Douglas-Fir Beetle Response to Artificial Creation of Down Wood in the Oregon Coast Range

Darrell W. Ross, Department of Forest Science, Oregon State University, Corvallis, OR 97331; **Bruce B. Hostetler,** USDA Forest Service, Forest Health Protection, Sandy, OR 97055; and John Johansen, USDA Forest Service, Siuslaw National Forest, Hebo Ranger District, Hebo, OR 97122.

ABSTRACT: Douglas-fir beetle populations were monitored before and after thinning and felling of trees to create down wood in an 88-year-old Douglas-fir plantation in the Oregon Coast Range. Treatments included an unthinned control, thinning to a target of 75 trees/ha, and thinning to a target of 150 trees/ha. Actual mean tree densities on the plots after thinning were 406, 102, and 154, for the control, 75 trees/ha, and 150 trees/ha treatments, respectively. Fifty trees/ha were felled and left on all thinned plots to create down wood for ecological values. Catches in pheromone-baited traps indicated that the local beetle population increased for 1 year in response to felling and leaving large diameter trees in partial shade. Douglas-fir beetle entrance holes and brood were significantly more abundant on the sides of felled trees and wood borers were significantly more abundant on the upper surface suggesting that treatments that provide maximum exposure of felled trees will create the least favorable habitat for Douglas-fir beetles. However, there were no differences in Douglas-fir beetle entrance holes or brood densities in felled trees between the two thinning intensities. Douglas-fir beetle-caused tree mortality was significantly higher on thinned plots with residual felled trees compared with unthinned controls, although infestation levels were low on all plots (<2 trees/ha). The small increase in beetle-caused tree mortality associated with leaving felled trees would be unlikely to interfere with resource management objectives. These results are applicable to mature, managed forests west of the Cascades with relatively low Douglas-fir beetle populations. In different regions and stand types, or under different environmental conditions, beetle populations could increase to higher densities, remain at high densities longer, and cause higher levels of tree mortality. West. J. Appl. For. 21(3):117-122.

Key Words: *Dendroctonus pseudotsugae*, thinning, felled trees, retention, down wood, population dynamics.

The importance of dead wood, both standing and down, to the maintenance of healthy forest ecosystems has become increasingly apparent in recent years (Maser and Trappe 1984, Harmon et al. 1986, Laudenslayer et al. 2002). During the early years of forest management in the Pacific Northwest, down wood (sometimes called coarse woody debris or coarse woody detritus) left after harvest operations was often at or greater than the levels historically found in

natural forests. However, as utilization standards improved and a perceived need to reduce waste developed in the mid-1900s, down wood left after harvesting declined to very low levels (Harmon 2002). As a result, many areas in the Pacific Northwest are now deficient in standing and down dead wood needed to maintain ecological processes. Currently, silvicultural systems are being developed that include active management of down and standing dead wood (Franklin et al. 1997, Harmon 2002). Until these systems are fully implemented and have time to develop the woody structural elements that are missing from some forests, it will be necessary to use remedial treatments to ensure healthy forest ecosystems. Federal land managers in Oregon and Washington are required to leave minimum amounts of large down wood after any stand management activities (USDA and USDI 1994a, USDA and USDI

NOTE: Darrell W. Ross can be reached at (541) 737-6566; Fax: (541) 737-1393; darrell.ross@oregonstate.edu. This study was funded, in part, by the Hebo Ranger District, Siuslaw National Forest. We thank Lori Duley (Hebo Ranger District, Siuslaw National Forest) for maintaining and collecting beetles from the pheromone monitoring traps, and Rex Wheeler (retired) (Hebo Ranger District, Siuslaw National Forest) for assistance in collecting bark samples from down logs. Copyright © 2006 by the Society of American Foresters.

1994b). In plantations or other stands, where the current amount of down wood is limited, this may involve deliberate felling and leaving of merchantable-size trees to create the necessary levels of down wood. These large pieces of down wood are needed to provide habitat for vertebrates, invertebrates, plants, and microbes; to maintain soil productivity; and for other ecological values. Previously, these trees would have been removed for their timber values.

