Western North American Naturalist

Volume 63 | Number 4 Article 10

12-3-2003

Effects of Douglas-fir beetle (Coleoptera: Scolytidae) infestations on forest overstory and understory conditions in western Wyoming

Joel D. McMillin
USDA Forest Service, Forest Health Management, Rapid City, South Dakota

Kurt K. Allen
USDA Forest Service, Forest Health Management, Rapid City, South Dakota

Western North American Naturalist 63(4), ©2003, pp. 498–506

EFFECTS OF DOUGLAS-FIR BEETLE (COLEOPTERA: SCOLYTIDAE) INFESTATIONS ON FOREST OVERSTORY AND UNDERSTORY CONDITIONS IN WESTERN WYOMING

Joel D. McMillin[1,2] and Kurt K. Allen[1]

ABSTRACT.—Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.) infestations frequently result from disturbance events that create large volumes of weakened Douglas-fir trees, *Pseudotsuga menziesii* (Mirb.) Franco. Previous research has focused on determining susceptibility of forest stands to Douglas-fir beetle and predicting the amount of tree mortality from Douglas-fir beetle infestations following disturbance events. Little work has been done on consequent changes in the forest overstory and understory. In the early 1990s, populations of Douglas-fir beetle increased in fire-scorched trees, subsequently infesting undamaged neighboring stands in the Rocky Mountains of western Wyoming, USA. In 1999 transect sampling and 25 pairs of previously infested and uninfested plots were used to quantify changes in forest stand conditions and ensuing responses in the understory caused by Douglas-fir beetle infestations. Significant effects of the Douglas-fir beetle infestation comprised 3 general categories: (1) *overstory effects:* basal area was reduced by 40%–70%, average tree diameter decreased by 8%–40%, and the Douglas-fir component of the overstory decreased by more than 12%; (2) *regeneration effects:* conifer seedling regeneration increased nearly fourfold in infested plots and 90% of the regeneration was Douglas-fir; (3) *understory effects:* understory vegetation (forbs, grass, and shrubs) had a threefold increase in infested compared with uninfested plots. In addition, basal area of Douglas-fir killed by the Douglas-fir beetle was significantly correlated with initial Douglas-fir basal area and percentage of Douglas-fir, but not with stand density index, tree diameter, or trees per hectare. Significant inverse relationships also were found between post-infestation basal area and abundance of forbs, grass, and shrubs, and understory height. Thus, we found that Douglas-fir beetle infestations cause significant short-term effects in both the overstory and understory and contribute to an altered mosaic in forest structure.

Key words: Dendroctonus pseudotsugae, *bark beetles, Scolytidae, insect impact, forest dynamics.*

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., infests and kills Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, throughout its range in North America. Typically, the beetle reproduces in scattered trees that are highly stressed or recently killed, such as windfall, defoliated, or fire-scorched trees (Furniss 1962, 1965, Lessard and Schmid 1990). If enough suitable host material is present, beetles can increase in stressed trees and infest nearby healthy ones (Furniss et al. 1981). Previous research on Douglas-fir beetle infestations has examined forest stand and site characteristics associated with infestations (Furniss et al. 1979, 1981, Weatherby and Thier 1993, Negrón 1998, Shore et al. 1999) and developed models to predict the extent of tree mortality (Negrón et al. 1999). However, there is a paucity of research concerning subsequent changes to the forest overstory and understory and forest dynamics (Hadley and Veblen 1993, Schmid and Mata 1996).

Fires that started in Yellowstone National Park in 1988 burned onto the Clarks Fork Ranger District of the Shoshone National Forest, Wyoming, killing and scorching a large number of trees. Populations of the Douglas-fir beetle increased in scorched trees and began attacking neighboring green trees in subsequent years throughout this area (Pasek 1990). Similar events took place within Yellowstone National Park (Rasmussen et al. 1996). During the Douglas-fir beetle infestation in the Shoshone National Forest, an estimated 23,000 trees were killed over a 7-year period (USDA Forest Service, Forest Health Monitoring aerial surveys, 1992–1998). Additional mortality has occurred in this area since it was last surveyed to detect changes in beetle populations (Pasek 1990, 1991, 1996, Pasek and Schaupp 1992, 1995, Schaupp and Pasek 1993, 1995, Allen and Pasek 1996) and to develop a predictive mortality model (Negrón et al. 1999). Moreover, previous surveys did not quantify

[1]USDA Forest Service, Forest Health Management, Rapid City, SD 57702.
[2]Corresponding author.

changes in the level of tree cover, tree species composition, size classes of residual trees, and changes in the understory. To predict the effects of insect outbreaks on shaping future forest conditions, we find it critical to document changes occurring in both the overstory and understory based on recent outbreaks.

