2 of basal area per acre. From that first harvest, it took 20 years for the density to reach 78 feet^2 of basal area per acre, which indicated a harvest was needed to keep the forest structure resistant to MPBs. The simulated harvest in 2033 removed 25 trees per acre and netted 1,111 board feet of volume per acre (table 5). The silvicultural system tended seedlings and saplings left in 2013 and allowed 20 seedlings per acre to become established. These trees were subsequently tended in 2053, 2073, and 2093 maintaining an irregular uneven-aged stand. Being an irregular system, harvests occurred at 10- and 20-year intervals and the volume removed in these harvests varied from 486 to over 2,800 board feet per acre. Similarly, the number of commercial trees removed per acre ranged from 2 to 25. However, as Baker (1934) said, there is an infinite number of ways a stand can be treated and this series of treatments is only one of many that can provide for northern goshawks and be resistant to MPBs (table 5, figs. 155, 156).

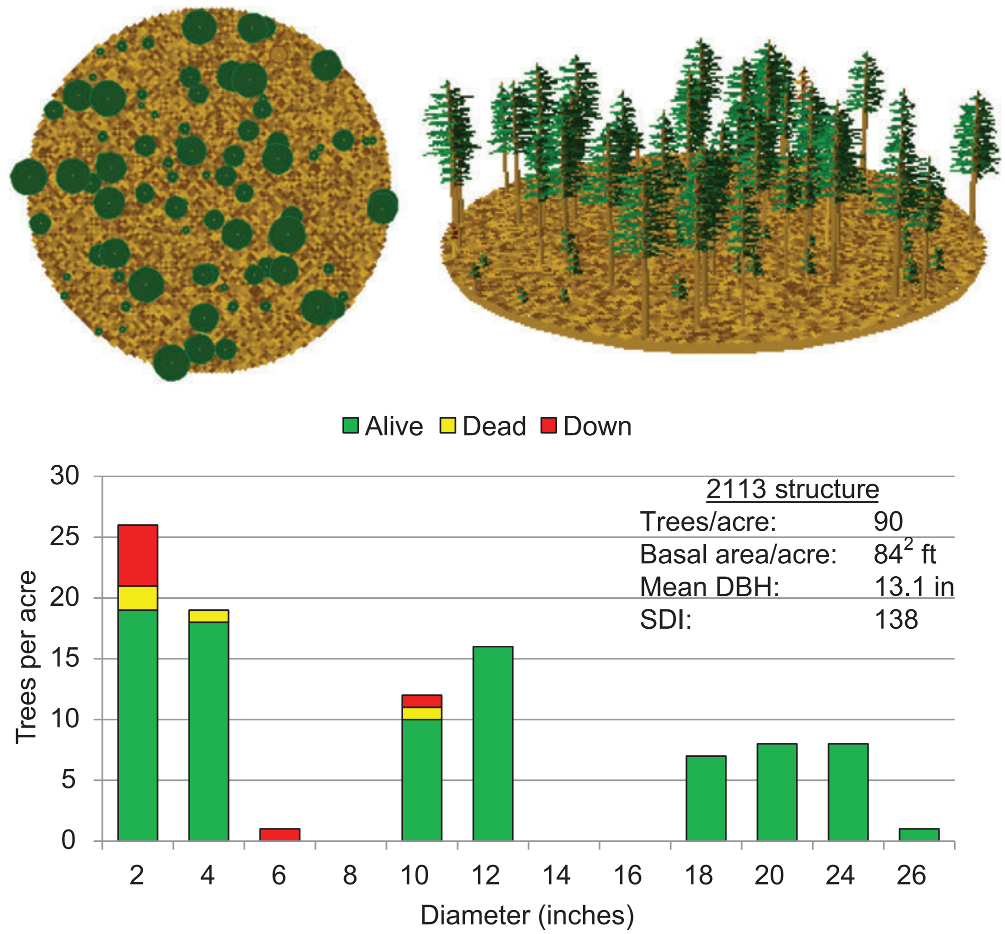

Figure 156—The resulting forest structure after a 100-year simulation (depicting year 2113) are shown of a stand located on the Black Hills Experimental Forest aimed at creating and maintaining MPB resistant structures while maintaining high forest cover. Note the tree diameters ranged from 2 to 26 inches and the trees, snags, and down logs are irregularly distributed.

As the simulation has shown, to maintain high forest cover while producing MPB-resistant stands, active management and harvests may be required every 10 to 20 years. Harmon (1955) postulated "the cutting cycle for the Black Hills ponderosa pine has now been established as 20 years" and is as true now (2015) as it was in 1955. Although the height growth of Black Hills ponderosa pine is not extraordinary, the basal area growth is quite remarkable. In general the productivity of a given stand and especially those even-aged and of a single species that occurs in the Black Hills are relatively constant over a wide range of densities (Langsaeter 1941). Using data from growth and yield plots established in 1964 and monitored through 2011 on the Black Hills Experimental Forest showed that basal area growth/acre/year averaged 1.8 feet^2 and the maximum was 3.5 feet^2 and the minimum was 0.5 feet^2/acre/year (fig. 157). It is interesting to note that the ≈minimum basal area growth occurred both at a tree density of 24 feet^2 of basal area per acre and at 152 feet^2 of basal area per acre (fig. 157). These data confirm that cutting cycles as short as 10 years and as Harmon (1955) suggested 20 years would likely be required to maintain high forest cover and MPB-resistant stands.

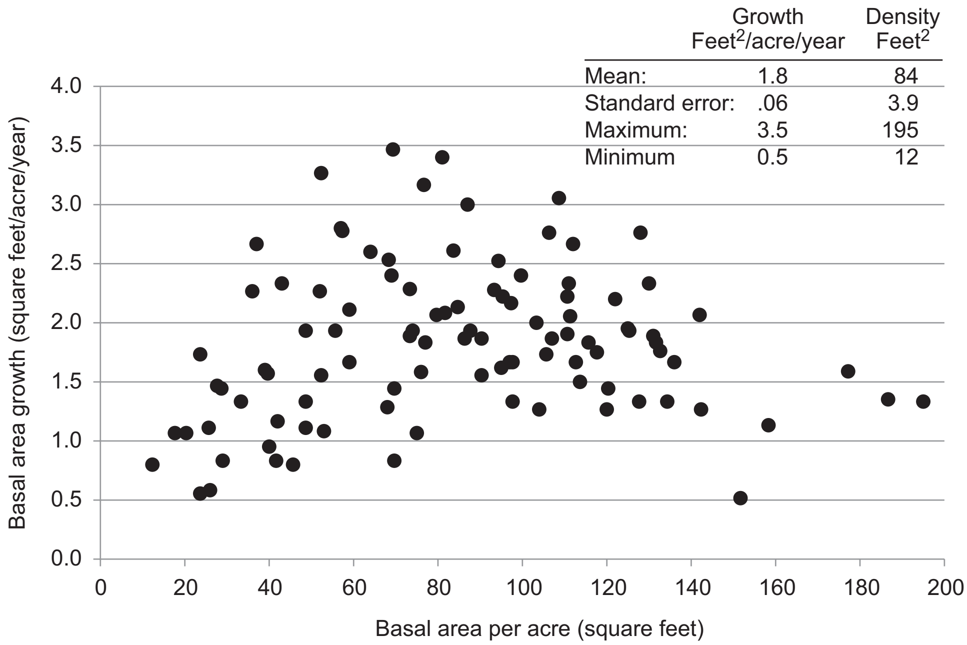

Figure 157—Basal area growth was similar over a wide range of tree densities in the Black Hills as Langsaeter (1941) postulated. These data are from 36 plots established on the Black Hills Experimental Forest in 1964 that were thinned to different densities and measured at ≈5 year intervals through 2012. As with the MPB plots located on the Experimental Forest, their site index was 61 and habitat type was kinnikinick.

Landscape Treatments

As shown by Miller and Keen (1960), Amman and Cole (1983), and Wickman (1987), WPBs and MPBs usually attack trees within yards of the tree in which they were reared, but have been known to travel miles to infest new trees. So treating a single stand to be resistant to MPBs would be insufficient to alter MPB dynamics and large areas or landscapes need to be in a resilient condition to keep MPB populations at endemic levels (Bentz et al. 2009; Fettig et al. 2014). Even though the Black Hills Experimental Forest is only 3,352 acres in size, the ponderosa pines within the Forest show considerable resistance to MPBs as a result of treatments it received in the 1980s, and again from 2011 through 2013.

The cuttings that occurred over the Black Hills Experimental Forest in the last ≈30 years have both intentionally and unintentionally created a variety of forest structures. As stated earlier, much of the Forest was treated with a two-step shelterwood: the northwestern corner was harvested by using a regular uneven-aged selection system, and the most recent cuttings used an irregular uneven-aged selection system (footnote 7, fig. 158). As a result of these treatments, tree densities ranging from 10 to 315 feet^2 of basal area per acre exist on the Experimental Forest in patches ranging from 2 to 71 acres in size (excluding the area where the nurseries occurred) (figs. 158, 159).

Forest Health Protection of the Rocky Mountain Region (USFS, Region 2) monitors the MPB populations yearly in the Hills (figs. 65–69). The 2014 survey showed the center of the Black Hills Experimental Forest heavily infested with MPBs, which, because of its inaccessibility due to topography, was not treated (Harris 2014) (fig. 158).

