The Douglas-fir beetle (Dendroctonus pseudotsugae Hopkins) occurs throughout the extensive range of its primary host, Douglas-fir, in western North America (Figure 1). In areas of the Northwest, it also infests downed western larch but not live larch trees. Douglas-fir is unique among North American trees by its adaptation to environments varying from mild maritime along the Pacific coast to seasonally drier and colder elevations inland up to 10,000 ft. as in the Escalante Mountains, Utah and the Sierras in Mexico. Botanists recognize two varieties of Douglas-fir. The coastal variety, Pseudotsuga menziesii var. menziesii (Mirb.) Franco, attains heights of over 300 ft. The inland form, var. glauca (Biessn) Franco, is of lesser size, with recorded tree heights ranging from 85 ft. in southern Utah to 140 ft. in Idaho. Douglas-fir stands become disjunct toward its southern distribution (Figure 1) and this isolation has resulted in a genetic divergence in Mexico indicative of a third variety and the development of a subspecies of the beetle, Dendroctonus pseudotsugae barragani Furniss (Furniss 2001), whereas the subspecies Dendroctonus pseudotsugae pseudotsugae Hopkins occurs northward in the United States and Canada.

The Douglas-fir beetle is normally kept in check primarily by resistance of live trees. Under endemic conditions, beetles typically inhabit individual trees or small groups of down or dying trees or...
trees infected with root disease. However, populations of the beetle have expanded exponentially in damaged trees following catastrophic environmental disturbances. In the Northwest, including Idaho and western Montana, windthrow and breakage from heavy snow or ice have consistently been associated with recorded outbreaks of the beetle. Other contributing agents reported less consistently over a wider geographic area are fire injury and defoliation by the Douglas-fir tussock moth and western spruce budworm. Drought, which lowers tree resistance, appears to sustain outbreaks and may play a role in initiating outbreaks in some areas.

Outbreaks differ in duration, lasting a year in coastal forests to about three years in northern Idaho before subsiding. However, this period has lasted longer in northwestern Wyoming where Douglas-fir stands are more extensive (Figure 2A). By contrast, in parts of the inland Northwest such as northern Idaho and western Montana, Douglas-fir grows in mixed stands or in relatively small groups surrounded by non-host trees, resulting in defined groups being infested (Figure 2B). This characteristic, and varying local history of logging and fire, have resulted in a mosaic in which Douglas-fir stands oscillate through time in their extent, species composition, age and density. Susceptible stands have a majority of Douglas-fir, are mature or older, and have above normal basal area. As the susceptible trees are killed during outbreaks or removed by logging, and as moisture conditions improve, resistance to beetle population expansion increases. The size of infested groups declines and a higher proportion of attacked trees survive. Douglas-fir beetle populations are maintained at an endemic level primarily by tree resistance aided by competition among broods, and from natural enemies.

Evidence of Infestation

Reddish-orange frass (Figure 3), consisting of fragments of phloem (inner bark) expelled from gallery entrances by invading beetles, is the first sign that a tree has been attacked. However, because wind and rain may remove much of the frass, a tree must be examined carefully for remnant frass in bark

Figure 1. Distribution of Douglas-fir. The broken green line separates the inland and coastal varieties. Little (1971).
crevices to determine if beetles are present. Sometimes, an infestation is signaled by streams of clear resin that flow downward from beetle entrance holes near the top of the infested portion of the trunk (Figure 4).

Several months after a tree is infested successfully, its foliage may begin to turn yellowish. At first, the fading appears mottled, involving only some branches as the flow of sap is gradually curtailed. Some trees, however, show no fading until a year after beetle attack. Then, foliage of successfully colonized trees becomes uniformly yellow and finally reddish brown (Figure 5). At this time, conks of the pouch fungus, Cryptoporus volvatus

Figure 4. Uppermost attacks sometimes cause pitch to stream downward on the outer bark, aiding in detection of groups of infested trees.
(Pk.) Shear, may form on the outer bark at beetle exit holes of some trees (Figure 6). Various trees in a group may resist attack (Figure 7) and survive while some are intermediate in their resistance. In the latter case, attacks are less dense and although brood establishment is mostly unsuccessful, the beetles succeed in inoculating the trunk with the pathogenic fungus, *Ophiostoma pseudotsugae* (Rumb.) von Arx. These trees of intermediate resistance fade a year later than others in a group, and are often mistaken for newer attacks.

