Douglas-Fir Beetle Infestations Are Associated with Certain Rock and Stand Types in the Inland Northwestern United States

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ABSTRACT Landscape-level geographic analysis was used to examine the occurrence of *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae) in association with geology (rock type) and forest stand types on the Panhandle National Forests of northern Idaho and northeastern Washington from 1996 to 1999. Beetle infestations occurred most often in mature stands comprised primarily of trees ≥23 cm in diameter at breast height (≈1.4 m), in habitat types likely to contain Douglas-fir. Douglas-fir stands growing on Prichard and lower Wallace formation metasedimentary rocks and intrusive dikes and sills were significantly more likely than Douglas-fir stands growing on other rock types to harbor beetle populations during nonoutbreak years early in the study period. By 1999 (when outbreak populations of Douglas-fir beetle were present), beetle infestations occurred across all rock types at rates proportional to the amount of stand area on those rocks, indicating a decrease in infestation rates for stands on particular rock types when beetle populations were large. Although the biological mechanisms influencing beetle preferences were not examined, information derived in this study could be useful in developing quantitative hazard-rating models for Douglas-fir beetle, and, subsequently, in designing silvicultural practices to reduce the amount of beetle-susceptible Douglas-fir stands on particular rock types.

KEY WORDS Douglas-fir beetle, *Dendroctonus pseudotsugae*, geology, geographic information system, landscape analysis

DOUGLAS-FIR (*Pseudotsuga menziesii*) is widely distributed across a variety of site conditions throughout the inland northwest of the United States, where it is one of the most important tree species. A diverse variety of insects and diseases affect Douglas-fir stands in the inland northwest, and many are capable of causing economic damage. Most of these insect and disease organisms are native to the area and experience natural cycles of buildup and decline. One of the major insect pests of Douglas-fir throughout the region is the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae). Douglas-fir beetle typically has one generation per year, and beetles normally attack dead or dying trees (McMullen and Atkins 1962, Furniss et al. 1981, Negron et al. 1999). Dense stands of Douglas-fir are more susceptible to attack by Douglas-fir beetles (Furniss 1979, Furniss et al. 1981, Negron et al. 1999), which typically attack large diameter (>30 cm in diameter at breast height [dbh], ≈1.4 m) trees (Furniss et al. 1979, Hagle et al. 1987). Furthermore, outbreaks of Douglas-fir beetle are often associated with forest disturbances such as wildfire or windstorms (McGregor et al. 1974, Furniss 1975, Furniss et al. 1981).

After a major ice storm in November 1997, an outbreak of Douglas-fir beetle occurred throughout much of northern Idaho and northeastern Washington. On the Panhandle National Forests, an average of 51 ha/yr was affected by new Douglas-fir beetle attacks in 1996 and 1997. In 1998, ≈479 ha were affected by Douglas-fir beetle, and in 1999, aerial surveys indicated that 31,093 ha were impacted (USDA 2001). Therefore, Panhandle National Forests initiated emergency salvage logging operations, both to reduce fire risk and the risk of beetles spreading to adjacent private lands.

As a prelude to our current study, Panhandle National Forests personnel noted that Douglas-fir beetle infestations seemed to occur more frequently on certain rock types than others, even though adjacent stands on various rock types were otherwise very similar. Although not implicated in previous studies of Douglas-fir beetle susceptibility (Furniss 1979, Furniss et al. 1979, Shore et al. 1999, Negron et al. 1999), research suggests that bedrock geology underlying forest stands affects forest nutrition (Moore et al. 1998), which in turn could impact tree susceptibility to insects and disease (Mandzak and Moore 1994). Rock type has been demonstrated to affect tree

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growth and growth response to nitrogen fertilization (Shen et al. 2000). Rock type also significantly affects tree mortality rates on both control and nitrogen-fertilized plots (Shen et al. 2001). Rock type may thus result in broad differences in site nutrient conditions. Potassium nutrition can significantly affect Douglas-fir root biochemistry, including the concentration of phenolic compounds (Shaw et al. 1998), and there are significant differences in Douglas-fir foliar potassium (K) concentration by rock type (Shen et al. 2001). For example, trees growing on metasedimentary rocks had the lowest foliar K concentrations of all rock types sampled (Shen et al. 2001). Nutrient-stressed trees may be unable to successfully defend themselves against bark beetle attacks due to an insufficient response of either the constitutive or induced resistance mechanisms (Cook and Hain 1988).