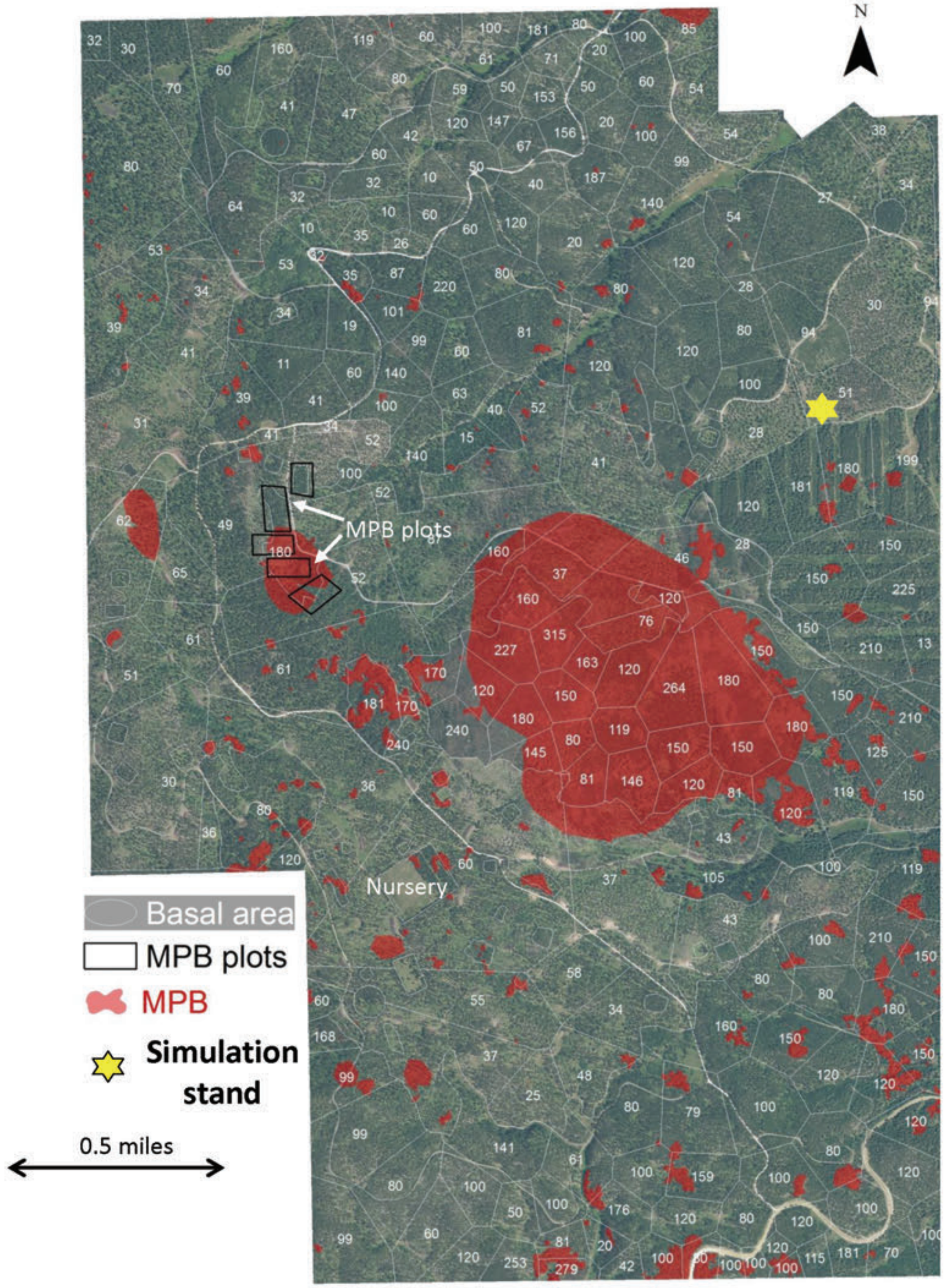

Figure 158— Thiessen polygons were generated using 206 forest inventory plots distributed across the Black Hills Experimental Forest that sampled stand density as basal area. Each Thiessen polygon defines an area of influence around its sample point so that any location inside the polygon is closer to that point and the basal area per acre it represents than any of the other sample points. The polygons were drawn over a 2012 National Agriculture Imagery Program (NAIP) image (1-m resolution), and the 2014 Forest Health Protection areas of MPB infestation are shown in red (Harris 2014).

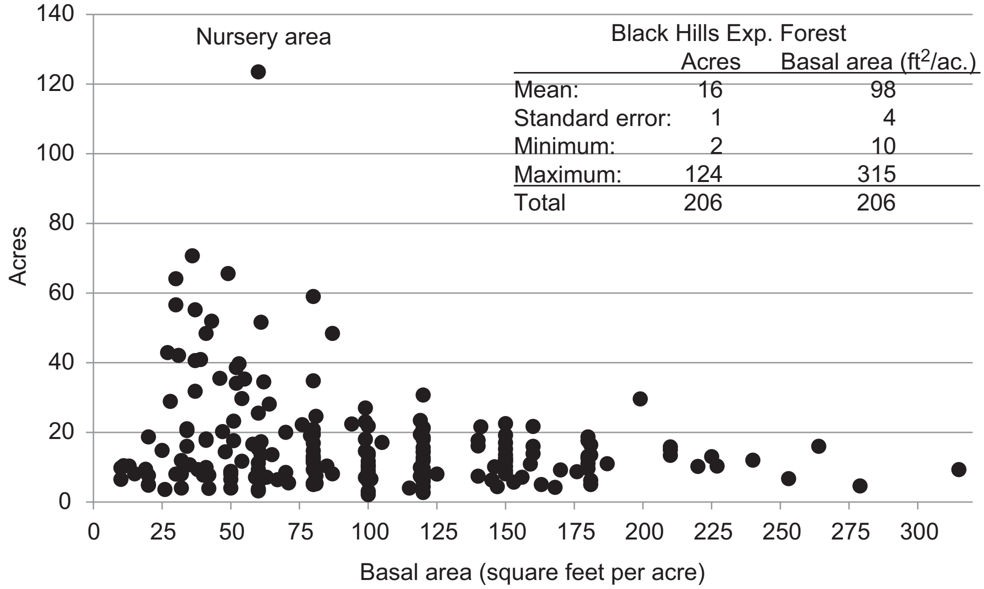

Figure 159—The 206 Thiessen polygons based on the plot basal areas ranged in size from 2 to 124 acres in size and their tree densities ranged from 10 to 315 feet^2 of basal area per acre.

Within this area, a variety of tree densities occurred, but they all tended to exceed 100 feet^2 of basal area per acre, with 9.3 acres having 315 feet^2 per acre of basal area per acre, the highest observed on the Experimental Forest (fig. 158). Also, the MPB survey of the Experimental Forest showed how MPBs were attracted to small patches of dense trees. For example, the area where plot EF154 was located experienced high MPB-caused mortality and the 4.6 acres with a density of 279 feet^2 per acre of basal area located on the southern boundary of the Black Hills Experimental Forest were heavily infested with MPBs (figs. 76, 158). However, this patch located on the southern boundary was most likely in the vicinity, if not adjacent to, a high amount of MPB activity on minimally treated lands located south and west of the Black Hills Experimental Forest (fig. 158).

The center of the Black Hills Experimental Forest was heavily infested with MPBs and a large number of trees were killed that reflected the tree mortality occurring on plot EF154, which lost 309 trees per acre and plot EF112 that lost 164 trees per acre to MPBs (figs. 128-plots 31, 19, 158). This area of high MPB infestation covered approximately 400 acres or 12 percent of the Experimental Forest. What could be termed an endemic MPB infestation occurred over the remaining 88 percent (2,900 acres) of the Experimental Forest, giving rise to the suggestion that heterogeneous landscapes composed of stands with heterogeneous structures and containing densities in the neighborhood of 80 feet^2 of basal area are resistant to MPB infestations (figs. 154–156, 158, 159). This suggestion is reinforced by the area surrounding the Experimental Forest that was severely infested with MPBs and has sustained high tree mortality as a result of MPBs in stark contrast to the Experimental Forest (fig. 160).

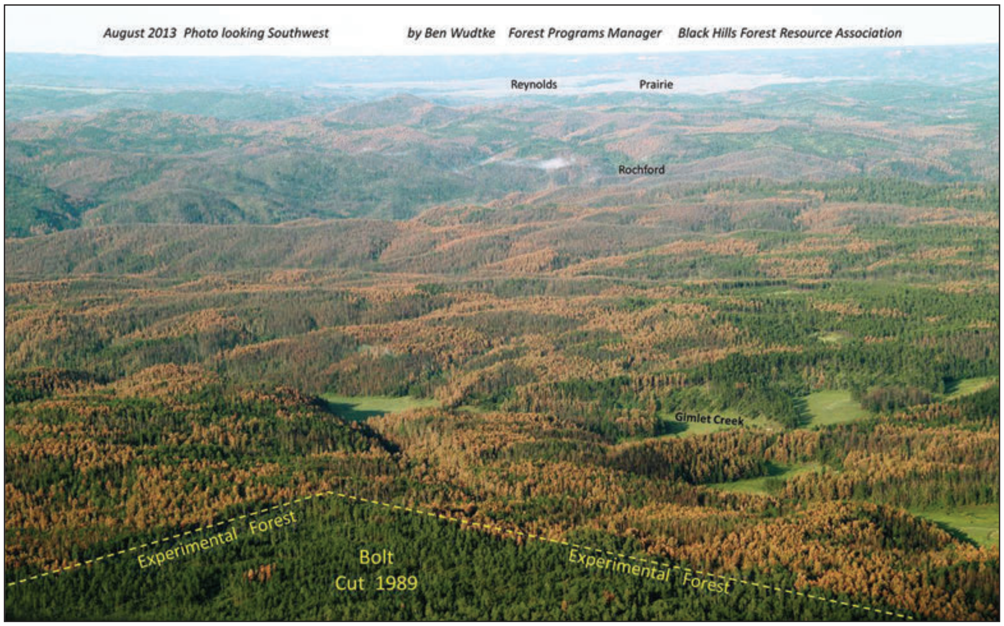

Figure 160—MPBs were very active around the Black Hills Experimental Forest beginning in 2010 and in 2013 the effect of reducing stand density on the Experimental Forest beginning in 1989 through 2013 was very effective in reducing MPB attacks (see figs. 158, 161) (photo taken in August 2013 looking southwest by Ben Wudtke, Black Hills Forest Resource Association).

Discussion

MPBs are amazing critters with an abundance of associated organisms. MPBs are native to North America; they were killing trees some 35 million years ago in what is now Colorado (Furniss and Carolin 1977; Leng 1920). Using their sense of smell, touch, feel, sight, and taste they have evolved into a complex and very destructive agent to the forests of North America and the World. Bark beetles have developed sophisticated communication systems by using pheromones and sounds to attract and repel other bark beetles and organize their tree attacks. They can distinguish among different tree species and have evolved into multiple bark beetle species that each attack and kill only one or a few tree species. Being so destructive, bark beetles have been studied and classified for over 250 years; Google Scholar lists several publications discussing the insect order Coleoptera and bark beetles dating to the middle 1700s. Also, Google Scholar lists over 120,000 publications and citations (2016) related to bark beetles. The Black Hills "tree destroying" bark beetle, which is now called the mountain pine beetle (MPB), was first described in the Black Hills in 1901 by Andrew D. Hopkins. From this beginning, the Black Hills became the center for studying MPBs and testing methods of controlling them and minimizing their impacts for many decades (Furniss 1997, 2007; Hopkins 1902).