The overall objective of this study was to determine the effect of Douglas-fir beetle on both the over- and understory of Douglas-fir stands in the Shoshone National Forest. Specific objectives were to (1) describe the effects of Douglas-fir beetle on tree species composition, basal area, and diameter on the Shoshone National Forest; (2) document forest conditions present in areas that have experienced high levels of mortality over the past 10 years; and (3) quantify changes in the understory of infested Douglas-fir stands. These objectives are of value not only to managers on the Shoshone National Forest but also to other areas of the northern and central Rockies where extensive stands of Douglas-fir exist.

STUDY SITE

The study was conducted in the drainages of Sunlight Creek and Clarks Fork River (44°50′N, 109°30′W), adjacent to the eastern border of Yellowstone National Park, Wyoming. These areas are characterized by predominantly pure stands of Douglas-fir and, to a lesser extent, by mixed stands consisting of Douglas-fir, Engelmann spruce (*Picea engelmannii* Parry), subalpine fir [*Abies lasiocarpa* (Hook) Nutt.], and lodgepole (*Pinus contorta* Dougl.), whitebark (*P. albicaulis* Engelm.), or limber pine (*P. flexilis* James). Elevation in the study area ranges from 1980 m to 2600 m asl. The most common habitat types for this area are *Pseudotsuga menziesii / Symphoricarpus albus*, *P. menziesii / Physocarpus malvaceous*, and *P. menziesii / Calamagrostis rubescens* (Negrón et al. 1999).

METHODS

Effect of Douglas-fir Beetle on Forest Overstory Conditions

To measure the effects of Douglas-fir beetle on forest stand conditions, we followed the design of McCambridge et al. (1982a) but included additional measurements as described below. Measurements of forest conditions and Douglas-fir beetle effect were conducted using sampling through stands that were predominantly Douglas-fir and had experienced older mortality (e.g., mortality that had occurred primarily 5 years or more before our 1999 study). A 20–basal area factor (BAF) variable-radius plot was installed every 10 chains (201.2 m) on 15 transects throughout these areas, totaling 153 plots. Transects were distributed at random throughout the area of infestation and each transect was contained within an individual stand.

For all plots data were recorded on tree species, diameter at breast height (dbh, cm), crown class, crown condition/damages, and year of Douglas-fir beetle attack. Other than Douglas-fir beetle–caused tree mortality, no other causes of Douglas-fir mortality were observed within the areas surveyed. Using this information, we obtained basal area ($m^2 \cdot ha^{-1}$) and stand density index estimates. Information on percent slope, aspect, and other general site characteristics was gleaned from earlier reports of the area (Negrón et al. 1999, W.C. Schaupp unpublished data). Using the following categories, we recorded the year of attack: *current-year attack:* green tree under attack, resin flow, and fresh boring dust evident; *1-year-old attack:* foliage fading but some green perhaps still present, bark still hard and tight, galleries evident, and exit holes present; *2-year-old attack:* most foliage missing, remaining foliage (if any) orange, galleries still identifiable, small twigs present, secondary wood borers may be present but not abundant, and exit holes present; *3-year-old attack:* all foliage gone but small twigs still present, bark loose, galleries hard to find, burrowing secondary wood borers abundant, and exit holes present; *4-year-old and older attack:* smaller twigs gone and exit holes present (Negrón 1998).

Effect of Douglas-fir Beetle on Understory Conditions

In addition to the transect-survey method of evaluating beetle effect, we also took measurements at permanent plots established in the early 1990s. These plots were originally established to develop hazard rating systems and a prediction model for Douglas-fir beetle–caused mortality using pairs of infested and uninfested plots (Negrón et al. 1999, W.C. Schaupp unpublished data). The methods for plot inspection follow those reported by Negrón (1998), which resulted in infested and uninfested points being intermingled. Areas of infestation were determined by aerial survey detection and ground-based information. Infested plots were then installed randomly in areas of mortality in the stand. Uninfested plots were installed in a random direction from the infested plots in unaffected areas of the stand. Although these plots were originally labeled uninfested, we detected a limited amount of tree mortality during our subsequent surveys. Plots were separated by ≥40 m and <100 m. Twenty-five paired plots installed in 1992 and 1993 were reexamined in 1999 throughout the Clarks Fork and Sunlight Creek drainages. The objectives of using these paired plots in the present study were to quantify changes in the overstory and understory as a result of Douglas-fir beetle infestation and, in turn, to quantify changes in forest structure that may be occurring.