Large diameter recently downed trees in partial shade are ideal habitat for the Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins (McMullen and Atkins 1962). Historically, outbreaks of this insect in the Pacific Northwest have followed winter wind events or other disturbances that created an abundance of breeding sites (Cornelius 1955, Hagenstein and Furniss 1956, Furniss 1965, Furniss et al. 1979, Schmitz and Gibson 1996). The new silvicultural treatments being used on federal lands such as felling and leaving large diameter trees create similar conditions and may potentially lead to increases in beetle-caused tree mortality conflicting with management objectives. In this study, our objective was to quantitatively describe the response of low-density Douglas-fir beetle populations to the artificial creation of down wood through felling and leaving of large diameter Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco]. We quantified beetle populations on and near the plots by using pheromone-baited traps, sampling the bark on felled trees, and surveying the live trees for beetle infestations. We also quantified Douglas-fir beetle predators in pheromone-baited trap catches, and predators, parasites, and competitors (wood borers) in bark samples to better understand responses of Douglas-fir beetle populations to the treatments.

Methods

This study was part of a larger USDA Forest Service forest ecosystem productivity research network that is comprised of several long-term, large-scale experimental sites. The overall purpose of this continuing project is "... to apply adaptive management concepts to restore late-successional habitat and at the same time produce some timber commodities to support local economies" (Bormann et al. 1998). Our plots were established within the Mount Hebo Old-Growth Restoration Study site located in the 2,400-ha Hebo burn plantation, the oldest large-scale plantation on federal land in the Oregon Coast Range, approximately 5 km east of Hebo, OR. The plantation was established in 1910 with Douglas-fir seedlings apparently from a Puget Sound, WA, seed source. The soils within the plantation suggest that significant erosion occurred before planting. Trees in the plantation were growing slowly and had thin crowns compared with trees growing in other parts of the Coast Range, presumably because of the off-site seed source and degraded soils. In addition, there was evidence of Swiss needle cast [Phaeocryptopus gaeumannii (Rhode) Petrak] infections in the trees during the time of our data collection, and this also would have contributed to the thinning of crowns in these trees. A complete survey of the central 1-ha mensuration plots set up by other researchers for long-term

studies before establishment of this study found a very low level of *Phellinus weirii* (Murr.) Gilb. infection. In addition, no obvious symptoms of root disease were observed in the remainder of the plot areas during our tree mortality surveys. Trees infected with this root pathogen often provide habitat for low-density Douglas-fir beetle populations between outbreaks in the Oregon Coast Range.

The study included three replications of three thinning treatments. Treatments included no thinning, thinning to a target of 75 residual trees/ha, and thinning to a target of 150 residual trees/ha. The larger study included an additional treatment based on two different underplanted tree species on plots thinned to 75 trees/ha, which was irrelevant to our objective of monitoring short-term Douglas-fir beetle response to treatments. Therefore, we pooled all of the plots thinned to 75 trees/ha into one treatment regardless of the underplanted tree species, resulting in three control plots, six plots thinned to 75 trees/ha, and three plots thinned to 150 trees/ha. Two replicates were thinned during September through November 1997, and the other was thinned during August and September 1998. On plots with either level of thinning, all felled trees were removed except 50 trees per ha that were left on the ground evenly spaced throughout the plot. Trees were felled for down wood during August and September 1998 on all plots. All trees were limbed and topped at the time of felling. After thinning, the actual mean tree densities on the plots were 406, 102, and 154, for the control, 75 trees/ha, and 150 trees/ha treatments, respectively (unpublished data; Robyn Darbyshire, Siskiyou National Forest, Brookings, OR). Plots ranged in size from 4.5 to 8.5 ha.

Douglas-fir beetle populations were monitored from 1996 through 2001 with 12 pheromone-baited multiple-funnel traps placed in four groups of three traps in young plantations located near the study plots. Traps were placed in plantations as far away from potential host trees as possible to minimize the chances that trees near the traps would become infested and influence trap catches. The purpose of trapping was to compare relative beetle population densities from year to year in the forests near the plots before, during, and after thinning. Trap catches were not used to compare beetle response to different treatments. The minimum distance from each group of traps to the nearest plot boundary ranged from 176 to 3,430 m (average = 2,064 m), and, within groups, the traps were approximately 10 m apart. Traps were baited with frontalin and seudenol in polyvinyl chloride formulations (Daterman 1974), releasing 5 and 2.5 mg/day at 25° C, respectively, and ethanol pouches (Phero Tech, Inc., Delta, BC, Canada) releasing 88 mg/day at 25° C. Chemical purities of semiochemicals were: frontalin, 95.0%; seudenol, 99.3%; and ethanol, \geq 98%. Traps were placed in the same locations each year. Traps were deployed in mid-late March and emptied at 1- to 4-week intervals until the end of September. All Douglas-fir beetles and associated predators in each sample were counted. The gender of Douglas-fir beetles was determined based on morphological characteristics of the elytral declivity (Jantz and Johnsey 1964).