Metropolis Under the Bark

Hundreds of different species of fungi, yeasts, nematodes, mites, algae, viruses, and bacteria are carried by MPBs as they move from tree to tree as they complete their lifecycle (Hofstetter et al. 2015). An unknown number of individuals of each of these species, probably numbering in the thousands, have both antagonistic and beneficial relations with MPBs. The relationships among all of the entities living under the bark can change depending on organism populations, MPB condition, weather, and tree condition (Amman and

Cole 1983; Mercado et al. 2014). Most notable of these organisms are the blue-stain fungi that MPBs carry with them; within 10 days these fungi can impede xylem function and most likely within the same time-frame impede phloem function, which dooms the tree to death (Hubbard et al. 2013; Six and Wingfield 2011). By obstructing water movement, the fungi reduce sap and pitch flow, which helps the MPB to mass attack and colonize a tree within 48 hours, ensuring their production of a new generation of MPBs. The fungi benefit because they are transported from tree to tree, which ensures that they can reproduce and minimize inbreeding that can be detrimental to both the fungi and the MPB (Amman and Cole 1983; Six 2012). As a result of both the fungi and the MPB, the tree is killed within 1 year, which would not occur if the 2 species did not work together (Hubbard et al. 2013; Mercado et al. 2014; Yamoka et al. 1990).

The relations between blue-stain fungi and MPBs are minimally understood but documented and the relations among all of the other species carried by the MPB are obviously as complex and intriguing, but our understanding of these relations is rudimentary at best (Six 2012; Six and Bracewell 2015;). For example, mites, these small but ferocious microscopic carnivorous arthropods, are carriers of blue-stain fungi, and 96 species of mites have been identified as being associated with the southern pine beetle (Bridges and Moser 1983; Moser and Roton 1971). Similarly, Massey (1974) lists 32 mite species and 112 associated nematode species that are parasitic on MPBs and there is an unknown number of other fungi, yeasts, and bacteria species linked to MPBs (Hofstetter et al. 2015; Six 2012; Wegensteiner et al. 2015). As with the MPBs themselves, all of these under-the-bark organisms are influenced by the physical and climatic environments they are exposed to. What is intriguing about all of the potential interactions among all of these organisms, the MPBs, and the trees they inhabit, is that they kill their home and food supply (i.e., tree). As a result, these associated organisms need to make sure they are represented and transported when MPBs emerge to colonize new trees. When fewer and fewer suitable trees for colonization become available and when bark beetle populations are high, the beetles have more difficulty avoiding the increasing deleterious effects of these associated organisms. Most likely, inbreeding, parasitism, necrophilous (eating the dead), cannibalism, predation, and a host of other interactions within and among all of these organisms lead to the fitness decline of the MPBs and lead to subsequent declines in their populations along with the depletion of suitable hosts. With this battle of creatures going on in the metropolis under the bark of infested trees and the MPB surviving for centuries, it was no wonder that the direct control of MPBs had minimal success.

Direct Control

The narrative of MPBs is a story about the insects and their associates, but it is also a story about the people who studied them and tried to control them, the administrators who directed these activities, and the public who witnessed their destruction. Similar to wildfire, the control of insects and diseases were paramount to the early development of the Forest Service and were a rationale for its creation (Keen 1952; Lewis 2005). Brilliant and observant scientists have studied bark beetles in the western United States for over 100 years and have made valiant attempts to understand them and devise ways of controlling them (Furniss 2007; Furniss and Carolin 1977; Keen 1958; Wickman 1987). With this understanding, there was the tendency for them to be advocates for bark beetle control even though their own work and work of others had shown that all of the peel, burn, trap tree, oils, insecticides, and a myriad of other direct control treatments at best saved one tree for every tree that was treated (Miller and Keen 1960; Smith 1990; Thompson 1975; Wickman 1987). Also, more than one scientist was adamant that direct control of MPBs was responsible for the end of an epidemic even though the evidence was to the contrary (Barker 2003; Blackman 1931; Furniss 1997; Hopkins 1909; Wickman 1987). It wasn't that the control treatments were not effective in killing bark beetle broods (sometimes with difficulty) under the bark to prevent bark beetle spread, it was the difficulty in locating and finding every infested tree. Keen attempted to visit every ponderosa pine tree on 18,560 acres, section by section (640 acres per section), and found it impossible to locate every WPB infested tree and treat it (Miller and Keen 1960). In some sections, if 4 to 5 infested trees were missed, in the same section the next year 18 to 36 trees were infested (fig. 40). Similarly, in the Black Hills they used build-up ratios of 1:2, 1:3, and 1:4 indicating that for every tree they missed that was infested by MPBs, they could expect 2 to 4 additional trees attacked the next year (Thompson 1975). Even though direct control of MPBs was minimally effective, administrators driven by public opinion continued to spend millions of dollars trying to control these insects.

Spruce beetle control in the northeastern United States and southern pine beetle control commenced in the late 19th and beginning of the 20th centuries as a response to protecting timber resources from the damage bark beetles were causing (Hopkins 1909). Similarly in the western United States, again for the protection of timber resources, direct control of bark beetles began in the early 1900s (Hopkins 1909; Miller and Keen 1960). Timber company executives, State legislators and governors, and the general public clamored for bark beetle control and both State and Federal agencies responded (Freeman 2015; Newport 1956; Thompson 1975; Wickman 1987). There was tremendous pressure on rangers, forest workers, park superintendents, and other administrators to solve the bark beetle problem and the scientists were providing them with information and often participated in major bark beetle control efforts (Craighead et al. 1931; Thompson 1975; Wickman 1987). Clark (1978) indicated that direct control of MPB-infested lodgepole pine trees had little or no success. For the most part, it was an exercise in futility, undoubtedly because symptoms were being treated rather than the underlying problem. In addition, there are so many instances where glowing reports of success in controlling MPBs were written but very often they would include a statement alluding to the fact that a little more work and money were needed and the problem would be solved. Or the corollary that the MPB epidemic was suppressed because of the direct control measures (Blackman 1931; Hopkins 1909; Wickman 1987). There was organizational pressure to ensure that the control measures would succeed as their failure would look bad for the organization charged with controlling the MPBs. As a result, scientists, administrators, and policy makers were all pushing for the success of bark beetle control, much like trying to control blister rust in the northern Rocky Mountains where major control efforts for both timber killing organisms continued into the mid-1960s and occasionally into the early 1970s (Ketcham et al. 1968; Thompson 1975). All efforts failed to control blister rust and bark beetles even though many scientists, managers, and policy makers argued convincingly that the efforts informed by science worked even though for both disturbances there was evidence in the 1920s that the control efforts were not effective (Maloy 1997; Miller and Keen 1960). Whether it was fatigue, lack of money, or shear hopelessness, such direct bark beetle control efforts greatly diminished by the 1970s and other methods were sought to lessen the damage MPBs were causing (Barker 2003; Clark 1978; Thompson 1975; Wickman 1987).

Indirect Control of Bark Beetles

F. P. Keen, both a forester and entomologist and once again being a superb observer, pioneered the concepts of using tree and stand characteristics for selecting trees to remove or leave to increase stand resistance to WPBs and MPBs (Keen 1936; Keen and Salman 1942; Miller and Keen 1960). His crown vigor classes and tree risk ratings have been used for nearly a 100 years in choosing ponderosa pine trees to remove or leave when treating stands to increase tree vigor and improve forest resilience to disturbance (Freeman 2015; Jain et al. 2014; Jain 2015, personal communication; Keen and Salman 1942; Newport 1956). Within the Black Hills, Keen recognized his tree risk ratings for bark beetle attack in the early 1950s would not work and suggested another approach was needed to manage the second growth ponderosa pine stands for MPB resistance (Furniss 2007). By 1962, within the Black Hills, tree density control was more frequently mentioned as a need for decreasing MPB risk and the pulp wood market that developed in the Hills in the 1960s allowed for many stands to be thinned (Freeman 2015; Graham 2015c, personal communication; Thompson 1975). And Sartwell and Stevens (1975) suggested stand densities of less than 125 feet^2 of basal area per acre as being resistant to MPBs in the Black Hills, providing the impetus for Schmid and Mata to establish the MPB study plots across the Black Hills.

From 1985 through 1994 Schmid and Mata (1992) established 46 MPB study plots but 4 were lost to wildfire and 3 were not treated. As a result 39 useable plots containing tree densities ranging from 44 to 199 feet^2 of basal area per acre were distributed throughout the northern and central portions of the South Dakota Black Hills. The plots were visited at varying intervals from the time they were established through 2012, with the plots on the Black Hills Experimental Forest being measured 7 times and the Medicine Mountain plots measured 4 times. As a result, thousands of tree observations were taken describing the fate of each tree on the plots, with some facing intense pressure from MPBs and others not. Major tree mortality caused by MPBs occurred at tree densities as low as 77 feet^2 and high as to 220 feet^2 of basal area per acre (fig. 127). Also, it is worth noting that plots beginning with 80 feet^2 of basal area per acre and subsequently increasing to 100 feet^2 and those increasing to 125 feet^2 per acre had substantially more MPB-caused mortality than those increasing to 90 feet^2 of basal area per acre. Amazingly, these subtle changes in tree density could have such contrasting outcomes (figs. 128–138). Similarly, the findings that MPB-caused tree losses were both quantitatively and proportionally less on plots with 150 to 220 feet^2 of basal area per acre compared to plots with 120 to 150 feet^2 of basal area per acre were contrary to what was expected. However, the tree losses caused by MPBs on both density clusters were substantial (figs. 128–141). Even though MPB-caused tree mortality occurred at tree densities below 80 feet^2 of basal area per acre, stands with tree densities ranging from 40 to 80 feet^2 per acre of basal area per acre showed considerable resistance to MPBs (figs. 120, 121, 128–138, 152–156).

Although not definitive, these MPB-resistant tree densities could be related to the weather created by the open and heterogeneous stand conditions created by thinnings (Edburg et al. 2010). Air inversions under tree canopies create ideal conditions for pheromone plumes to develop and allow for effective MPB communication. Such conditions could be minimized by opening the forest canopy through thinning. The open stand conditions could cause differential forest floor heating that could increase air turbulence, which would disrupt pheromone plumes (Rosenberg et al. 1983). Similarly, openings in the tree canopy would let pheromone plumes vent out of the tree canopy so they would be torn apart by winds blowing above the canopy (Fares et al. 1980). These within-stand heterogeneous conditions in concert with a mixture of such conditions across the landscape look to be the preferred forest conditions to reduce the impacts of MPBs, as the condition of the Black Hills Experimental Forest exemplified (figs. 158–160).