At each plot location (20 BAF variable-radius plot), we took overstory measurements as described earlier for the transect surveys. In addition, understory growth and abundance were measured using the Canfield (1941) line-intercept method. The percentage of each understory component (grass, forb, and shrub) was calculated from total area (cm) of each component along 3-m lines running north–south and east–west from plot center. Understory height also was measured by recording height of the understory at plot center and 3 m from plot center in each cardinal direction. Species, number, and type of tree regeneration (saplings [2.54 ≤ dbh <12.7 cm], seedlings [dbh <2.54 cm]) were measured using 3.59-m radius plots (0.004 ha).

Data Analysis

Data collected from the transect portion of the study were used to quantify Douglas-fir beetle effects on stand conditions. We used transect means of the measured variables to compute linear regressions between stand characteristics and amount of basal area killed by the Douglas-fir beetle. Transect means were used in regression analysis because they represent average conditions for a given stand. Summary statistics also provided a description of stand conditions before and after Douglas-fir beetle infestations.

Paired plots were used to quantify changes to the overstory and understory. Measurements collected from infested and uninfested plot pairs were evaluated in paired-sample t tests of variable means. Data were used also to calculate coefficients of determination using simple linear regression analysis between post-infestation basal area and understory variables. Percent data in both the transect and paired-plot studies were normalized by arcsine transformation prior to paired t-test and regression analyses. Figures and tables both present original untransformed data. All statistical analyses were conducted using Systat® software (Wilkinson 1991).

RESULTS

Effect of Douglas-fir Beetle on Forest Overstory Conditions

Douglas-fir beetle infestations caused significant changes to forest conditions of the areas studied (Tables 1, 2). Approximately two-thirds of the mortality occurred more than 3 years before we began the study (Table 1), and the greatest proportion probably occurred 5–8 years ago (Negrón et al. 1999). Aerial surveys within the area of interest detected a resurgence in Douglas-fir beetle–caused tree mortality in 1998. However, the amount of mortality was less than occurred in the early to mid-1990s (USDA Forest Service, Forest Health Management). Uninfested plots had sustained basal area losses $<3.0\ m^2 \cdot ha^{-1}$ (5%) by 1999, with most of this occurring in the previous 2 years (Table 2). This suggests that the Douglas-fir beetle may infest areas within stands that are less preferred as suitable hosts and within areas that are depleted.

Douglas-fir beetles caused significant reductions in the overstory of Douglas-fir stands. Based on transect studies, we determined that the Douglas-fir beetle caused reductions in Douglas-fir basal area by more than $16\ m^2 \cdot ha^{-1}$ (46%), pre-outbreak basal area of all tree species by 43%, and average stand diameter by more than 2.5 cm (8%; Table 1). Using a subsample of the plots reported in Negrón et al. (1999), we found basal area was reduced nearly 80% in infested plots compared with uninfested plots (Table 2). Similarly, reduction in tree diameter was greater using paired plots than the transect portion of the study. Post-outbreak tree diameters averaged 11 cm less in infested than in uninfested plots.

Percentages of Douglas-fir stems in the stand and Douglas-fir basal area were important in determining the level of Douglas-fir beetle effect. Regressing basal area of Douglas-fir

TABLE 1. Summary of stand conditions and Douglas-fir beetle effect on stand conditions based on transect sampling on the Shoshone National Forest, Wyoming, in 1999.