Bark samples were collected from 10 trees randomly selected from among the 50 felled trees/ha that were left after thinning within the central portion of each thinned plot between Sept. 21 to 29, 1999. All sample trees were at least 30 m from the nearest plot boundary. Nine 100-cm^2 samples were collected from each tree using a power drill and hole saw. Samples were removed from the top and each side of the tree at 2 m from the base, at a location where the bole was 30 cm in diameter, and midway between these locations. For each sample tree, the following data were recorded: length from the base to a 30-cm diameter top, diameter at the base, and diameter at each of the three locations where bark samples were removed.

In the laboratory, bark samples were dissected and the following data were recorded: number of entrance holes; numbers of Douglas-fir beetle larvae, pupae, and adults; numbers of predators and parasites; and percent of surface area covered by wood borer feeding galleries. The gender of all Douglas-fir beetle brood adults was determined. Percent of the bark surface area covered by wood borer feeding galleries was visually estimated using the following categories: 0, no feeding galleries; 1, 0-5%; 2, 6-25%; 3, 26-50%; 4, 51-75%; 5, 76-95%; and 6, 96-100%. Mean bark surface area covered by wood borer feeding galleries was determined using the mid-point values for each category.

All of the Douglas-fir beetle, natural enemy, and wood borer data were subjected to analysis of variance to test for effects of position along the bole, position around the circumference of the bole, and residual overstory density using the SAS procedure GLM (SAS System for Windows Release 8.02, SAS Institute, Inc., Cary, NC). Means were compared and separated by Fisher's protected least significant difference test when P < 0.05 as needed (Steel and Torrie 1980). The measurements of felled trees were used to calculate the bark surface area and, along with brood densities, the number of brood produced per tree.

The plots were surveyed on July 17 and 18, 2001 to determine beetle-caused tree mortality. The dbh of all infested trees was recorded. The Douglas-fir beetle infestation data were subjected to analysis of variance to test for differences among the thinning treatments using the SAS procedure GLM. Means were compared and separated by Fisher's protected least significant difference test when P < 0.05 (Steel and Torrie 1980).

Results

Douglas-fir beetle catches for the 12 pheromone-baited traps increased from an average of 148 beetles/trap to 1,073 beetles/trap from 1996 to 1998 before thinning and tree felling (Figure 1). In 1999, the first year after tree felling, trap catches dropped to an average of 197 beetles/trap. The highest catches for the 6-year period of 2,199 beetles/trap occurred in 2000, 2 years after felling and coinciding with beetle emergence from the felled trees. In 2001, trap catches declined to an average of 958 beetles/trap. The overall percentages of Douglas-fir beetles that were male each year varied from 78 to 90%. Predator catches ranged from zero

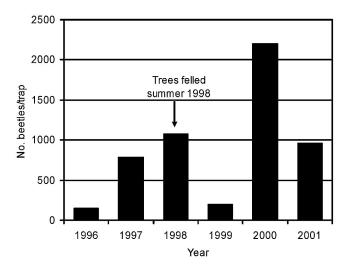


Figure 1. Average number of Douglas-fir beetles caught in pheromone-baited multiple-funnel traps near the Mount Hebo Old-Growth Restoration Study from 1996 to 2001.

to six per year with 22 *Thanasimus undatulus* (Say) and 1 *Temnochila chlorodia* (Mannerheim) collected during the 6 years of trapping.

Location along the bole of felled trees had no effect on Douglas-fir beetle entrance holes (F = 0.84; df = 2,16; P = 0.4305), larvae (F = 0.25; df = 2,16; P = 0.7752), or pupae (F = 0.91; df = 2,16; P = 0.4013), but numbers of brood adults were significantly higher (F = 4.21; df = 2,16; P = 0.0152) in samples collected from the middle of the bole compared with those from the base or 30-cm diameter top (Table 1). There were no significant differences in abundance of wood borer feeding galleries along the bole of felled trees (F = 0.14; df = 2,16; P = 0.8659) (Table 1).