Exceptions

However convincing the data and resultant arguments are that heterogeneous stands and landscapes with tree densities less than 80 feet^2 of basal area per acre are resistant to MPB attacks, there are exceptions. Most notable are the stands located at Crook Mountain. Three thinned and one unthinned plot were established in 1986 with tree densities ranging from 84 to 158 feet^2 of basal area per acre (fig. 122). In 1986, right after the plots were established, MPBs killed two trees per acre on plot CMt84, four trees per acre on plot CMt104, one tree per acre on plot CMt119, and one tree per acre on plot CMt158. As a result, MPBs have been in the vicinity of Crook Mountain since 1986 and through 2012 they have caused less mortality than weather (fig. 122). In 2012, the tree densities on the thinned plots ranged from 103 to 176 feet^2 of basal area per acre and compared to the other 35 plots, the trees on these plots are at high to very high risk of being attacked and killed by MPBs. It is not that the stands in the area did not have MPB infestations because this latest MPB epidemic had its genesis (circa 1999) a few miles south and east of Crook Mountain (fig. 66). And by 2012 the central and northern part of the South Dakota portion of the Black Hills were heavily infested with MPBs (fig. 161). So this outcome begs the question: “why?”

Also, figure 161 shows numerous infestations by MPBs west of the Wyoming border, south of Sundance and north of Newcastle, but not the severe infestations occurring just east of the border in South Dakota. Similarly the Bear Lodge north of Sundance is peppered with MPB infestations, but again not the severe damage that occurred within the central Black Hills. The argument can be made that these areas, not severely infested by MPBs, will succumb to MPBs in the future. However, possibly because the fitness of the MPB is declining, the epidemic in the Black Hills is subsiding (Allen 2014, personal communication). But that assertion most readily applies in the area that has been severely impacted and not these areas where MPBs have tended to be endemic. In the epidemic of MPBs at Crater Lake in the 1930s, it was suggested that the insects would continue to spread until they ran out of mature lodgepole pines trees (food) to infest (Wickman 1987). This rationale for declining MPB populations is quite plausible in lodgepole pine forests but appears to be less so in ponderosa pine forests as the MPB dynamics in the Black Hills has shown over the last 15 years or so.

A cogent argument can be made that heterogeneous stands and landscapes that likely occurred before the advent of fire suppression and timber harvesting, and shown by the data in this publication, were resistant to MPB attacks (Bentz et al. 2009; Fettig et al. 2014). As suggested by Sartell and Stevens (1975), Amman and Cole (1983), and Fettig et al. (2014) and tested by Schmid and Mata (1992) and validated and rationalized in this publication, basal area is a well suited stand metric for describing MPB risk. Moreover, data presented in this publication suggest a MPB threshold 80 feet^2 of basal area per acre as a target for producing MPB-resistant stands in the Black Hills. The data presented here and suggested by Bentz et al. (2009) and Fettig et al. (2014) are heterogeneous within and among stands across landscapes and are additional measures for creating and maintaining MPB-resistant forests (fig. 152–160).

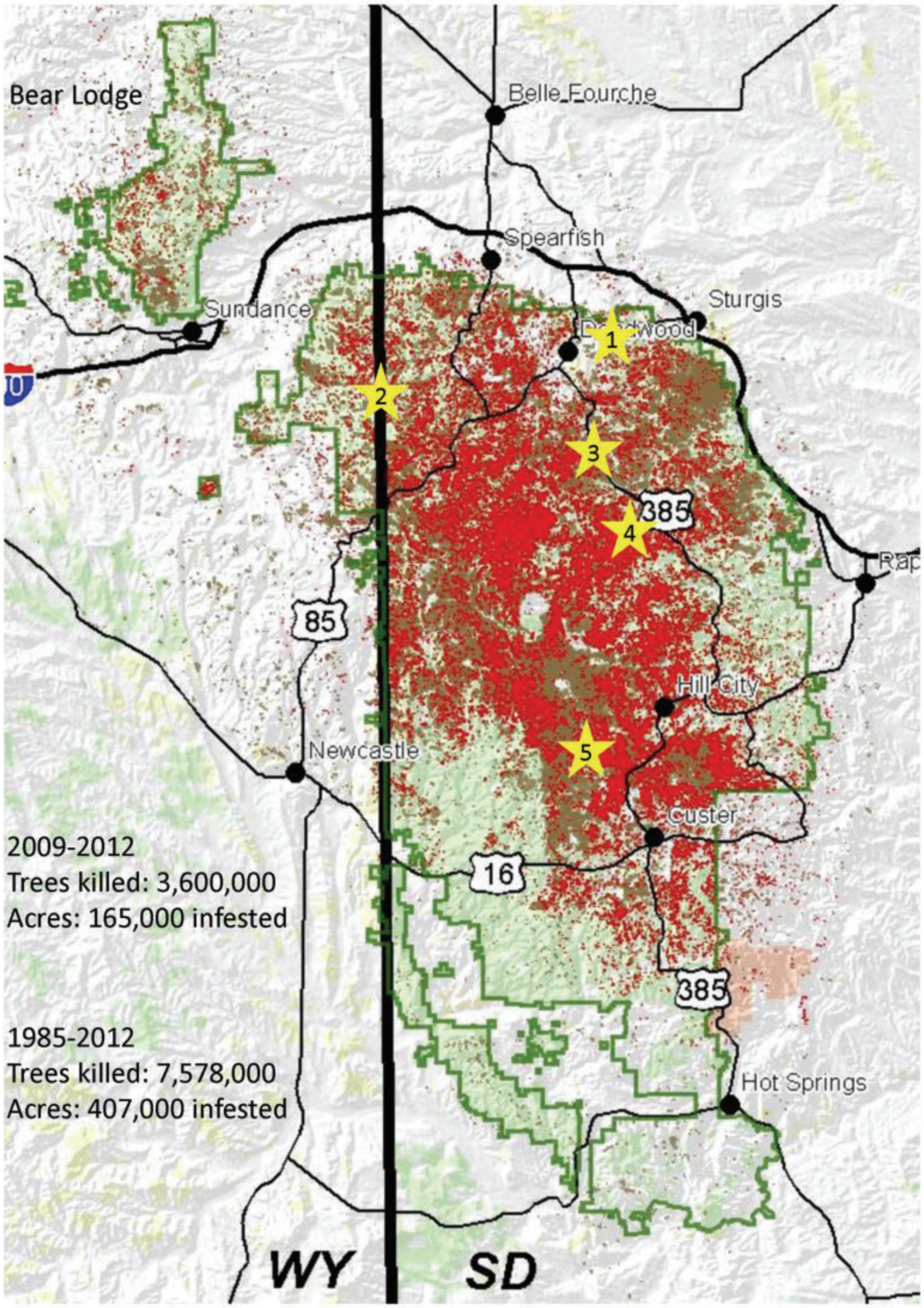

Figure 161—By 2012 the border (2), Custer Crossing, Custer Peak, Brownsville (3), the Experimental Forest (4), Boy Scout, Medicine Mountain, White House Gulch, and Bear Mountain One and Two (5) plots were intensely exposed to MPB attack. MPBs were in the vicinity of Crook Mountain (1) but minimal bark beetle caused mortality occurred on those plots.

Early Settlement Forest Structure in the Black Hills and Mountain Pine Beetles

Prior to 1900 and photographed by Illingworth when he travelled with General Custer as they explored the Black Hills from July 2 through August 30, 1874, the stands and the forests of the Black Hills were very heterogeneous (Grafe and Horsted 2002). They contained a mix of openings, meadows, and variable sized trees (fig. 162). Brown and Cook (2006) reconstructed stand density expressed by basal area per acre of large trees circa 1900 before tree harvests occurred in the Black Hills. They sampled 112 ponderosa pine stands and found that large tree basal area averaged 69 feet^2 per acre although there was a great deal of diversity in tree density. Approximately 35 percent of all stands contained 0 to 44 feet^2 of basal area per acre in large trees but seven stands (6 percent) contained greater than 174 feet^2 of basal area per acre. They went on to say historical ponderosa pine forests in the

Illingworth Valley No. 824
6.2 miles north of Custer east of Hwy 385
on Custer County line.

Gold Quartz Mt. No. 822
5.7 miles north of Custer
east of Hwy 385

Sunshine and Shadow Mount No. 832
Near Mickelson Trail 2.5 mi
north of Custer

Organ Pipe Range No. 826
5.0 miles north of Custer in
Norbeck Reserve

Figure 162—Illingworth, a photographer traveling with Custer in 1874, took several photos of the Black Hills. The forests tended to have open tree canopies and were highly variable as these photos taken just north of Custer show. See Grafe and Horsted (2002) for full descriptions and locations of where the photos were taken and a view of what the area looked like in 2000 (photos: Grafe and Horsted 2002).

Black Hills consisted of a diverse landscape mosaic that varied from non-forested patches and open stands of few large trees to quite dense stands with many similar-sized and -aged trees (fig. 162). In 1897, Graves (1899) indicated the stand basal area in the Rifle Pit area near the Wyoming border (east of Sundance, Wyoming) was 139 feet^2 per acre and in the Slate Creek area the tree density was 121 feet^2 of basal area per acre (north of Hill City, South Dakota). Based on the data presented in this publication, the appearance of these heterogeneous stands and landscapes that occurred in 1874, and the forest metrics supplied by Graves (1899) and Brown and Cook (2006), the forests of the Black Hills pre-1900 would be highly resistant to MPBs (Bentz et al. 2009; Fettig et al. 2014; Grafe and Horsted 2002). With that being the case, then why in 1884 did the largest MPB epidemic ever to occur in the Black Hills commence (fig. 163)? Graves first discovered "bark borers, a species of the Scolytidae," killing trees within the Black Hills in 1897 and Hopkins with Pinchot's help documented and described the "Black Hills beetle" as the cause in 1901 (Graves 1899; Hopkins 1902)—a very interesting conundrum.