Transect	BA[a]	DFBA[b]	TPH[c]	DBH[d]	SDI[e]	Live DBH[f]	% DF[g]	CY[h]	Basal area killed by year of attack				Total
									1 yr	2 yr	3 yr	4 yr+	
1	35.6	20.6	274.6	42.9	103.3	44.2	58.1	0.0	0.0	0.0	0.0	0.0	0.00
2	41.3	40.2	276.9	43.4	106.1	33.8	97.2	4.6	0.6	2.9	4.0	10.9	23.1
3	35.6	31.5	289.7	39.4	94.8	35.1	87.0	2.8	0.0	0.0	0.6	9.2	12.6
4	39.0	35.6	384.1	36.6	111.7	35.6	92.4	2.3	4.0	1.7	2.3	6.3	16.7
5	42.5	40.2	254.7	40.6	87.7	37.1	94.3	1.1	2.3	4.6	8.0	10.3	26.4
6	39.8	39.0	265.8	44.7	106.6	40.9	98.1	1.9	1.1	2.7	5.4	6.1	17.2
7	31.0	29.8	287.6	36.6	83.5	31.2	92.3	1.2	0.0	2.3	2.3	8.0	13.8
8	36.7	37.4	537.9	30.2	115.2	28.2	100.0	1.2	1.7	1.7	1.4	8.3	14.4
9	42.5	42.5	440.2	35.6	122.3	37.1	100.0	4.6	4.0	0.6	2.3	20.1	31.6
10	36.5	36.5	448.3	32.0	105.2	29.2	100.0	4.0	0.6	1.5	3.8	7.5	17.4
11	36.3	34.4	502.4	27.9	94.8	24.6	96.2	2.3	1.4	3.2	4.1	5.5	16.5
12	33.0	33.1	305.5	35.3	83.9	33.8	100.0	4.6	0.5	2.8	2.3	3.7	13.8
13	39.8	39.0	659.7	27.7	122.7	26.9	98.1	2.7	0.4	1.1	0.0	6.5	10.7
14	29.6	25.0	360.4	33.0	88.9	32.3	84.2	0.5	0.0	0.3	1.8	1.8	4.4
15	36.3	34.2	334.9	37.4	100.7	33.8	94.4	1.1	2.3	2.9	2.3	7.5	16.1
Mean	*37.0*	*34.6*	*374.8*	*36.2*	*101.8*	*33.5*	*92.8*	*2.3*	*1.3*	*1.9*	*2.7*	*7.5*	*15.6*
$s_{\bar{x}}$	*1.0*	*1.5*	*30.0*	*1.3*	*3.2*	*1.2*	*2.7*	*0.4*	*0.3*	*0.3*	*0.5*	*1.1*	*1.9*

[a]Average pre-outbreak basal area ($m^2 \cdot ha^{-1}$) found for all points in the transect
[b]Average Douglas-fir basal area ($m^2 \cdot ha^{-1}$)
[c]Trees per hectare
[d]Diameter at breast height (cm) for all tree species
[e]Stand density index
[f]Diameter at breast height for all post-outbreak living Douglas-fir trees
[g]Percentage of stems in plot that were Douglas-fir
[h]Basal area currently infested by Douglas-fir beetle

TABLE 2. Summary of Douglas-fir beetle–caused changes to overstory and understory conditions based on 25 paired variable-radius plots on the Shoshone National Forest, Wyoming, in 1999. Mean (± s) for each variable is presented.

Variable	Uninfested plots	Infested plots	t-value	$P > t$
Pre-outbreak all species basal area ($m^2 \cdot ha^{-1}$)	43.0 (2.3)	44.5 (2.0)	0.489	0.630
Pre-outbreak Douglas-fir basal area ($m^2 \cdot ha^{-1}$)	40.8 (2.9)	44.1 (2.0)	0.931	0.361
Post-outbreak all species basal area ($m^2 \cdot ha^{-1}$)	40.8 (2.4)	8.3 (1.3)	11.862	***
Post-outbreak Douglas-fir basal area ($m^2 \cdot ha^{-1}$)	38.6 (2.8)	7.9 (1.2)	10.006	***
Pre-outbreak DBH for all species (cm)	33.2 (1.4)	37.9 (1.4)	4.111	***
Post-outbreak Douglas-fir DBH (cm)	32.8 (1.4)	21.9 (2.9)	3.188	**
Basal area killed ($m^2 \cdot ha^{-1}$)	2.2 (0.8)	36.2 (2.0)	14.513	***
Percent Douglas-fir[a]				
Pre-infestation	93.8 (3.0)	99.6 (0.4)	2.362	0
Post-infestation	93.6 (3.0)	78.0 (7.6)	1.890	0.071
Seedling regeneration[b]	8.3 (2.5)	30.6 (8.5)	3.020	**
Understory height (cm)	14.8 (2.0)	49.4 (5.1)	7.810	***

[a]Percentage of Douglas-fir stems per plot
[b]Number of seedling recorded per 0.004-ha plot
* <0.05
** <0.01
*** <0.001

killed by Douglas-fir beetle, we found significant relationships with (1) percentage of Douglas-fir stems ($y = -30.3 + 0.50DF\%$, $r^2 = 0.466$, $P < 0.006$), (2) pre-outbreak basal area of all tree species ($y = -36.9 + 1.426BA$, $r^2 = 0.50$, $P < 0.003$), and (3) Douglas-fir basal area ($y = -23.4 + 1.13BA$, $r^2 = 0.744$, $P < 0.001$; Table 1, Fig. 1). Douglas-fir diameter, trees per hectare, and stand density index were not found to be significant ($P > 0.50$). No Douglas-fir beetle–related tree mortality was measured in the only transect (T1) that had <80% Douglas-fir component in the overstory. Moreover, the 3 transects having the highest average basal areas (T2, T5, and T9) also had the 3 highest total mortality values.