Douglas-fir beetle entrance holes (F = 11.99; df = 1.8; P = 0.0006), larvae (F = 9.34; df = 1.8; P = 0.0023), pupae (F = 8.82; df = 1.8; P = 0.0031), and brood adults (F = 13.58; df = 1.8; P = 0.0002) were all significantly more abundant on the sides of the felled trees compared with the upper surface (Table 2). In contrast, wood borer feeding galleries were significantly more abundant (F = 227.69; df = 1.8; P < 0.0001) on the upper surface of felled trees compared with the sides (Table 2).

Density of residual overstory trees had no effect on Douglas-fir beetle entrance holes (F = 0.42; df = 1.5; P = 0.5447), larvae (F = 1.27; df = 1.5; P = 0.3103), pupae

Table 1.	Douglas-fir beetle and wood borer abundance			
at three locations along the bole of residual felled trees				
	wn wood in the Mt. Hebo Old-Growth Resto-			
ration Stu	ldy.*			

Douglas-fir beetle					% Area of	
Location along the bole	No. entrance holes/m ²	No. larvae/m ²	No. pupae/m²	No. adults/m²	wood borer feeding galleries	
Base Middle 30-cm Top	2.8 a 3.9 a 5.6 a	6.9 a 9.4 a 11.4 a	4.0 a 3.3 a 8.3 a	15.9 b 58.6 a 30.0 b	8.9 a 9.1 a 8.5 a	

*Values within a column followed by different letters are significantly different (P < 0.05).

Table 2.Douglas-fir beetle and wood borer abundanceon the sides and top of residual felled trees left for downwood in the Mt. Hebo Old-Growth Restoration Study.*

	Douglas-fir beetle				% Area of
Location around the hole	No. entrance holes/m ²	No. larvae/m ²	No. pupae/m ²	No. adults/m ²	wood borer feeding galleries
Side Top	7.1 a 1.1 b	17.0 a 1.5 b	10.1 a 0.4 b	57.5 a 12.3 b	2.1 a 15.6 b

*Values within a column followed by different letters are significantly different (P < 0.05).

(F = 0.55; df = 1,5; P = 0.4922), or brood adults (F = 0.21; df = 1,5; P = 0.6648) (Table 3). However, the abundance of wood borer feeding galleries was significantly higher (F = 17.39; df = 1,5; P = 0.0087) in the plots with a target residual overstory of 75 trees/ha compared with those having a target residual overstory of 150 trees/ha (Table 3).

Of a total of 342 brood adult Douglas-fir beetles found in all of the bark samples, 164 were male and 178 were female. The most abundant natural enemies found in the bark samples were cocoons of *Coeloides brunneri* Viereck, a parasitic wasp, and larvae of *Medetera aldrichii* Wheeler, a predacious fly. Densities of both natural enemies were low and there were no significant differences among sample positions on the bole or between thinning treatments (P > 0.05). Only one predacious clerid beetle, a *T. undatulus* larva, was found in all of the bark samples.

The number of Douglas-fir beetle-infested trees was low (<2/ha) on all plots, but a significantly higher density of trees (F = 14.01; df = 2.7; P = 0.0036) was infested on thinned plots with residual felled trees compared with unthinned controls (Table 4). There was no difference in infestation level between the two intensities of thinning. There was no difference in size of Douglas-fir beetle-infested trees among the treatments (F = 0.08; df = 2.6; P = 0.9283).

Discussion

Before thinning, the Douglas-fir beetle population in the vicinity of the research plots was at a relatively low level, but increasing (Figure 1). From 1996 to 1998, the highest Douglas-fir beetle catch occurred in 1998 averaging 1,073 beetles/trap. In comparison, similar traps caught an average

Table 3. Douglas-fir beetle and wood borer abundance in felled trees left for down wood in stands with different overstory densities in the Mt. Hebo Old-Growth Restoration Study.*

Target	Douglas-fir beetle				% Area of
residual overstory trees/ha	No. entrance holes/m ²	No. larvae/m ²	No. pupae/m ²	No. adults/m ²	wood borer feeding galleries
75 150	4.7 a 6.0 a	14.7 a 5.9 a	6.2 a 8.2 a	40.0 a 47.5 a	7.8 a 4.3 b

*Values within a column followed by different letters are significantly different (P < 0.05).