Bark beetles have been killing trees throughout western North America for centuries and Hopkins postulated a large portion of the damaged and killed trees attributed to fires were actually the result of MPBs (Furniss and Carolin 1977; Hopkins 1909). When Custer

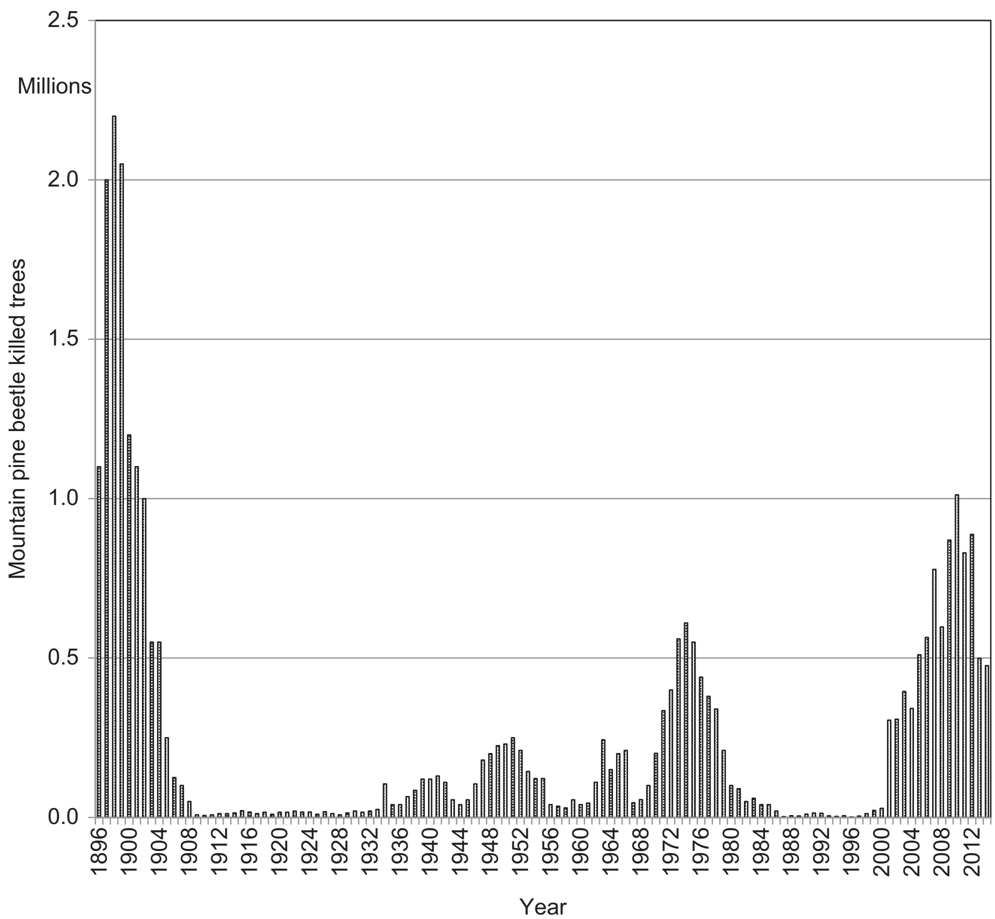

Figure 163—Within the forests of the Black Hills, there has been a continuous endemic and several epidemics of MPBs over the last 129 years. There is an uncertainty about how many trees were killed but the above graph provides estimates from descriptions and values provided by Graves (1899), Hopkins (1910), Murdoch (1910), Furniss (1997), Thompson (1975), Lessard et al. (1987), Freeman (2015), Harris (2003, 2004, 2005, 2006, 2010, 2011, 2012, 2013, 2014), and Harris et al. (2001, 2002).

descended Harney Peak on July 31, 1874, he encountered large amounts of dead and downed timber that were likely killed by MPBs, indicating some areas in the Hills had endemic populations of MPBs (Ludlow 1875). In 1897 Graves (1899) estimated about 3,000 acres of ponderosa pine trees had been killed by MPBs near Crook Tower and within the headwaters of little Spearfish Creek (fig. 9). In 1901, a more detailed estimate of the timber in the Black Hills Reserve was completed and 116,000 acres of trees were estimated to have been killed by MPBs (Hopkins 1902). Also, Hopkins (1902) suggested that a major portion of the trees that were thought to have been killed by fire in the Black Hills in the 1870s and 1880s were actually killed by MPBs. A resident living near Piedmont, South Dakota, (located 10 miles north of Rapid City on Interstate 90, fig. 2) in 1898 described many trees dying that had small holes drilled in them most likely caused by a small black insect. Hopkins (1910) reported that a billion board feet of ponderosa pine were killed in the Black Hills National Forest from 1900 through 1910 by MPBs and Furniss (1997) indicated that one and a half billion board feet of timber had been killed during the same time period. Hopkins suggested during this MPB epidemic that about 2,000 board feet of timber per acre were killed, indicating that this first recorded MPB epidemic in the Black Hills covered 500,000 to 750,000 acres. This assemblage of anecdotal information on MPBs indicates that the tree mortality caused by MPBs was extensive but most likely concentrated in the South Dakota portion of the Black Hills and adjacent lands just west of the Wyoming border. The Bear Lodge in northeastern Wyoming likely had MPB activity; but with fewer people and no major mining activity, MPB mortality would not have been readily described or reported (fig. 2).

These historical descriptions of the forests of the Black Hills and the anecdotal evidence of a major epidemic of MPBs occurring in these relatively low density and heterogeneous stands and landscapes underscores how little we really know about bark beetle dynamics. As presented in this publication, a very cogent argument can be made that stand densities ranging from 40 to 80 feet^2 of basal area per acre and heterogeneous landscapes containing such tree densities are resistant to MPBs. Nevertheless, such forests in the Black Hills were severely impacted by MPBs from 1895 through 1909 (fig. 163). Whatever the cause—weather, bark beetle fitness, food supply, or stand and landscape structure—the initiation and cessation of MPB epidemics, especially in ponderosa pine forests, is poorly understood. MPB outbreaks in the Black Hills from 1894 through 2014 had a mean return interval of 20 years and a mean duration of 13 years that ranged from 6 to 18 years (fig. 163). The intensity of these MPB epidemics also varied with the 1900 MPB activity considered the most severe and followed by the 1974 and 2012 MPB out-breaks. Even with over 100 years of studying, observing, trying to control, and treating forests to lessen their impacts with the Black Hills being the epicenter of such activities, the understanding of MPB dynamics is far from complete.

Bark beetles and forest trees have coevolved for millions of years and both have adapted to a myriad of biophysical conditions and disturbances (Conkle and Critchfield 1988; Furniss and Carolin 1977). The Pleistocene era contained widely fluctuating environments during the full- and interglacial periods and ponderosa pine most likely was only able to expand its range during the warm interglacial periods like the present. As a result, the species has experienced major shifts in climate and has adapted to be one of the most wide ranging conifers in North America. Nevertheless, how the current varieties and races of ponderosa pine and the MPBs and WPBs respond to a changing climate is unknown. For example, the *scopulorum* variety of ponderosa pine occurring east of the Continental Divide and in the southwestern United States tends to be inbred more than the *ponderosa* variety that occurs west of the Continental Divide (fig. 164). Because of inbreeding, this ponderosa pine variety may be less able to adapt to a changing climate and possibly more readily attacked by MPBs (Potter et al. 2013). Another MPB and climate interaction is occurring on the east side of the Continental Divide in Canada. MPBs have killed ≈25 million acres of lodgepole pine trees in British Columbia and Alberta, Canada, and are approaching stands of lodgepole pine and jack pine, (*Pinus banksiana*) hybrids located in central Alberta. As climate warms, there are concerns that the jack pines of the boreal forests across Canada could be at risk to MPB infestations (Safranyik et al. 2010). Why and how an endemic population of MPBs becomes epidemic is not known, but as these examples show, climate will most likely be an important factor in MPB dynamics in the future.

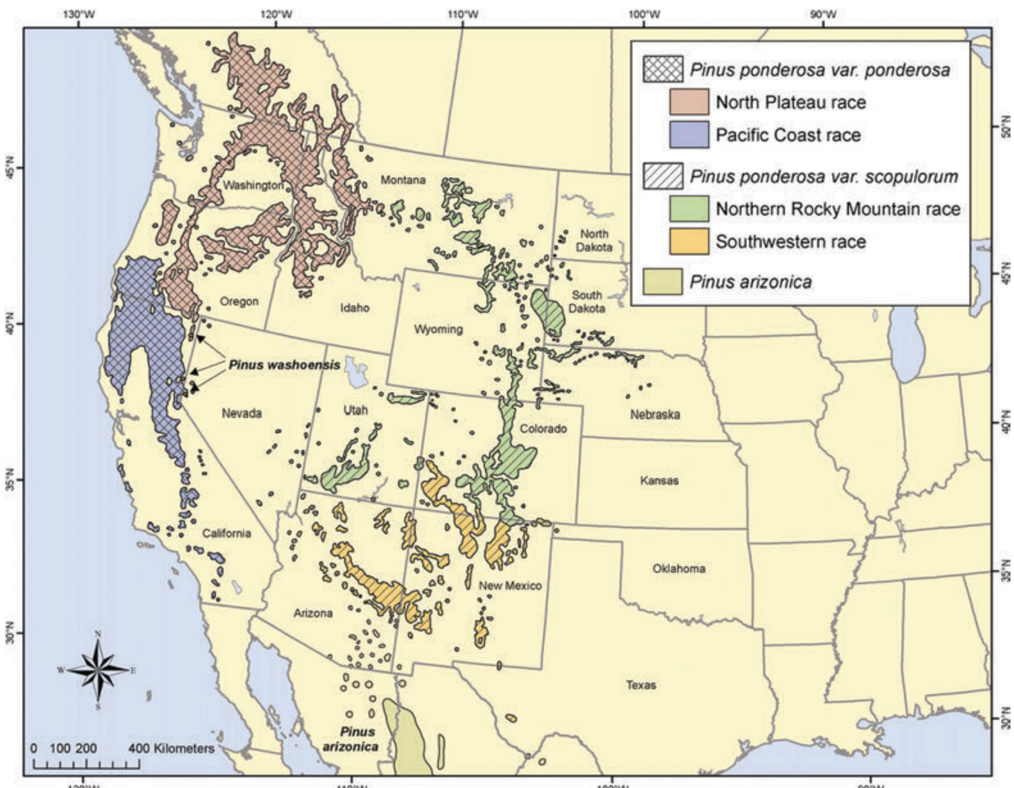

Figure 164—Over the range of ponderosa pine there are two recognized varieties and two races in each variety (Potter et al. 2013).

Concluding Remarks

MPBs are amazing critters. It seems the more we know about them the more we need to know. Most likely because the wood of trees attacked by MPBs quickly turned blue after boring dust and pitch tubes appeared on a tree, fungi were recognized as being associated with MPBs in the late 1800s and early 1900s. Along with these blue-stain fungi, mites, nematodes, bacteria, yeasts, and other fungi are moved from tree to tree by MPBs. This metropolis under the bark associated with MPBs in itself is a fascinating story. Similarly, how MPBs use sight, smell, feel, touch, and sound to locate and colonize trees is a testament to how they have evolved over the last 35 million years. They know if the wind speeds are favorable for flying and if air and tree temperatures are conducive for egg gallery construction and brood survival. MPBs work together to overcome the defenses of a tree and know when a tree is mass attacked and send pioneering MPBs to other trees so inbreeding is minimized as is competition for food and shelter within one tree.