Douglas-fir beetle also caused >20% reduction in Douglas-fir in the overstory relative to other tree species (Table 2). The percentage of Douglas-fir did not differ between infested and uninfested plots when measured post-infestation because of the large variance in infested plots (Table 2). However, when examining only infested plots, we noted that the percentage of post-infestation Douglas-fir stems was significantly lower than the pre-infestation percentage ($t = 2.605$, $P = 0.016$). Consequently, percentages of Engelmann spruce, white pine, and lodgepole pine increased relative to Douglas-fir in the overstory of infested plots.

Effect of Douglas-fir Beetle on Understory Conditions

Douglas-fir beetle also had a significant effect on understory abundance. Infested plots had approximately a threefold increase in total abundance of understory plant categories compared with uninfested plots (Fig. 2). However, the abundance of forbs, shrubs, and grass did not change relative to each other (e.g., forbs were the most prevalent in both infested and uninfested plots). Grass species had the greatest percentage increase (nearly 12-fold on average) in abundance among the 3 groups of understory plants. In addition, average understory height more than tripled in infested plots (Table 2). Because mortality of tree species other than Douglas-fir was less than 1% (Table 2), these changes in understory are assumed to be a result of Douglas-fir mortality.

Regressing basal area of Douglas-fir killed by Douglas-fir beetle, we found significant, but weak, inverse relationships with (1) abundance of forbs ($y = 44.8 - 0.11BA$, $r^2 = 0.266$, $P < 0.001$), (2) grass ($y = 21.3 - 0.10BA$, $r^2 = 0.24$, $P = 0.003$), (3) shrubs ($y = 29.4 - 0.07BA$, $r^2 = 0.10$, $P = 0.027$), and (4) understory height ($y = 21.6 - 0.10BA$, $r^2 = 0.468$, $P = 0.005$). The amount of seedling regeneration was not found to be significant ($P = 0.174$). The relatively low coefficient of determination for each understory component suggests, however, that there are other important, but unexplained, sources of variation that lead to their abundance. One source of variation may be the timing of tree mortality in relation to timing of plot measurements; i.e., plots with "older mortality" had more time for understory response than plots with more recent tree mortality. Other sources of variation may include differences in

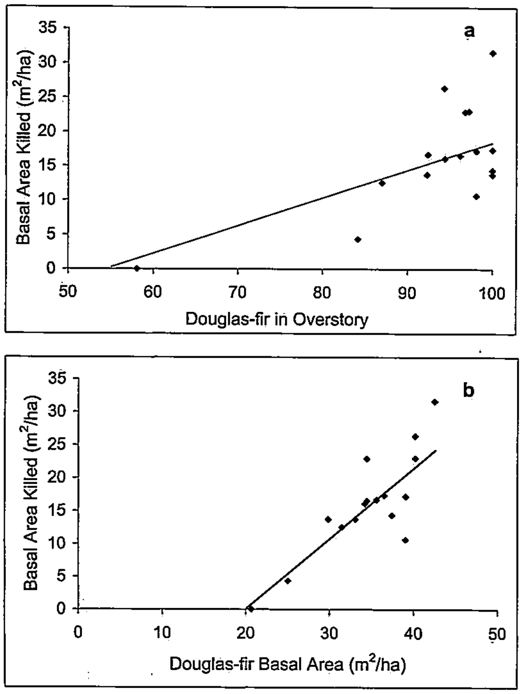

Fig. 1. Relationship between basal area of Douglas-fir killed by Douglas-fir beetle ($m^2 \cdot ha^{-1}$) and (a) percentage of Douglas-fir and (b) pre-outbreak Douglas-fir basal area ($m^2 \cdot ha^{-1}$) on the Shoshone National Forest, Wyoming. Data symbols represent transect means (153 plots total).

