

Mountain Pine Beetle, a Major Disturbance Agent in US Western Coniferous Forests: A Synthesis of the State of Knowledge

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It is well documented in the scientific and popular literature that large-scale bark beetle outbreaks are occurring across many coniferous forests in the western United States. One of the major species exhibiting extensive eruptive populations resulting in high levels of tree mortality is the mountain pine beetle, *Dendroctonus ponderosae* (Hopkins) (Negrón et al. 2008) (Figure 1). The literature on *D. ponderosae* is extensive and “navigating” through the many outlets in seeking information and summarizing it can be a daunting task. This special section of *Forest Science* contains 10 papers concerning different aspects of the biology, ecology, and management of *D. ponderosae*. A number of relevant topics are reviewed and available literature synthesized for use by land managers, forest health specialists, scientists, and students from a variety of disciplines. Novel research results are also presented in select papers.

The host range of *D. ponderosae* encompasses at least 15 native pines (Table 1). However, suitability for successful colonization, development, and reproduction varies among host species (Langor 1989, Cerezke 1995). Phloem thickness is a major factor in the performance of *D. ponderosae* (Amman and Pace 1976), and therefore, species with thick phloem tend to be more suitable hosts. Preferred hosts are lodgepole pine, *Pinus contorta* Dougl. ex Loud.; sugar pine, *P. lambertiana* Dougl.; ponderosa pine, *P. ponderosae* P. Lawson and C. Lawson; and limber pine, *P. flexilis* E. James. *D. ponderosae* also attacks and successfully reproduces in some pines that have been introduced into the western United States, e.g., Scots pine (also referred to as Scotch pine), *Pinus sylvestris* L., and occasionally other Pinaceae during severe outbreaks e.g., Engelmann spruce, *Picea engelmanni* Parry ex Engelm.).

The geographic distribution of *D. ponderosae* comprises southern British Columbia, Canada, east to South Dakota, and south to Baja, California, Mexico, and New Mexico (S. Wood 1982). Recently, *D. ponderosae* has been reported in Nebraska (Costello and Schaupp 2011). Figure 2 portrays the distribution as presented by S. Wood (1982), however, the insect is expanding its range northward in British Columbia and eastward in Alberta, Canada (Fauria and Johnson 2009, Robertson et al. 2009, de la Giroday 2012) and is

now colonizing jack pine, *Pinus banksiana* Lamb., in eastern Alberta (Cullingham et al. 2011).

Many years of research have focused on the biology, ecology, and management of *D. ponderosae* and its impacts on forest resources. These efforts have generated a wealth of knowledge (Waters et al. 1985, Schowalter and Filip 1993, Safranyik and Wilson 2006). Alternatives for managing populations and preventing or mitigating undesirable levels of tree mortality attributed to *D. ponderosae* have been and continue to be developed. Although we have accumulated extensive knowledge on the natural role of *D. ponderosae* in forests there is still much to learn as we continue our pursuit of understanding forest ecosystems, interactions among disturbance agents that shape them, and how best to maintain resilient ecosystems for future generations.

In the majority of its range, *D. ponderosae* exhibits a 1-year life cycle, but colder regions may extend development to a 2-year life cycle (Logan and Powell 2001). Although with some variation in geographic location, the primary dispersal flight of *D. ponderosae* occurs toward the end of July to early August during which time females initiate host selection and colonization. Attraction to host volatiles has not been conclusively demonstrated in *D. ponderosae*, suggesting that initial host selection may be through random landing (Hynum and Berryman 1980, Byers 1996, Pureswaran and Borden 2003, 2005, Raffa et al. 2008). On identification and acceptance of a host tree, involving gustatory stimuli, a very sophisticated chemical communication system comes into play (D. Wood 1982, Raffa and Berryman 1982, Raffa et al. 1993). In short, aggregation pheromones are produced to attract other *D. ponderosae* to attack the tree in a process referred to as “mass attack.” The release of antiaggregation pheromones results in the termination of attack of the focal tree causing additional *D. ponderosae* to switch attacks to adjacent trees (Geiszler et al. 1980). In this issue, Progar et al. (2014) synthesize information related to the chemical ecology of *D. ponderosae* relevant to host location, selection and colonization, and mating behaviors. To that end, an abundance of studies have evaluated protection of trees from *D. ponderosae* with verbenone, the