The story of MPBs is also a story about people. As articulated by Google Scholar and attributed to Bernard of Chartres in 1159 and Isaac Newton in 1676, current scientists stand on the shoulders of giants who lived before them. So true with the study of western U.S. bark beetles. Hopkins, Keen, Miller, Eaton, Amman, Cole, Furniss, Blackman, Wickman, Sartwell, Stevens, Schmid, Fettig, Negrón, Allen, and Bentz are just a few of the scientists upon which the body of western bark beetle knowledge is based. As fascinating and very destructive organisms, bark beetles have been studied for over 100 years by intelligent, creative, and determined individuals. Hopkins with very likely only a grade to high school education was extraordinary in the knowledge he discovered and developed about bark beetles. Along with his exceptional intellect came stubbornness in his views on the success of direct control of bark beetles. He postulated that the failure to adequately address the MPBs in the Black Hills was the cause of the 1900 epidemic. Nevertheless, when the epidemic waned he was convinced that the direct control measures he suggested and applied were the reason the epidemic subsided.

In forestry and in observing and studying natural systems there is a tendency to look for and more often than not accept simple solutions to what turn out to be very complex problems. Most management decisions have a political element and some are more political than others. Also, politicians, administrators, and managers all struggled over the years at trying to find a solution to one of the most destructive agents in western forests equal to if not greater than fire in many locales. Most likely more than one ranger or forester were transferred or even lost their jobs because they failed to locate all of the trees attacked by MPBs in an area, failed to "mop-up" an infestation, or made the organization look bad by not controlling MPBs.

The role of science is not to advocate but rather inform decisions and decisions do not necessarily need to conform to science. Within this context it was amazing that even though the science and scientists knew that direct control of MPBs was futile, it went on for decades after the knowledge was discovered (≈1920). Moreover, some scientists continued to advocate for the direct control of WPBs and MPBs even though their own and findings of others showed that it was ineffective. For years, beginning with Hopkins in the Black Hills, direct control of MPBs was advocated and for more than 75 years burning, peeling, spraying, and many more methods were used in an effort to kill these insects with little success. Of special note was the toxic insecticides used to such an extent that trees "glistened" with chemicals that are now banned from use in the United States. Many of these control efforts were credited for the demise of MPB populations; however, most likely beetle fitness, lack of suitable hosts, or other unknown reasons caused the epidemic populations' return to endemic levels.

So with all of the great minds, money, and time spent trying to understand and control MPBs, a comprehensive understanding of them is elusive. As survivors for 35 million years, western bark beetles and their life histories are far more complex than anyone ever imagined. With this complexity there was always the search for a quick and simple solution to the damage they caused. If just all of the infested trees would have been located or a cold winter would occur the trouble would be over. History has proved otherwise—there are no simple solutions. Heterogeneous stands and landscapes still appear to be the most logical approach to living with MPBs. Even that assertion based on data initiated by Schmid and Mata and reported in this publication does not align with the major MPB epidemic that occurred in the Black Hills in the late 1800s and early 1900s when such forest conditions dominated. Nevertheless, such heterogeneous stand and landscape conditions appear to be a worthwhile alternative for producing wildfire resilient forests, producing wildlife habitat, maintaining functioning watersheds, producing forest products, and producing bark beetle-resistant forests in the face of a changing climate.

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Appendix A: Stand Density Index and Mountain Pine Beetles

Stand density index (SDI) is a very robust and widely used stand descriptor that offers many forest management applications. SDI is based on size-density relationships and is a valuable tool in translating management objectives into practical density management regimes. Commonly, management objectives involve some form of compromise between the mutually exclusive goals of maximizing either stand or individual tree growth. SDI, which is independent of site quality and stand age, allows management objectives to be translated into specific target levels of growing stock (Long 1985). In addition, no direct conversion from SDI to basal area per acre is possible, because many combinations of mean stand diameter and number of trees will produce identical SDIs at different basal areas (Oliver 1995) (fig. A1). Even with this limitation, SDI is very useful for describing MPB-resistant structures in the Black Hills. The figures A2 through A11 show how MPBs impacted the trees on each of the 39 plots as described by SDI. To offer an ease of comparison to how basal area changed because of MPBs, the plots are clustered by the same basal area clusters (table A1).

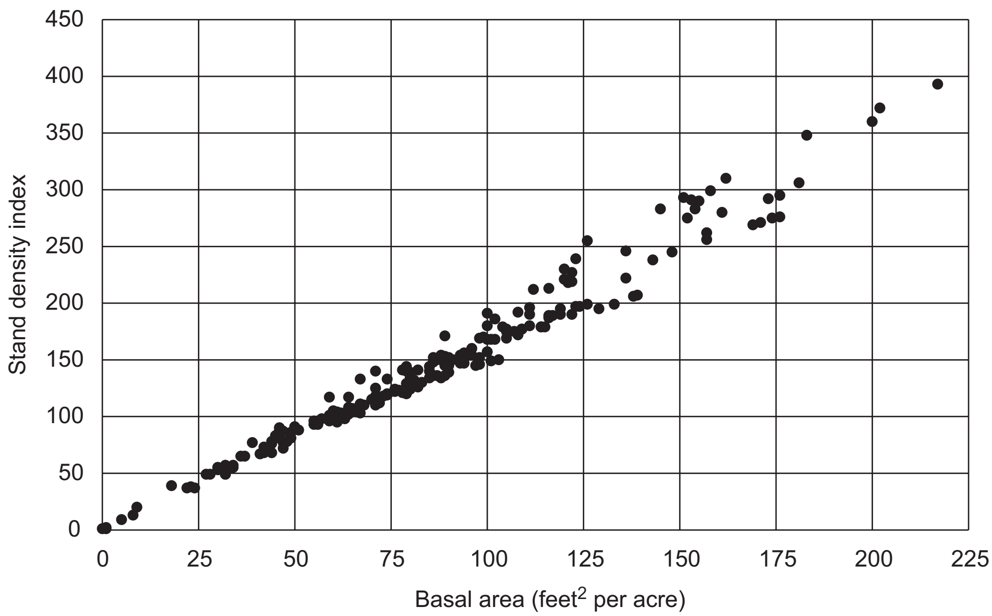

Figure A1—Over the 39 MPB plots both tree density measured by basal area per acre and stand density index (SDI) varied considerably, and for a given SDI, the basal area could vary considerably.

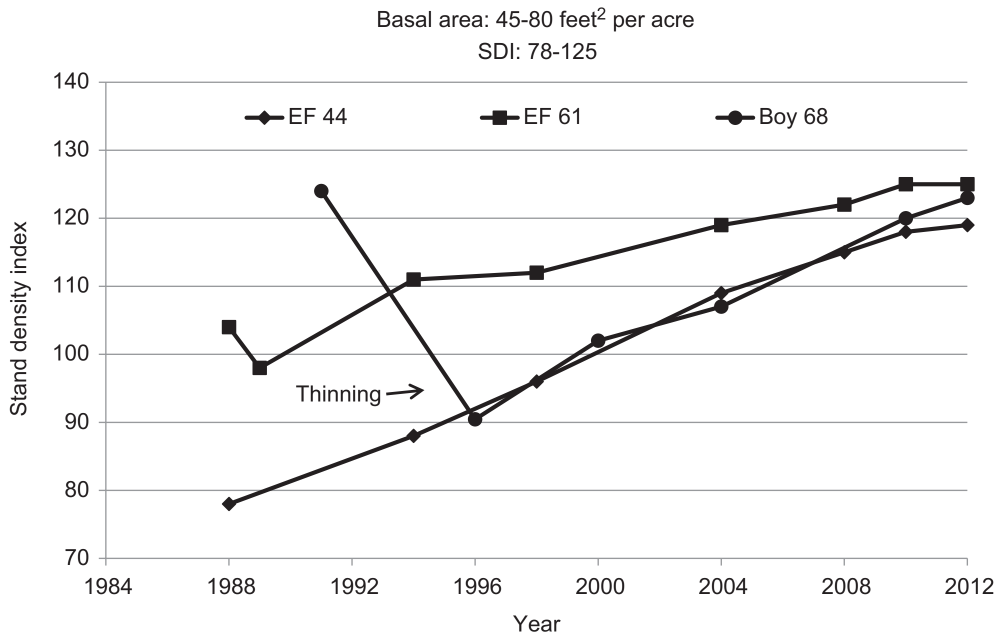

Figure A2—Trees on plots EF44, EF61, and Boy68 were minimally impacted by MPBs. Their basal areas per acre ranged from 45 to 80 feet^2 and their establishment and maximum SDIs ranged from 78 to 125.

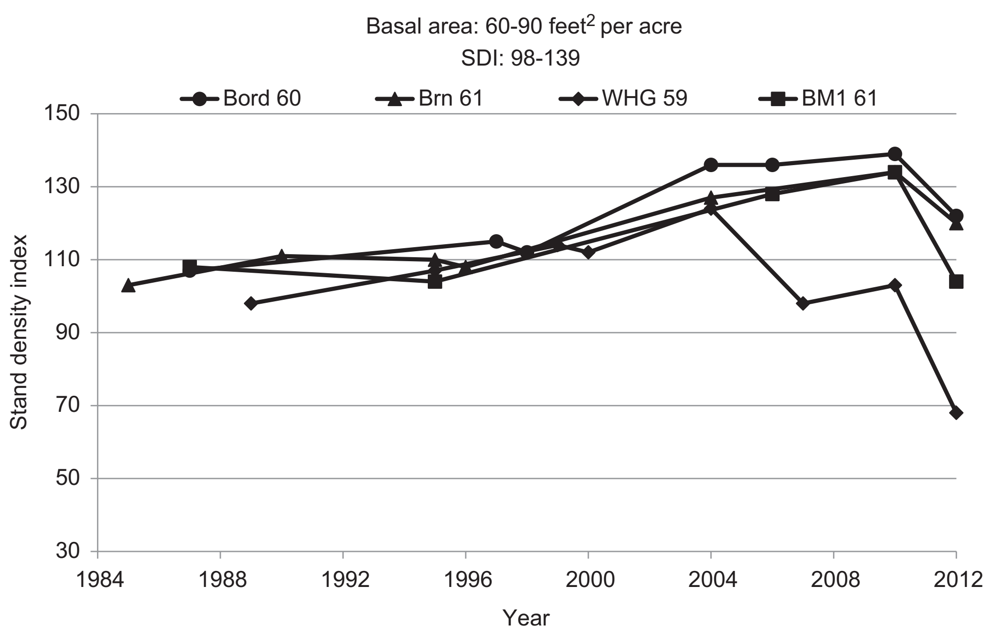

Figure A3—Trees on plots Bord60, Brn61, WHG59, and MM161 all had many trees killed by MPBs. Their establishment and maximum basal areas per acre ranged from 60 to 90 feet^2 and their establishment and maximum SDIs ranged from 98 to 139.