Table 4.Diameter and density of Douglas-fir beetle-in-fested trees on thinned and unthinned control plots inthe Mt. Hebo Old-Growth Restoration Study.*

Treatment	Diameter at breast height (cm)	No. infested trees per ha
Control	49.5 a	0.20 a
75 Residual trees/ha	51.8 a	1.95 b
150 Residual trees/ha	51.3 a	1.33 b

*Values within a column followed by different letters are significantly different (P < 0.05).

of approximately 7,000 beetles during an outbreak in northeastern Oregon in the early 1990s (Ross and Daterman 1997). Thinning and felling of residual trees occurred in the summer of 1998 after Douglas-fir beetle flight had ended. As a result, the felled trees were not infested until the spring of 1999 when they provided a strong alternative source of attraction for flying beetles that competed with the pheromone-baited traps. The low trap catch in 1999 was probably the result of many beetles colonizing felled trees before they encountered a trap. The peak trap catch of 2,199 beetles/trap occurred in 2000 corresponding with beetle emergence from the felled trees. However, trap catches were reduced that year as a result of logging in the vicinity of one of the groups of traps during the peak period of beetle dispersal. Trees were attacked by Douglas-fir beetles immediately after felling and many logs were heavily infested by the time they were removed from the forest. Apparently, these freshly downed trees competed effectively with the pheromone-baited traps for flying beetles. In the absence of this logging operation, the traps would have caught more beetles, but the extent to which logging affected trap catches is unknown. In 2001, trap catches declined to levels similar to those that occurred before thinning and tree felling.

Predator catches were low throughout the study reflecting low-density bark beetle populations. The lowest ratio of Douglas-fir beetles to predators of 297:1 occurred in 1996. In comparison, the same ratio was approximately 7:1 during the latter stages of a Douglas-fir beetle outbreak in northeastern Oregon (Ross and Daterman 1994, Ross and Daterman 1997). Overall, entrance hole densities on felled trees averaged $5.1/m^2$, somewhat lower than the $19.0/m^2$ observed on felled trees in western Washington (Hedden and Gara 1976) or the $22.6/m^2$ observed on windthrown trees in southern Idaho (Furniss 1962) providing further evidence that beetle populations were at low densities at the time of the study.

Although generally there were trends of increasing entrance hole, larval, and pupal densities moving from the base to the top of felled trees, the differences were not statistically significant. However, brood adult densities were significantly higher in the middle of the bole compared with those at the base or 30-cm diameter top (Table 1). A similar infestation pattern was observed in a previous study of windthrown Douglas-fir trees in southern Idaho (Furniss 1962). However, in that study, as in the present one, infestations varied more around the circumference of downed trees than along the bole. In this study, Douglas-fir beetle entrance holes, larvae, pupae, and brood adults were all significantly more abundant on the sides of felled trees compared with the top, and wood borer feeding galleries were more abundant on the tops of felled trees compared with the sides (Table 2). This suggests that treatments that maximize the exposure of felled trees to direct sunlight will create the least favorable habitat for Douglas-fir beetles.

The Douglas-fir beetle is known to preferentially infest down trees in partial shade more than those in full sunlight most of the time (Rudinsky and Vité 1956, McMullen and Atkins 1962). Apparently, the different intensities of thinning in this study did not create significant differences in the quality of habitat for Douglas-fir beetles, because there were no differences in entrance hole densities or brood production between the two levels of thinning (Table 3). In contrast, many wood borers, particularly those in the Buprestidae family, commonly known as flatheaded or metallic wood borers, prefer standing or down trees in full sunlight (Furniss and Carolin 1977). The greater abundance of wood borer feeding galleries in felled trees on plots with the lower residual overstory density is consistent with this preference.