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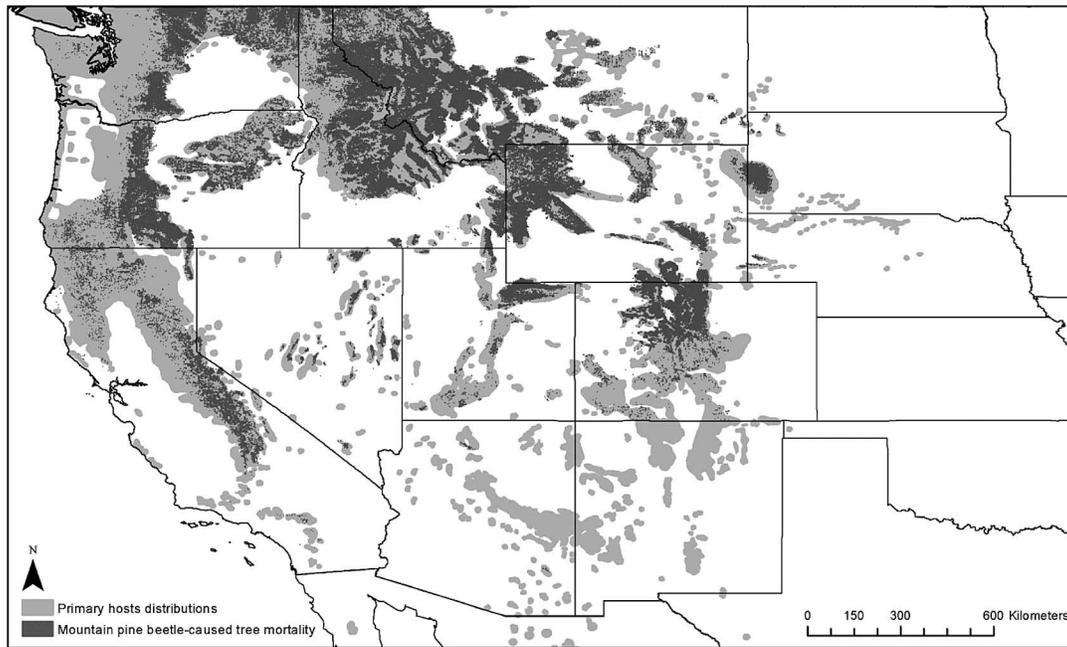


Figure 1. Areas (dark gray) impacted by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in the western United States during 2001–2011 based on aerial survey data provided by the USDA Forest Service. Distributions of the primary hosts are represented in light gray. Prepared with the assistance of Z. Heath, USDA Forest Service.

Table 1. Reported *Pinus* spp. that are hosts for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins.

Species	Common name
<i>Pinus albicaulis</i>	whitebark pine
<i>Pinus aristata</i>	Rocky Mountain bristlecone pine
<i>Pinus banksiana</i> <i>Pinus balfouriana</i>	jack pine foxtail pine
<i>Pinus contorta</i>	lodgepole pine
<i>Pinus coulteri</i>	Coulter pine
<i>Pinus edulis</i>	piñon pine
<i>Pinus flexilis</i>	limber pine
<i>Pinus jeffreyi</i>	Jeffrey pine
<i>Pinus lambertiana</i>	sugar pine
<i>Pinus longaeva</i>	Great Basin bristlecone pine
<i>Pinus monophylla</i>	single-leaf piñon
<i>Pinus monticola</i>	western white pine
<i>Pinus ponderosa</i>	ponderosa pine
<i>Pinus strobiformis</i>	southwestern white pine

principle antiaggregation pheromone of *D. ponderosae*, with mixed results. Progar et al. (2014) also identify factors limiting the effectiveness and utility of this and other semiochemical treatments.

If *D. ponderosae* are successful in entering the tree, they mate and the female begins construction of an egg gallery and lays eggs on both sides of the gallery in excavations called “egg niches.” The egg niches are then covered with frass, likely to reduce the potential for egg desiccation. A few days later eclosion occurs and larvae begin to feed, constructing galleries perpendicular to the egg gallery. Larvae continue feeding excavating galleries and develop into mature larvae, which is the predominant overwintering stage. Development resumes in the spring when *D. ponderosae* builds pupal chambers in the inner bark in which pupation occurs. The pupae later transform into brownish callow adults that remain in place until completely hardened and emerge from the tree when suitable environmental conditions occur, and the cycle begins once more. In this issue, Bentz et al. (2014) highlight novel findings on the effects of tem-