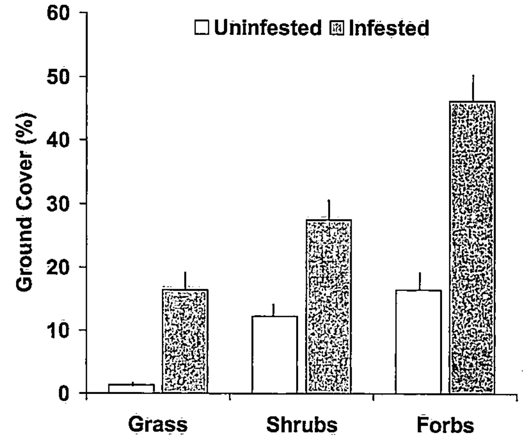

Fig. 2. Effect of Douglas-fir beetle on understory (grass, shrubs, forbs) abundance on the Shoshone National Forest, Wyoming. Bars represent plot means + $s_{\bar{x}}$. Significant differences were detected between infested and uninfested plot means for all understory components ($P < 0.005$).

grazing pressure, short- and long-term fire effects, aspect, and moisture.

In addition to the increase in the understory herbaceous layer, the amount of conifer regeneration also increased significantly (Table 2). Regeneration in infested plots was more than 3 times greater than in uninfested plots, and approximately 90% in both plot types was Douglas-fir. The remaining 10% included Engelmann spruce, subalpine fir, and lodgepole, whitebark, and limber pine seedlings.

Discussion

Effect of Douglas-fir Beetle on Forest Overstory Conditions

The percent reduction in basal area found in the transect portion of this study was either lower or higher than reported by Negrón et al. (1999) for the same general area depending on the method of measurement. Negrón et al. (1999) selected points at random distance and direction from infested spots to develop mortality models, whereas in our transect study whole stands were surveyed, thus including areas of high and low infestations. Using the same plots established by Negrón et al. (1999), we documented greater mortality because of continued beetle activity within the areas studied. Tree mortality observed in infested plots is probably representative of stands that have experienced heavy mortality, and mortality levels found along the transects are likely more reflective of the type of mortality that occurs across a watershed.

Percentages of Douglas-fir stems in the stand and basal area were important in determining level of Douglas-fir beetle effect. Coefficient of determination and slope between Douglas-fir basal area and basal area killed ($r^2 = 0.70$ and slope = 1.12) were higher than those reported earlier for the area (e.g., $r^2 = 0.46$ and slope = 0.6; Negrón et al. 1999). Perhaps these differences occurred because the beetles had more fully utilized their food resources since the earlier study, or because we based the regression on stand averages, whereas Negrón et al. used plot-level means to compute relationships. Thus, stand averages may have reduced some between-plot variation, resulting in tighter regressions. Care must be taken when using linear regression equations of this kind because, although actual mortality can be derived, relatively low precision estimates may be generated (Negrón et al. 1999). In addition, because a relatively small range of basal area and percentage of Douglas-fir was found in our study, caution should be used in interpreting these results.

Relationships between amount of tree mortality and basal area or percentage of Douglas-fir are, in general, consistent with previous studies on Douglas-fir beetle in other geographical locations (Furniss et al. 1979, 1981, Weatherby and Thier 1993, Negrón 1998). Hypotheses as to why Douglas-fir beetles prefer stands of higher basal area include (1) tree subjection to greater moisture stress and (2) beetle preference for trees with shaded stems (Furniss et al. 1981). Furthermore, trees growing in overstocked conditions may have reduced growth rates, leading to competition for carbon resources needed for the production of defensive compounds (discussed in Negrón 1998).

Although tree diameter was not significantly correlated with basal area killed in the transect portion of our study, tree diameter has been linked with Douglas-fir susceptibility to Douglas-fir beetle in Idaho and Montana (Furniss et al. 1979, 1981) and British Columbia (Shore et al. 1999). One reason a significant relationship did not occur may be that we measured effects at, or near, the conclusion of the infestation. Therefore, most of the largest trees may had already been attacked and the beetles had moved on to smaller trees, thus causing a dilution effect of initial beetle preferences for larger tree size. Pasek (1990) reported that Douglas-fir beetles preferentially attacked the largest-diameter trees first in this area following the 1988 fires. In the paired plots, tree diameter prior to infestation was significantly higher in infested plots and significantly lower after the infestation than in uninfested plots (Table 2). Moreover, tree diameter of live trees was lower than initial tree diameter for all transects except 1 and 9. This reinforces the argument that the Douglas-fir beetle initially attacks larger-diameter trees and is reducing average Douglas-fir diameter.