Using the mean bark surface area from the base to a 30-cm diameter top of 20.4 m², the mean densities of Douglas-fir beetle brood adults and total brood (i.e., adults plus larvae and pupae) were calculated for an average felled tree. For those calculations, it was assumed that the brood densities on the sides of the bole were representative of three-quarters of the bark surface (sides and bottom) and the brood densities on the top were representative of one-quarter of the bark surface. Those calculations yielded estimates of 942 brood adults or 1,365 total brood per felled tree. Because 50 felled trees/ha were left on these plots, they approximately 50,000 Douglas-fir would produce beetles/ha. Assuming an infestation density of 60/m² is optimal for overcoming the defenses of live trees and minimizing intraspecific competition (McMullen and Atkins 1961), approximately 1,200 infestations or mated pairs of beetles would be required to successfully infest live trees similar in size to the felled trees on these plots. Therefore, with a sex ratio of 1:1, the 50,000 Douglas-fir beetles per ha in the felled trees (25,000 pairs) would have the potential to kill approximately 21 live trees.

It was not possible to document the actual number of trees killed by beetles emerging from the felled trees, because adult Douglas-fir beetles are capable of flying at least several miles and possibly as far as 20 miles before locating a host tree (Atkins 1961). Beetles emerging from felled trees on the research plots may have flown considerable distances before colonizing a potential host. However, the actual number of live trees killed by the Douglas-fir beetle brood found in 50 felled trees/ha would likely be less than our estimate of 21 for several reasons. First, we collected bark samples in the early fall. Some overwintering mortality would be expected so that the actual numbers of brood adults emerging the following spring would be less than the numbers present when we collected samples. Second, some of the beetles emerging in the spring would probably infest trees that died during the previous winter from natural causes such as windstorms. Third, not all of the beetles emerging in the spring would be successful in locating a suitable host tree or would be killed by predators after arriving at a potential host.

Douglas-fir beetle-caused tree mortality was significantly higher on plots with trees felled for down wood than on control plots (Table 4). On visits to the plots in 2000, there was no evidence of standing trees that had been infested in 1999. Furthermore, because all of the beetlekilled trees had relatively tight, intact bark and some red needles when surveyed in 2001, we assume that they were all infested in spring of 2000 by beetles emerging from the felled trees. The higher mortality on thinned plots was most likely due to higher beetle populations on those plots associated with the felled trees. However, beetle-caused tree mortality was less than two trees/ha on all plots. It is unlikely that this level of tree mortality would have any significant detrimental impacts on management objectives. Furthermore, in the absence of additional disturbance, beetle populations quickly declined to prethinning levels (Figure 1), and it is unlikely that tree mortality remained at elevated levels on the thinned plots. In the long term, beetle-caused mortality is likely to be less on the thinned plots because of improved growing conditions for the residual trees (Williamson and Price 1971).

Our results show that a low-density Douglas-fir beetle population increased in response to improved habitat provided by felling and leaving large diameter Douglas-fir trees in partial shade. The felled trees provided ideal breeding sites for the local beetle population. Beetle-caused mortality to live trees surrounding the felled trees was elevated compared with trees on unthinned control plots. However, the increase in mortality was small, and beetle populations declined to prethinning levels the third year after thinning and felling trees for down wood. Still, resource managers must be careful when using the fell and leave method to create down wood. The risk of beetle-caused tree mortality after such treatments will depend on a variety of factors including the scale of the operation, weather, silvicultural activities in adjacent stands, ages and sizes of Douglas-fir trees in adjacent stands, natural disturbances, beetle population levels at the time of the treatment, geographic location, and stand conditions. For example, the logging that occurred near the study plots in 2000 removed some unknown portion of the Douglas-fir beetle population that was emerging from the felled trees that might have otherwise infested trees on the plots. Furthermore, beetle populations would likely respond differently in forests east of the Cascades or in old-growth stands west of the Cascades. Under more favorable conditions for beetle population growth, higher levels of mortality in residual live trees could occur.

Literature Cited

ATKINS, M.D. 1961. A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) III. Flight capacity. Can. Entomol. 93:467–474.