Geology of the area is dominated by a group of Precambrian metasedimentary rocks known as the Belt Supergroup. The Belt Supergroup is comprised of a series of formations, including the Wallace, Prichard, Burke, Revett, St. Regis, Striped Peak, and Libby (Harrison and Campbell 1963, Lewis and Burmester 1999). The Wallace formation is further subdivided into upper and lower members, whereas the Burke, Revett, and St. Regis formations are often grouped together and called the Ravalli group. The formal nomenclature of Belt rocks is based on their stratigraphy, or the order in which they were laid down during the original process of sedimentation. Almost all of the Belt rocks underwent low-level metamorphism after sedimentation, such that their original protolith (parent rock) is still identifiable. The lithology of Belt rocks reflects this metamorphism, such that all formations contain argillite, siltite, and/or quartzite, which are metamorphosed claystone, siltstone, and sandstone, respectively. The dominant lithologies of the Belt formations include quartzite for the Revett and portions of the Striped Peak, layered gray siltite and argillite for the Prichard and portions of the upper Wallace and Striped Peak, layered green or red siltite and argillite for the Burke, St. Regis, and Libby formations, and carbonate-bearing siltite and quartzite for the lower Wallace and portions of the upper Wallace and Striped Peak (Munts and Idaho Geological Survey [IGS] 2000). Other lithologies common to the area include glacial deposits and intrusive (granitic) rocks. Some of the intrusive rocks occur as plutons, which are deep-seated granitic intrusions characterized by very large grain sizes.

Our analysis used Forest Service data on forest vegetative cover and Douglas-fir beetle attack distributions combined with published geological data to assess whether infestations of Douglas-fir beetles were significantly associated with Douglas-fir stands on certain rock types. Rock type differences may be associated with other environmental or spatial factors that could themselves account for perceived relationships between rock type and beetle infestations. Therefore, additional analyses were conducted to examine these potential alternative explanations for the rock type/Douglas-fir beetle association.

Materials and Methods

Geographic information system (GIS) data layers were obtained for the Bonner's Ferry, Priest Lake, St. Joe, St. Maries, and Sandpoint ranger districts of the Idaho Panhandle National Forests. The total analysis area consisted of ≈445,000 ha, and the insect survey data spanned a 4-yr period (1996–1999). The Forest Service provided two data sets (USDA 2001). The first was a vegetative cover layer mapping stands comprised primarily of trees >12.9 cm in dbh, which occurred on various habitat types (Daubenmire and Daubenmire 1968) likely to contain Douglas-fir (Zack, personal communication). The second data set delineated infestations of Douglas-fir beetle from 1996 to 1999 and was digitized from aerial surveys conducted by the Forest Service's Forest Health Protection group. Infested areas ranged from a few square meters to several hundred hectares, and although the digitized areas probably included some live trees, the majority of trees within the affected areas were dead or dying. These surveys primarily detect trees that were attacked the previous year because most trees do not fade and become visible until at least 1 yr after beetle attack/infestation. For example, trees detected in 1996 were actually attacked and killed by beetles in 1995. Throughout this article, the years referred to will be the years in which infestations were detected by aerial survey.