Despite both basal area and stand density index being calculated from tree diameter and quantity of trees per unit area, previous studies have demonstrated that basal area is in general a better predictor of tree mortality than stand density index (Negrón 1998, Negrón et al. 1999). We also found that stand density index is not a good estimator of basal area killed. Transect 13 had the highest stand density as a result of the high number of trees per hectare; however, the lower-than-average dbh probably resulted in less basal area being killed. Similarly, transect 5 had a low stand density index caused by fewer trees per hectare, but larger-than-average dbh and thus relatively higher basal area killed.

The percent reduction of Douglas-fir in the overstory caused by Douglas-fir beetles likely depends on the initial proportion of Douglas-fir in the overstory as indicated by the regression analysis. For example, compared with the current study, reductions in the percentage of Douglas-fir in the overstory were greater (e.g., 20%) in Idaho where stands initially were only 60% or higher Douglas-fir (Furniss et al. 1979).

Effect of Douglas-fir Beetle on Understory Conditions

Douglas-fir beetle–caused mortality of the forest overstory resulted in understory growth response. The relative abundance of understory plants changes over time as the amount and height of conifer regeneration increases and, therefore, the data presented here should not be considered to reflect a permanent change. However, in the short-term, previously infested spots may serve as areas of increased forage suitable for large ungulates (Schmid and Amman 1992). Also, mountain pine beetle (*D. ponderosae* Hopkins) outbreaks have caused increased herb production in Colorado (McCambridge et al. 1982b). That study reported forb, sedge, and grass production increases following beetle-caused mortality of ponderosa pine in the overstory. Similarly, spruce beetle (*D. rufipennis* Kirby) outbreaks have been shown to increase grass and forb production in Colorado (Yeager and Riordan 1953). However, in contrast to the effects caused by the Douglas-fir beetle, browse (woody) plants showed a steady, unexplainable decrease following the spruce beetle epidemic. Differences in understory response are probably a function of seed sources on the site prior to the bark beetle–caused disturbances and the biotic potential of on-site vegetation. Further and additional long-term studies are needed to determine how long these understory effects are measurable and what differences occur between forest types.

In addition to increased abundance of understory plants, conifer regeneration also increased significantly. It seems, however, that areas experiencing heavy Douglas-fir mortality will remain predominantly Douglas-fir. These findings were anticipated inasmuch as the stands were initially almost pure Douglas-fir. Similar studies in more mixed stands may detect a greater increase in regeneration of other species. These results mirror Hadley and Veblen (1993), where Douglas-fir in the Colorado Front Range remained the dominant tree species after repeated and overlapping outbreaks of western spruce budworm and Douglas-fir beetle.

CONCLUSIONS

Douglas-fir beetle changed both overstory and understory conditions of the forest. There were both significant reductions in the overstory and consequent increases of conifer regeneration, forbs, grass, and shrubs in the understory. This dynamic will probably continue until after the Douglas-fir beetle population collapses to endemic levels. However, it is important to remember that overstory reductions are temporary, as diameter growth may be accelerated in the remaining live trees and as the regeneration matures. Based on average tree size and age reported by Negron et al. (1999), we estimate that a return to pre-infestation overstory conditions will probably take between 25 and 200 years, depending on the severity of tree mortality for a given stand. Moreover, we emphasize that changes are characteristic of a dynamic forest ecosystem. Insect-caused disturbances work with other disturbances such as fire to shape the continually changing spatial and temporal patterns of the forest (Schmid and Mata 1996).

ACKNOWLEDGMENTS

We acknowledge the field and data entry assistance of Denise Hardesty and Daniel F. Long. In addition, we thank David Bailey, Shoshone National Forest, for supplying GIS maps of the area, and José F. Negrón, David Leatherman, and Matt Hansen for providing valuable comments on an earlier version of this manuscript. The Forest Health Monitoring, Evaluation Monitoring Program, provided funding for this project.

LITERATURE CITED

ALLEN, K.K., AND J.E. PASEK. 1996. Emergence and overwintering brood of Douglas-fir beetle eight years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-97-03, USDA Forest Service, Rocky Mountain Region. 16 pp.

CANFIELD, R. 1941. Application of the line-intercept method in sampling range vegetation. Journal of Forestry 39: 388–394.

FURNISS, M.M. 1962. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. Journal Economic of Entomology 55:486–491.

______. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. Journal of Forestry 63:8–11.

FURNISS, M.M., R.L. LIVINGSTON, AND D.M. MCGREGOR. 1981. Development of a stand susceptibility classification for Douglas-fir beetle. Pages 115–128 *in* Proceedings: Symposium on Hazard Rating Systems in Forest Pest Management, 31 July–1 August 1980, University of Georgia, Athens. General Technical Report WO-27, USDA Forest Service, Washington, DC.