- BORMANN, B., J. JOHANSEN, P. CUNNINGHAM, M. BROOKES, R. DARBYSHIRE, AND J. MARTIN. 1998. Mt. Hebo old-growth restoration project—A PILOT adaptive management research study and prescription experiment (DRAFT). USDA For. Serv. Pacific Northwest Research Station, Corvallis, OR.
- CORNELIUS, R.O. 1955. How forest pests upset management plans in the Douglas-fir region. J. For. 53:711–713.
- DATERMAN, G.E. 1974. Synthetic sex pheromone for detection survey of European pine shoot moth. USDA For. Serv. Res. Paper PNW-180.
- FRANKLIN, J.F., D.R. BERG, D.A. THORNBURGH, AND J.C. TAPPEINER. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. P. 111–139 in Creating a forestry for the 21st century; the science of ecosystem management, Kohm, K.A., and J.F. Franklin (eds.). Island Press, Washington, DC.
- FURNISS, M.M. 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. J. Econ. Entomol. 55:486–491.
- FURNISS, M.M. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. J. For. 63:8–11.
- FURNISS, M.M., M.D. MCGREGOR, M.W. FOILES, AND A.D. PARTRIDGE. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. USDA For. Serv. Gen. Tech. Rep. INT-59.
- FURNISS, R.L., AND V.M. CAROLIN. 1977. Western forest insects. USDA For. Serv. Misc. Publ. No. 1339.
- HAGENSTEIN, W.D., AND R.L. FURNISS. 1956. Cooperation speeds salvage of windthrown and beetle-killed timber in Oregon and Washington. P. 167–168 *in* Proc. Soc. Amer. For., 1955. Society of American Foresters, Bethesda, MD.
- HARMON, M.E. 2002. Moving toward a new paradigm for woody detritus management. P. 929–944 *in* Proc. of the symposium on the ecology and management of dead wood in western forests. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181.
- HARMON, M.E., J.F. FRANKLIN, F.J. SWANSON, P. SOLLINS, J.D. LATTIN, N.H. ANDERSON, S. GREGORY, S.P. CLINE, N.G. AUMEN, J.R. SEDELL, G.W. LIENKAEMPER, K. CROMACK JR., AND K.W. CUMMINS. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15:133–302.
- HEDDEN, R.L., AND R.I. GARA. 1976. Spatial attack pattern of a western Washington Douglas-fir beetle population. For. Sci. 22:100–102.

- JANTZ, O.K., AND R.L. JOHNSEY. 1964. Determination of sex of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 96:1326–1329.
- LAUDENSLAYER, W.F. JR., P.J. SHEA, B.E. VALENTINE, C.P. WEATHERSPOON, AND T.E. LISLE (TECH. COORD.). 2002. Proceedings of the symposium on the ecology and management of dead wood in western forests. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181.
- MASER, C., AND J.M. TRAPPE. 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164.
- MCMULLEN, L.H., AND M.D. ATKINS. 1961. Intraspecific competition as a factor in the natural control of the Douglas-fir beetle. For. Sci. 7:197–203.
- MCMULLEN, L.H., AND M.D. ATKINS. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera:Scolytidae). Can. Entomol. 94:1309–1325.
- Ross, D.W., AND G.E. DATERMAN. 1994. Reduction of Douglas-fir beetle infestation of high-risk stands by antiaggregation and aggregation pheromones. Can. J. For. Res. 24:2184–2190.
- Ross, D.W., AND G.E. DATERMAN. 1997. Using pheromone-baited traps to control the amount and distribution of tree mortality during outbreaks of the Douglas-fir beetle. For. Sci. 43:65–70.
- RUDINSKY, J.A., AND J.P. VITE. 1956. Effects of temperature upon the activity and behavior of the Douglas-fir beetle. For. Sci. 2:258–267.
- SCHMITZ, R.F., AND K.E. GIBSON. 1996. Douglas-fir beetle. USDA For. Serv. Forest Insect and Disease Leaflet 5. Washington, DC. 8 p.
- STEEL, R.G.D., AND J.H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill, Inc., New York, NY.
- USDA AND USDI. 1994a. Final supplement environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. US Dept. Agric. For. Serv.; US Dept. Interior, Bureau of Land Management. 2 vol.
- USDA AND USDI. 1994b. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl (plus Attachment A: standards and guidelines). US Dept. Agric. For. Serv.; US Dept. Interior, Bureau of Land Management.
- WILLIAMSON, R.L., AND F.E. PRICE. 1971. Initial thinning effects in 70- to 150-year-old Douglas-fir—Western Oregon and Washington. USDA For. Serv. Res. Paper PNW-117.