**Life Stages**

The mature adult beetle (Figure 8A) is 4-6 mm long. Its head and body are black whereas the elytra vary from reddish brown to blackish, darkening with age; those from Mexico lack a reddish cast. Females have small tubercles on the elytral declivity; the male declivity is smooth and shiny. Eggs (Figure 8A) are oblong, pearly white, and about 1 mm long. Larvae (Figure 8B) have the typical weevil-like C-shape, with whitish body and a shiny brown, hardened
head with opposing black mandibles. Pupae (Figure 8C) are fragile, whitish throughout, and have rudimentary adult features.

**Seasonal History**

The beetle was reported by Bedard (1950) to have one generation per year with a predominant spring brood and a smaller summer brood in northeastern Washington. Subsequent investigations in other areas have shown that wide variations occur in the proportion of overwintering adults and larvae, evidently driven by weather and climate. Commonly, only adults overwinter and in one documented instance in Utah, broods spent two winters in their host, first as larvae and then as new adults (Furniss 1956) resulting in collapse of the population. Overwintering brood adults normally emerge in the spring and fly to new hosts when air temperatures exceed 60º F. Timing of flight varies with local elevation and sun exposure. Overwintering larvae normally mature and fly later in summer, as do some parent adults that re-emerge from egg galleries that they excavated in the spring. This later flight is much less intense, and rather than killing additional trees, the beetles may fill-in trees that are already attacked or damaged.

The circumstances under which a pioneer female beetle selects a new host
tree are not certain but her physiological state, tree odors, tree image and tactile response may all play a sequential role. Once a tree has been selected, the female produces attractant pheromones including the major component, frontalin. The attraction of frontalin is synergized by alpha-pinene, a constituent of tree resin. A resultant mass attack of thousands of both male and female beetles ensues that spills over into surrounding trees resulting in group kill. Each pair of beetles interacts by a sequence of sonic and chemical signals. The male reacts to the female attractant pheromone by chirping in a manner that causes the female to release methylcyclohexenone (MCH), resulting in a change in chirp and release of MCH by the male. MCH is an anti-aggregating pheromone that masks attraction to other beetles. This adaptation prevents overcrowding in the tree and enhances brood survival. After mating, females construct egg galleries in the phloem and lay eggs. Eggs hatch into larvae in 1 to 3 weeks, depending on prevailing temperatures. The duration of the larval stage is variable. Spring brood larvae normally pupate and transform to adults during July and August. Larvae of the summer broods, if they exist, overwinter in that stage.

**Galleries & Characteristics of Infestation**

Distinctive egg galleries (Cover Photo) are constructed by female beetles that bore through the bark and tunnel upward in the phloem, lightly engraving the sapwood. At first, the gallery runs at a slight angle, devoid of eggs, and then turns parallel to the wood grain commonly for lengths of 8 to 10 inches. In windthrown trees, galleries are less dense and longer. The galleries are packed with frass except where the beetles are actively tunneling. In complete galleries of similar length, female beetles of the U.S. and Canadian subspecies typically deposit eggs in 10-13 groups, each group deposited alternatively on opposite sides of the gallery; whereas females of the Mexican subspecies deposit eggs in three to four such groups. The newly hatched larvae mine apart from each other outward from the egg gallery (Figure 9). Their mines increase in width as larvae molt and grow through four stages. During the final stage of development, larvae construct pupal cells at the ends of their mines (Figure 8C), some of which are hidden in the inner bark.