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. General Technical Report INT-59, USDA Forest Service. 19 pp.

HADLEY, K.S., AND T.T. VEBLEN. 1993. Stand response to western spruce budworm and Douglas-fir bark beetle outbreaks, Colorado Front Range. Canadian Journal of Forest Research 23:479–491.

LESSARD, E.D., AND J.M. SCHMID. 1990. Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado. Great Basin Naturalist 50:333–338.

MCCAMBRIDGE, W.F., F.G. HAWKSWORTH, C.B. EDMINISTER, AND J.G. LAUT. 1982a. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-235, USDA Forest Service. 7 pp.

MCCAMBRIDGE, W.F., M.J. MORRIS, AND C.B. EDMINISTER. 1982b. Herbage production under ponderosa pine killed by the mountain pine beetle in Colorado. Research Note RM-416, USDA Forest Service. 3 pp.

NEGRÓN, J.F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. Forest Ecology and Management 107:71–85.

NEGRÓN, J.F., W.C. SCHAUPP, JR., K.E. GIBSON, J. ANHOLD, D. HANSEN, R. THIER, AND P. MOCETTINI. 1999. Estimating extent of mortality associated with the Douglas-fir beetle in the central and northern Rockies. Western Journal of Applied Forestry 14:121–127.

PASEK, J.E. 1990. Douglas-fir beetle infestations following the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-90-01, USDA Forest Service, Rocky Mountain Region. 10 pp.

______. 1991. Populations of Douglas-fir beetle in scorched and green trees two years following the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-91-01, USDA Forest Service, Rocky Mountain Region. 20 pp.

______. 1996. Emergence and overwintering brood of Douglas-fir beetle seven years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-96-01, USDA Forest Service, Rocky Mountain Region. 16 pp.

PASEK, J.E., AND W.C. SCHAUPP, JR. 1992. Populations of Douglas-fir beetle in green trees three years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-92-02, USDA Forest Service, Rocky Mountain Region. 13 pp.

______. 1995. Emergence and overwintering brood of Douglas-fir beetle six years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-95-02, USDA Forest Service, Rocky Mountain Region. 17 pp.

RASMUSSEN, L.A., G.D. AMMAN, J.C. VANDYGRIFF, R.D. OAKES, A.S. MUNSON, AND K.E. GIBSON. 1996. Bark beetle and wood borer infestation in the Greater Yellowstone Area during four postfire years. General Technical Report INT-RP-487, USDA Forest Service. 10 pp.

SCHAUPP, W.C., JR., AND J.E. PASEK. 1993. Emergence and overwintering brood of Douglas-fir beetle four years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-94-01, USDA Forest Service, Rocky Mountain Region. 14 pp.

______. 1995. Emergence and overwintering brood of Douglas-fir beetle five years after the Clover Mist Fire on the Clarks Fork Ranger District, Shoshone National Forest, Wyoming. Biological Evaluation R2-54-01, USDA Forest Service, Rocky Mountain Region. 19 pp.

SCHMID, J.M., AND G.D. AMMAN. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. Pages 51–59 *in* Proceedings: Workshop on Old-growth Forests in the Southwest and Rocky Mountain Regions, 9–13 March 1992, Portal, AZ. General Technical Report RM-213, USDA Forest Service, Fort Collins, CO.

SCHMID, J.M., AND S.A. MATA. 1996. Natural variability of specific forest insect populations and their associated effects in Colorado. General Technical Report RM-GTR-275, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 14 pp.

SHORE, T.L., L. SAFRANYIK, M. FURGUSON, J. CASTONGUAY, AND W.G. RIEL. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). Canadian Entomologist 131:831–839.

WEATHERBY, J.C., AND R.W. THIER. 1993. A preliminary validation of a Douglas-fir beetle hazard rating system, Mountain Home Ranger District, Boise National Forest, 1992. Forest Pest Management Report R4-93-05, USDA Forest Service, Intermountain Region. 7 pp.

WILKINSON, L. 1991. SYSTAT: the system for statistics. Evanston, IL.

YEAGER, L.E., AND L.E. RIORDAN. 1953. Effects of beetle-killed timber on range and wildlife in Colorado. Pages 596–616 *in* Proceedings of the 18th North American Wildlife Conference.

Received 5 February 2002
Accepted 10 December 2002