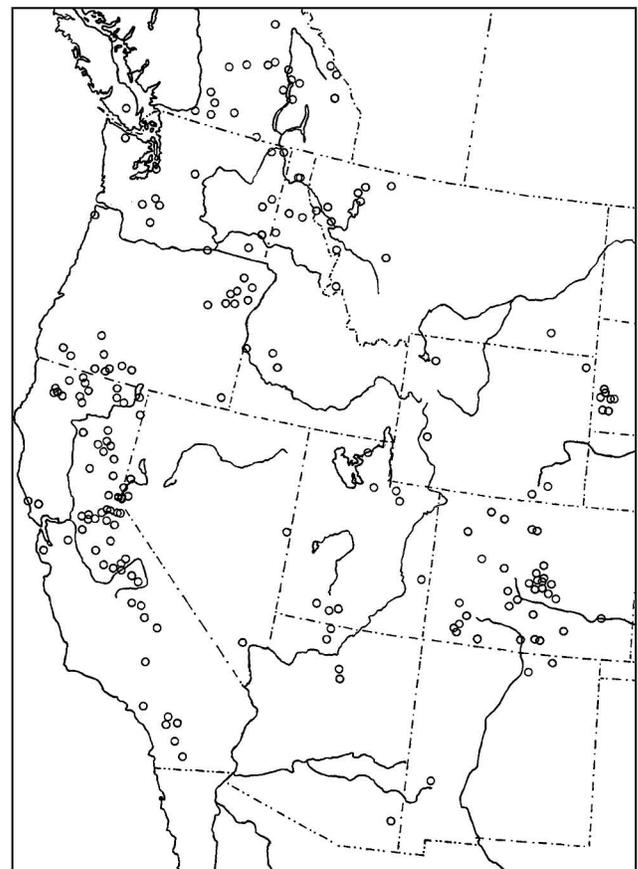


Figure 2. Geographic distribution of the mountain pine beetle, *Dendroctonus ponderosae*. Modified from S. Wood (1982). Circles indicate collection records. Used with permission from the Western North American Naturalist (formerly Great Basin Naturalist) and Brigham Young University.

perature on the ecology of *D. ponderosae*. They monitored lifecycle timing and associated temperatures at 15 sites across latitudinal and elevational gradients in the western United States and found the number of days required to complete a generation (~375) was surprisingly similar among most sites. The thermal units required, however, were significantly less for individuals at the coolest sites. An excellent illustration of the life history of *D. ponderosae* can be found in Gibson et al. (2009).

As *D. ponderosae* bores into the tree, resin ducts are severed, releasing resin. This resin exudation is the primary defensive mechanism of the tree in an attempt to prevent *D. ponderosae* from entering the tree. If the tree is able to produce enough resin it may be successful in resisting mass attack (Raffa and Berryman 1983). As *D. ponderosae* colonizes the tree, it inoculates the sapwood with fungi, including *Ophiostoma* spp. among others (Owen et al. 1987). The beetles carry fungal spores on their body surface and in a specialized structure called a “mycangium.” The fungi block the sapwood preventing translocation of water and nutrients, and serve as an important food source for developing brood. In addition to the fungi, a suite of mites, nematodes, and bacteria are common associates of the *D. ponderosae*. Their interactions are highly complex and fascinating yet not fully understood. In this issue, Mercado et al. (2014) present our current understanding of the ecto- and endofauna and flora associated with *D. ponderosae*.

The first significant outbreak of *D. ponderosae* on record in the United States occurred in the Black Hills of South Dakota (at the time referred to as the Black Hills Forest Reserve) and was first noted in 1895 (Blackman 1931). At the time *D. ponderosae* was viewed as an enemy of the forest as portrayed by a newspaper in Deadwood, South Dakota, published on Apr. 12, 1908 which stated, “After ruining a billion and a half feet of the choicest lumber in the Black Hills and ravaging thousands of acres of the finest pine trees in the West, the little bark beetle, which has robbed Uncle Sam’s forestry division of \$10,000,000 in the last ten years...” (Furniss 1997). This outbreak in the Black Hills was also the genesis of direct control strategies for *D. ponderosae*. In this issue, Fettig et al. (2014) review direct and indirect control methods for mitigating undesirable levels of tree mortality attributed to *D. ponderosae*, while Gillette et al. describe the potential long-term consequences of these treatments on forests.

Although the loss of timber was initially the primary concern, impacts on other resources were also soon recognized. For example, it was reported that “many pine stands valuable from an aesthetic or protection standpoint have been practically destroyed by its [*D. ponderosae*] activity. There is no way of estimating the real monetary value of such forests but there is no doubt that it often exceeds that of commercial timber” (Evenden et al. 1943, p. 3). Many questions remain about the unique role of *D. ponderosae* among other disturbances in western coniferous forests. Outbreaks of *D. ponderosae*, like other ecological processes in forests, do not operate in isolation but interact with other agents such as wildfires and forest pathogens, specifically root diseases or dwarf mistletoe (Schowalter and Filip 1993a, Lundquist 1995). Schowalter and Filip (1993b, p. 3) elegantly described this point when they stated: “Accumulating scientific evidence now supports a view of forests as integrated ecosystems in which species interactions respond to changes in forest conditions...” To that end, many experts consider bark beetle outbreaks and wildfires to be the principle drivers of change in western coniferous forests. In this issue, Jenkins et al. (2014) discuss how fires and *D. ponderosae* interact. They report that outbreaks of *D. ponderosae*

alter forest fuels with consequences to fire risk and severity, and, conversely, that fire injury to trees can promote *D. ponderosae* attack and increase their populations.