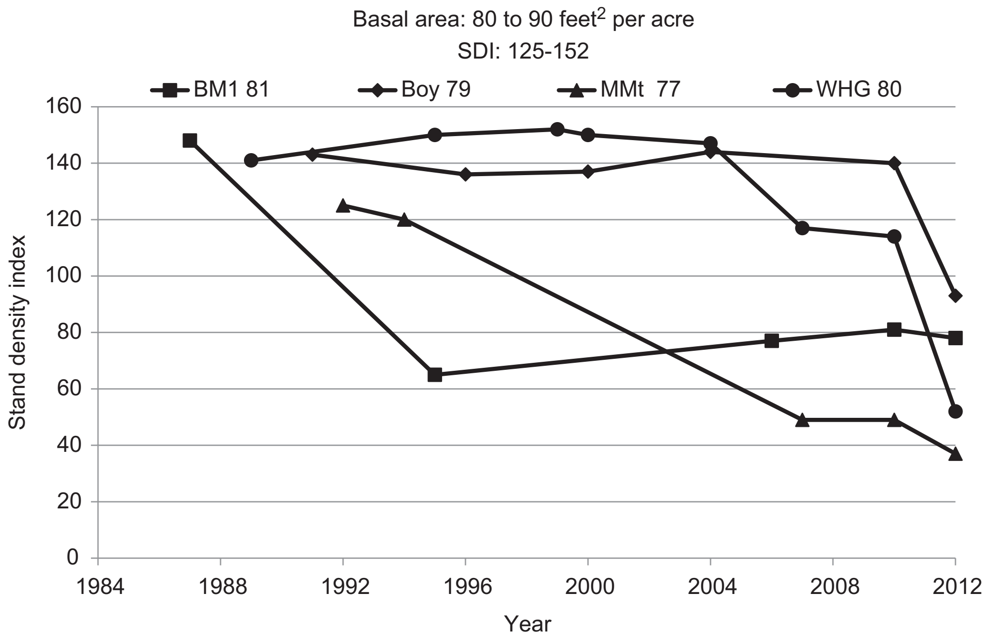

Figure A4—All of the trees on plots BM181, Boy79, MMt77, and WHG80 had major tree mortality caused by MPBs. Their establishment and maximum basal areas per acre ranged from 80 to 90 feet^2 and their establishment and maximum SDIs ranged from 125 to 152.

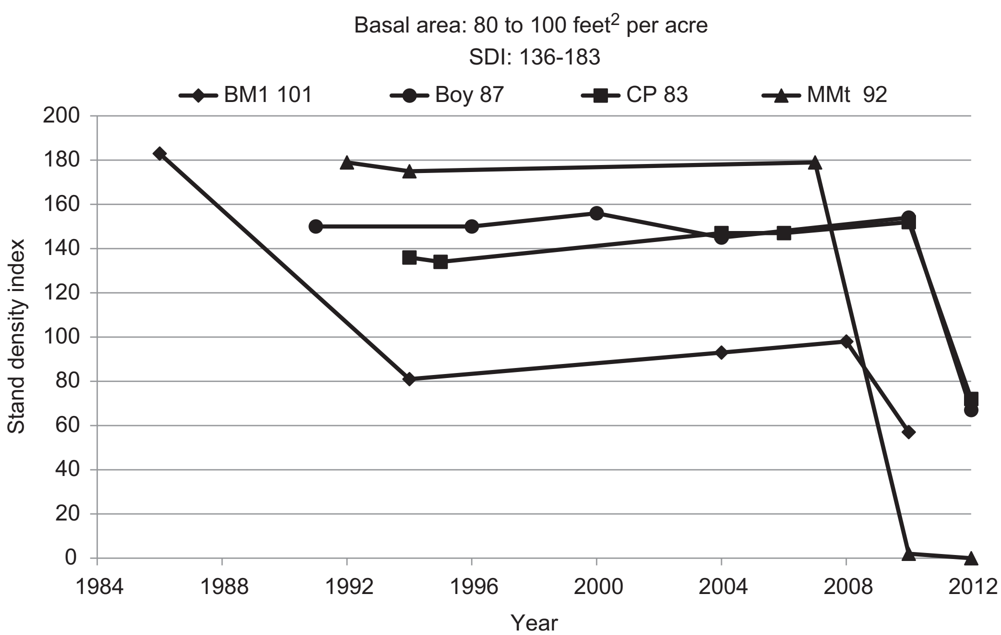

Figure A5—All of the trees on plots BM1101, Boy87, CP83, and MMt92 had major tree mortality caused by MPBs. All of the trees on plot MMt92 were killed. Their establishment and maximum basal areas per acre ranged from 80 to 100 feet^2 and their establishment and maximum SDIs ranged from 136 to 183.

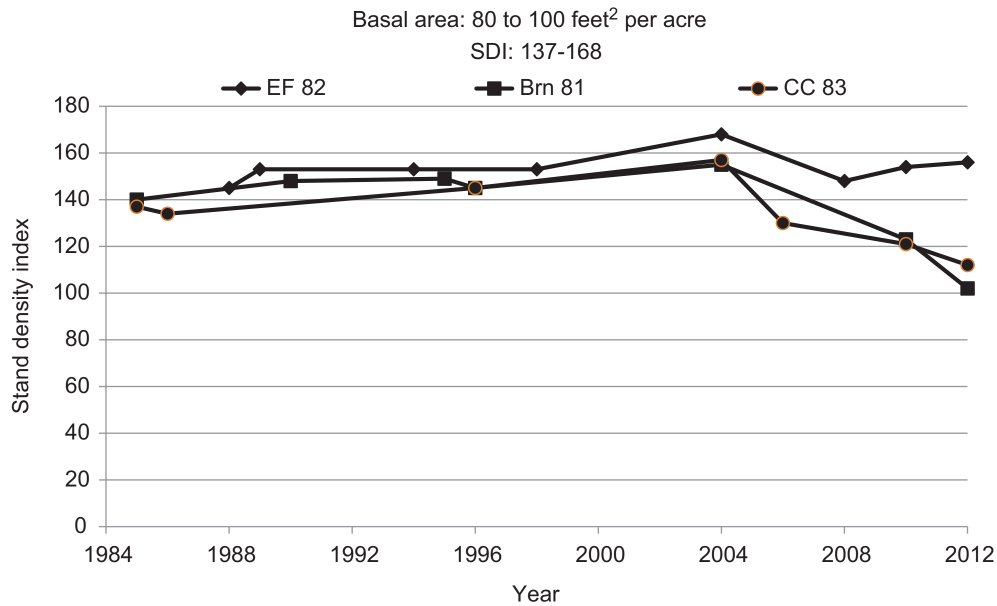

Figure A6—Trees on plots EF82, Brn81, and CC83 showed some resistance to MPBs even though their establishment and maximum basal areas per acre ranged from 80 to 100 feet^2 and their establishment and maximum SDIs ranged from 137 to 168. Contrasting outcome to the plots with the same basal area range shown in figure A5.

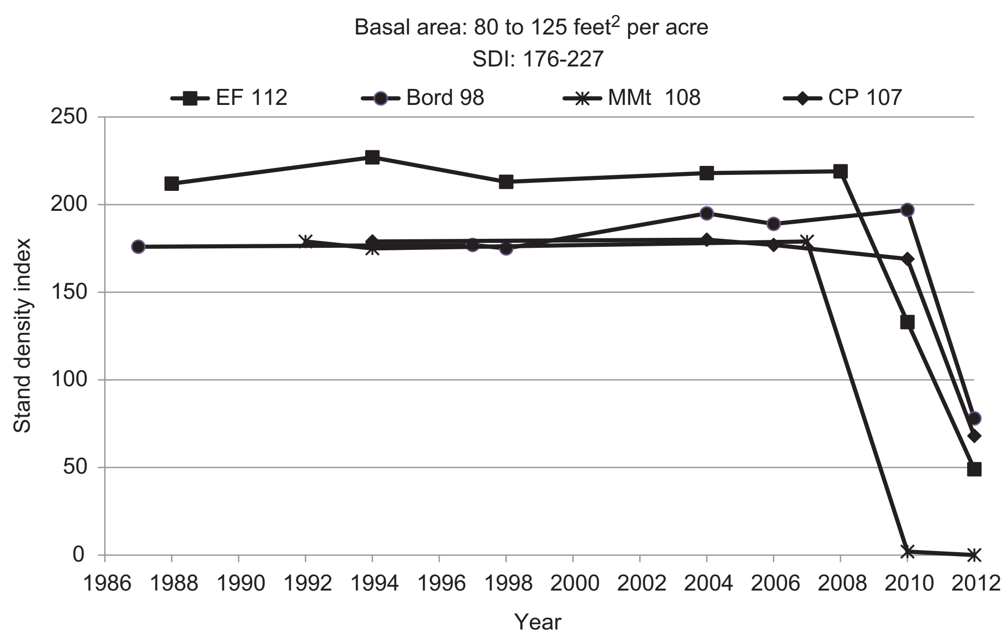

Figure A7—All of the trees on plots EF112, Bord98, MMt108, and CP107 had major tree mortality caused by MPBs with all of the trees killed on plot MMt108. Their establishment and maximum basal areas per acre ranged from 80 to 125 feet^2 and their establishment and maximum SDIs ranged from 176 to 227.