Trees are infested at varying heights, but seldom higher than a top diameter of 6 or 8 inches. Other bark beetles such as *Scolytus monticolae* Swaine and *Pseudohylesinus nebulosus* (LeConte)
often occur in the stem above the zone infested by the Douglas-fir beetle. In standing trees, Douglas-fir beetle egg galleries are twice as dense, and more successful, above a basal zone that is often occupied in part by wood borers. The extent of this basal zone differs with geographic area and increases with tree height. In Idaho and western Montana, representative samples must be taken at 12 ft. (Figure 10) or higher; in areas having smaller trees, such as southern Utah, samples have been taken at breast height. Attacks in windthrown trees average one-third as dense as in standing trees and are distributed uniformly lengthwise along the bole, but occur only on the shaded underside if the trunk is sun-exposed.

Natural Control
Mechanisms and Associated Organisms

Populations of the beetle are kept at endemic levels during normal conditions by defenses inherent in live trees. A primary defense consists of resin canals dispersed in the xylem. If the attack is not massive, rupturing of these canals by tunneling of beetles may flood resin into beetle galleries, suffocating eggs and displacing parent beetles. This action is aided by a secondary response to the introduction of a tree pathogenic blue stain fungus, *Ophiostoma pseudotsugae* (Rumbold). In some trees, the lesion created by the fungus may be walled off and overgrown by callus tissue (Figure 7).

Many organisms are associated with the beetle throughout its life cycle. Some, such as mites, nematodes and fungi, are carried by the beetle to a new host; others such as predacious beetles and a parasitic wasp greet it after landing on the bark. Still others find their way into the gallery system of the bark beetles. This assemblage forms a complex ecosystem with each participant having its own role. The role can be one that is mutualistic, or one that is harmful to the beetle either directly or indirectly. Others interact with each other independently in the gallery environment created by the beetle. However, not all of the insects involved have succeeded in accompanying the bark beetle throughout its range. This seems due, in part, to the isolation of populations of the Douglas-fir beetle where its tree host’s range is disjunct.

Examples of predacious insects are species of clerid beetles, including *Thanasimus undatulus* Say (Figure 11) and *Enoclerus sphegeus* (Fab), which occurs northward and is replaced by *Enoclerus arachnodes* (Klug) in Mex-
As well, among the predacious beetles is *Temnochila virescens* (Mann.). Adults of these beetles prey on the Douglas-fir beetle during its exposure on the bark before tunneling to safety; their larvae, however, are able to penetrate galleries (Figure 12) where they prey on immature broods. Larvae of a predacious fly, *Medetera aldrichii* Wheeler commonly prey on Douglas-fir beetle larvae. Parasitic wasps augment the array of insects of which the Douglas-fir beetle is a host. A braconid wasp, *Coeloides vancouverensis* (Dal-la Torre) (Figure 13 A, B), is able to sense, apparently by sound, the presence of Douglas-fir beetle larvae hidden from it beneath bark. The length of her ovipositor limits it to larvae in thinner bark, which is more prevalent in the upper portion of infested trunks. This parasite has not been reported yet from Mexico. Of special interest is a pteromalid wasp, *Karpinskiella par-atomicobia* Hagen and Caltagirone, which, in an instant, hops on and off a Douglas-fir beetle on the bark while inserting an egg inside the beetle’s ab-
domen (Figure 14). It is known to occur only in southern Utah and adjacent Arizona and is the only recorded hymenopterous parasite of an adult *Dendroctonus* species. Its effect, however, may be more beneficial than harmful to the survival of the beetle’s progeny. It does not immediately kill its host. Instead, it reduces egg production of parasitized females by two thirds, thus reducing competition among brood for space and allowing greater survival of larvae. Further, those fewer larvae may have better nutrition and greater fat reserves, thus strengthening their power of dispersal and ability to colonize a new host.