The structure and composition of today’s forests is the product of thousands of years of responses to climatic influences and disturbance agents (Fulé 2008, Minckley et al. 2012), and human activities have influenced how disturbances shape forests. For example, prior to Euro-American settlement, ponderosa forests in the southwestern United States were often dominated by park-like structures of widely dispersed trees, particularly on more xeric sites (Covington and Moore 1994, Johnson 1994). Low-intensity surface fires that frequently thinned small-diameter trees (e.g., <19 cm dbh) and fire-intolerant tree species, and understory grasses that excluded tree seedlings likely maintained these conditions. Today, many of these forests are denser, have more small trees and fewer large trees, and are dominated by more shade-tolerant and fire-intolerant tree species. This is primarily a result of fire exclusion and past harvesting practices, but it has unintended consequences as these forest conditions are of increased susceptibility to bark beetles as well as wildfires. To a certain extent, bark beetle outbreaks are indicative of the condition of the forest. For example, it is well established that high-density stands with large-diameter trees are of elevated susceptibility to *D. ponderosae* as trees begin to exhibit reductions in vigor as quantified by the production of wood as a ratio to leaf area (Waring and Pitnam 1980, Larsson et al. 1983). In this issue, Fettig et al. (2014) review tree, stand, and landscape factors associated with *D. ponderosae* infestations. In particular, landscape-level spatiotemporal dynamics of *D. ponderosae* are not well understood but have become a busy area of research, particularly with the use of satellite imagery. Lundquist and Reich (2014) review this rapidly growing body of literature. They report that landscape heterogeneity influences dispersal patterns in many ways and *D. ponderosae* exhibits patterns of large-scale dispersal, which interact with other biotic and abiotic disturbances or processes. High levels of tree mortality caused by *D. ponderosae* outbreaks cause changes in forest structure and composition, which in turn influence habitat suitability for wildlife. The impact will depend on the distribution and levels of tree mortality and the wildlife species in question. A crucial interaction in forest ecosystems, yet the research to date is scarce. Saab et al. (2014) review research on wildlife responses to *D. ponderosae* outbreaks and postoutbreak salvage logging. Only 15 studies were identified. They found avian studies reported positive responses to *D. ponderosae* outbreaks by cavity nesters, shrub nesters, and bark-drillers, while mammalian responses were mixed.

How *D. ponderosae* outbreaks influence biogeochemical cycles has not been extensively studied. Hansen (2014) examines carbon dynamics after a *D. ponderosae* outbreak and reports trees in the residual stand and recruited stems grow more quickly in response to the reduced competition, and stand net primary productivity (NPP) and live basal area recover to preoutbreak levels within a few years or decades. In unaffected stands, reductions in carbon storage last longer as a result of temporary reductions in NPP. Carbon losses due to decomposition are slow due to recalcitrance of snags and coarse woody debris. Combined with recovery of carbon stocks in live pools, ecosystem carbon storage remains high in absolute terms.

Although *D. ponderosae* is an integral part of the ecology of western coniferous forests, extensive levels of tree mortality caused by the insect poses a severe challenge to land managers. In some areas, beetle-killed trees remain suitable for wood production for several

years after being killed and provide a potential source of fiber. Accordingly, utilization of beetle-killed trees for biomass and energy production has become a topic of interest for private and public land managers but its processing is still in its infancy, and technology is being developed. As an example, Hoeger et al. (2014) present new data and methodology for production of submicron or nanometer lignocellulose fibrils using mechanical fibrillation. They report that *D. ponderosae*-killed trees are suitable feedstock for the production of lignocellulose micro/nanofibrils.

This project was sponsored by the USDA Forest Service, Research and Development. Most authors are members of the Western Bark Beetle Research Group, a consortium of scientists within Research and Development, whose research focuses on issues of relevance to bark beetle ecology and management in the western United States. In addition, several authors led papers in other areas of expertise (e.g., represented by Jenkins et al. 2014, Saab et al. 2014, and Hoeger et al. 2014). By no means should it be inferred that the authors represented in this special section are the sole authorities in any given field. Many other outstanding and prolific scientists have made significant contributions to the literature of relevance to this special issue. Much of their work is cited herein, and we encourage the reader to study their works. On behalf of all the authors we hope that the information presented in this special issue proves to be useful and insightful. We thank the editorial staff of *Forest Science* for their support of this work.

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