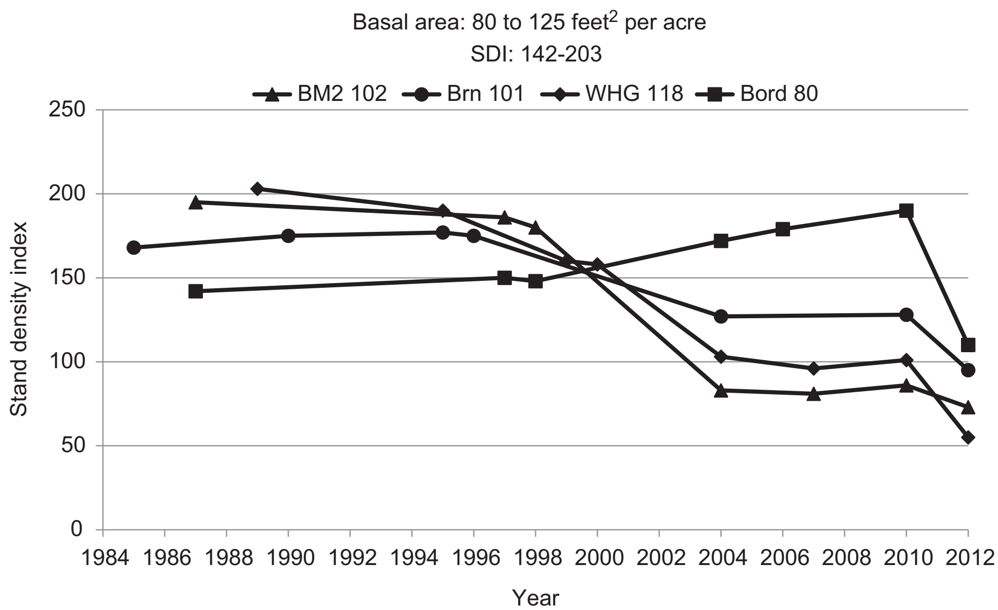

Figure A8—All of the trees on plots BM2102, Brn101, WHG118 and Bord80 had major tree mortality caused by MPBs. Their establishment and maximum basal areas per acre ranged from 80 to 125 feet^2 and their establishment and maximum SDIs ranged from 142 to 203.

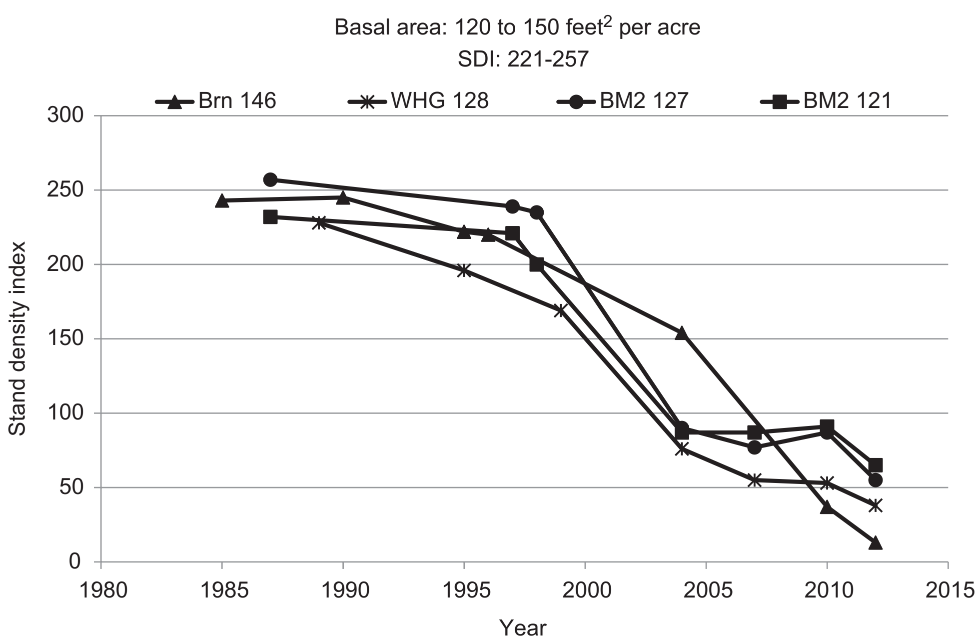

Figure A9—All of the trees on plots Brn146, WHG128, BM2127, and BM2121 had rather continual tree mortality caused by MPBs. Their establishment and maximum basal areas per acre ranged from 120 to 150 feet^2 and their establishment and maximum SDIs ranged from 221 to 257.

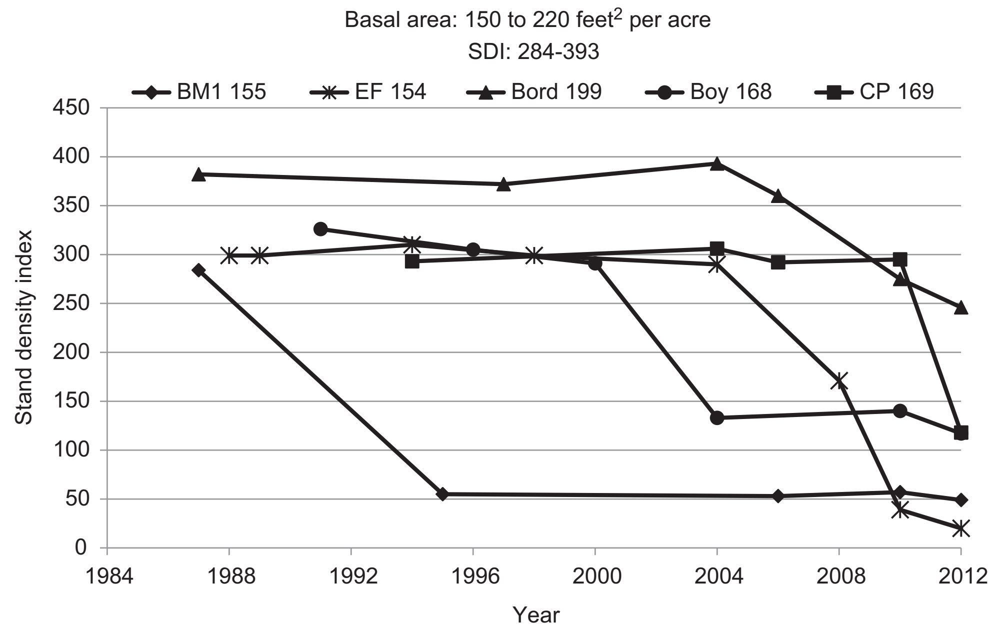

Figure A10—All of the trees on plots BM1155, EF154, Bord199, Boy168, and CP169 had major tree mortality caused by MPBs. Most notably, MPBs caused major tree mortality on plot BM1155 right after it was established in 1987. The plot establishment and maximum basal areas per acre ranged from 150 to 220 feet^2 and their establishment and maximum SDIs ranged from 284 to 393.

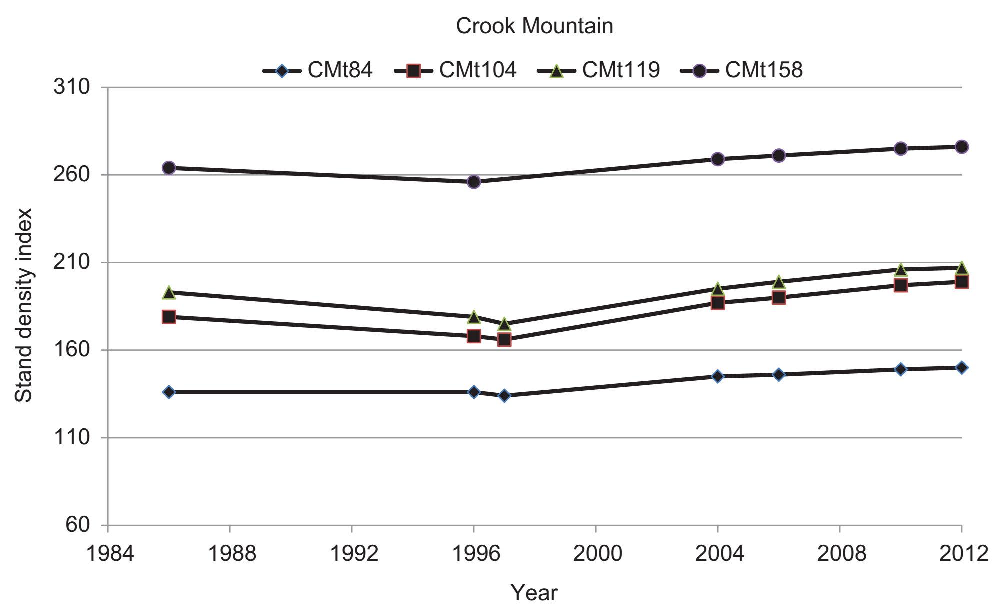

Figure A11—Very few trees were killed by MPBs on plots CMt84, CMt104, CMt119, and CMt158 located at Crook Mountain. In addition these data show how SDI can remain rather constant over a range of basal areas

Table A1—The 35 plots exposed to mountain pine beetles and experienced major mortality within them or near them were placed into clusters based on the minimum and maximum tree densities that occurred on them expressed as square feet of basal area per acre. Also included in the table are the tree densities of the Crook Mountain plots when they were established.

Tree densities that occurred from establishment through 2012							
BA 45–80 ft^2/ac		BA 60–90 ft^2/ac		BA 80–90 ft^2/ac		BA 80–100 ft^2/ac	
Plot[a]	Est BA[b]	Plot[a]	Est BA[b]	Plot[a]	Est BA[b]	Plot[a]	Est BA[b]
EF44	44	BM161	61	BM181	81	EF82	82
EF61	61	Bord60	60	Boy79	79	BM1101	101
Boy68	68	Brn61	61	MMt77	77	Boy87	87
		WHG59	59	WHG80	80	Brn81	81
						CP83	83
						CC83	83
						MMt92	92

Tree densities that occurred from establishment through 2012							
BA 80-125 ft^2/ac		BA 120-150 ft^2/ac		BA 150-220 ft^2/ac		Establishment density Crook Mountain	
Plot[a]	Est BA[b]	Plot[a]	Est BA[b]	Plot[a]	Est BA[b]	Plot[a]	BA[b] ft^2/ac
EF112	112	BM2121	121	EF154	154	CMt84	84
BM2102	102	BM2127	127	BM1155	155	CMt104	104
Bord80	80	Brn146	146	Bord199	199	CMt119	119
Bord98	98	WHG128	128	Boy168	168	CMt158	158
Brn101	101			CP169	169		
CP107	107						
MMT108	108						
WHG118	118						

[a] Plot names include the location and the tree density in square feet per acre when they were established. Plot locations: EF = Black Hills Experimental Forest, Boy = Boy Scout Camp, Bord = Border, Brn = Brownsville, WHG = White House Gulch, MMt = Medicine Mountain, BM1 = Bear Mountain One, BM2 = Bear Mountain Two, CC = Custer Crossing, CP = Custer Peak, and CMt = Crook Mountain.

[b] Est BA= established basal area, ft^2/acre.

Black Hills mountain pine beetle story: the principals

Clockwise from top left: John Schmid retired Research Entomologist Rocky Mountain Research Station, Stephen Mata retired Research Technician, Rocky Mountain Research Station, Blaine Cook (standing), Forest Silviculturist, Black Hills National Forest, Russ Graham, Research Silviculturist, Rocky Mountain Research Station, and Kurt Allen, Entomologist, Forest Health and Protection, Rocky Mountain Region.

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