Smaller, more obscure organisms that accompany the beetle from tree-to-tree include fungi, nematodes and mites. Ascospores of the tree pathogenic fungus, *O. pseudotsugae*, are carried on the beetle’s exoskeleton. In susceptible trees, this fungus invades and clogs the sapwood cells thereby stifling their ability to conduct nutrients vital to the life of the tree and contributing to survival of beetle offspring. Nematodes of several species occur externally in pods under beetle elytra and internally in their abdomen. These do not seem to have much harmful effect, with the exception of the large adult *Parasitaphelenchus reversus* (Thorne) which, by their activity in a beetle’s abdomen, may reduce fat reserve and possibly fecundity. Other hitch-hikers include several species of mites that cling to inter-segmental spaces of beetle abdomens, under the elytra, or attached to a leg by a pedicel. Most are scavengers, fungivorous, or feed on nematodes, and do not appear to be detrimental except possibly by interfering with flight when occurring at high density on occasional beetles.

These natural enemies help to keep Douglas-fir beetle populations in check under normal conditions but do not prevent outbreaks from occurring after a disturbance, nor have they been implicated in the collapse of an outbreak.

**Management**

Managers of Douglas-fir forests are helped in dealing with Douglas-fir beetles by taking the view that the beetle is a symptom, not the cause, of the perceived problem when large numbers of trees become infested. If an outbreak occurs, forest conditions have favored the beetle population. Such affected stands have a high proportion of Douglas-fir trees that are overly dense, mature, and of large diameter (Figure 15). Well-managed Douglas-fir stands may sometimes be attacked by Douglas-fir beetles, but never have been known to sustain a Douglas-fir beetle outbreak.
Silvicultural Treatment and Sanitation

Any treatment that reduces the basal area, average age, or percent of Douglas-fir in a stand will produce stand conditions unfavorable to Douglas-fir beetles. Alternatives include thinning or regeneration harvests which help meet resource objectives for the site.

In Douglas-fir forests in the Pacific Northwest and Northern Rocky Mountains, possible presence of root disease should be evaluated before cutting trees. If present, root diseases can rapidly colonize the root systems of Douglas-fir stumps and spread to residual live trees through root grafts. Conversion to less susceptible tree species, such as pines and western larch, may be a better alternative than partial cutting in root disease-affected forests.

Douglas-fir beetles readily infest trees blown down by wind or broken by heavy snow or ice storms in which disproportionately large numbers of their broods may develop. The resulting enlarged population of offspring typically kills groups of trees in surrounding susceptible stands. Such damaged trees should be removed wherever possible before adult broods emerge from them in the following spring.

Trap Trees

Because of the attractiveness of downed trees to Douglas-fir beetles, freshly-cut trap trees have been advocated in conjunction with logging on private and state land in Idaho and Montana to absorb emerging beetles during outbreaks. After the trap trees fill up with beetles, they are removed from the forest and processed. To be effective, trap trees must be felled in the shade and more than one trap tree is needed to absorb beetles emerging from one standing tree. This method is only used in conjunction with logging where timely removal of infested trees is assured.

Aggregative Pheromones

A tree bait containing the beetle’s primary aggregative pheromone, frontalin, is designed to concentrate beetles in a stand that is scheduled for clearcutting. The attractive power of this tree bait causes beetles to mass attack baited trees and to “spill over” into surrounding trees in proportion to the beetle population in the area. All infested trees must then be removed before beetles emerge in the following spring.
**Anti-aggregative Pheromones**

The odor of the antiaggregative pheromone, MCH, causes beetles to fly elsewhere, interrupting their aggregation and prolonging their exposure to environmental hazards. These beetles are more likely to attack less susceptible hosts, which absorb rather than generate populations of beetles. When applied aerially to damaged stands prior to spring flight, controlled-release formulations of MCH are effective in preventing population build-up in inaccessible locations. This pheromone is also available as a bubble cap (Figure 16) for attachment to high value trees such as in campgrounds, around lodges, or in forest areas where expected beetle-caused mortality would negatively impact resource objectives.

**Additional Information**

Forest landowners can obtain more information from County Extension Agents, State Forestry Agencies or State Agriculture Departments. Federal resource managers should contact USDA Forest Service, Forest Health Protection (www.fs.fed.us/foresthcalth). This publication and other Forest Insect and Disease Leaflets can be found at www.fs.usda.gov/goto/fhp/fidls.

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**References**


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