Digital geology maps for the region were obtained from the United States Geological Survey (USGS) and the IGS. The Sandpoint 1:250,000 quadrangle was merged with the Coeur d'Alene, Thompson Falls, Wallace, St. Maries, and Headquarters 1:100,000 scale digital geology maps (IGS 1996, Miller et al. 1999, Lewis and Derkey 1999, Lewis et al. 1999, Munts and IGS 2000, Burmester et al. 2001). The geology maps were edge-matched at the quadrangle boundaries. Some relabeling of map units was necessary to maintain a consistent naming convention across the different maps; however, rock class aggregation was the same across all geology maps. The relabeling of maps was necessary because different authors used different names for the same rock units, a problem commonly encountered in Belt rocks.

Personnel of the Idaho Panhandle National Forests had observed that the Douglas-fir beetle infestations seemed to be more prevalent on stands occurring on Prichard formation rocks. Therefore, Belt Supergroup rocks were categorized using their formal names, whereas other rock types in the analysis area were categorized by lithology. The resulting eight categories used in statistical analyses were the Prichard, Wallace, Libby, and Striped Peak formations, the Ravalli group (undivided), glacial deposits, intrusive rocks, and other rocks.

Geographic analyses were conducted using ArcView (Environmental Systems Research Institute 1992–1999). The first step of the geographical analysis was to intersect the vegetative cover layer with the geological information layer. By intersecting these layers, new polygons were created that preserved individual stand size class and geological information. The areas infested by Douglas-fir beetle from 1996 through 1999 were then clipped to the intersected Douglas-fir/geology layer. Using this clipping technique, the subsequent analyses were only conducted on beetle infestations that occurred in stands for which both stand attribute and geological data were available. The area infested by Douglas-fir beetle in 1996 and 1997 were combined because infestations were small during those 2 yr compared with 1998 and 1999. A series of frequency tables tabulating the total affected area by timber stand type, rock type, and vegetation category for each year were then created for use in statistical analysis. All frequency tables were created in ArcView (ESRI 1992–1999) and exported to Excel (Microsoft Corporation 1985–1999) worksheets.

Only stands that provided suitable habitat for Douglas-fir beetle were included in analysis, and attack frequency was analyzed by stand size class. The Panhandle National Forests define the various timber size classes as follows: 1) Sawtimber stands have a minimum of 10% of the growing stock trees with a dbh ≥12.5 cm and the stocking of trees ≥23 cm dbh and larger is at least equal to the stocking of trees 12.5–22.9 cm dbh; 2) Poletimber stands have a minimum of 10% of the growing stock trees with a dbh ≥12.5 cm and the stocking of trees from 12.5 to 22.9 cm dbh exceeds the stocking of trees 23 cm dbh and larger; and 3) multisized stands contain trees in two or more size classes. To remain consistent with Forest Service measurement protocols and defined terminologies, we used these size classes for analysis, and abbreviated them as sawtimber, poletimber, and multisized stands for use throughout this article.

Stand maturity classification was also based on Panhandle National Forests stand inventory definitions and refers to stage of development for a given stand. Mature stands are those in which the growth stage has nearly reached full site potential, whereas immature stands are still actively growing. To include all habitats suitable for Douglas-fir beetle, the initial vegetative cover data set consisted of all stands that were pole-size and larger (including multisized stands), in both immature and mature growth stages, in all habitat types likely to contain Douglas-fir. The resulting data set included five categories, which were immature poletimber, immature sawtimber, multisized, mature poletimber, and mature sawtimber.

For analysis, the total stand area in each of the five size and maturity class categories was calculated to determine the baseline distribution of these stand types in the analysis area. This baseline distribution was considered to be the expected distribution of Douglas-fir beetle in the absence of a size and maturity class preference. The total beetle-infested area in each size and maturity class category was then calculated for each year during the analysis period of 1996 through 1999. These yearly distributions were considered to be the observed distributions of Douglas-fir beetle for each year studied. Chi-square analysis (Ott 1988) was used to detect significant differences between the expected and observed distributions. Based on this analysis, only those size and maturity classes that showed expected or greater than expected occurrences of beetle infestation were selected for additional testing.

Geological differences in beetle infestation preferences were examined using the selected size and maturity class categories. Total stand area on each rock type was calculated for this subset of Douglas-fir stands. This served as the baseline distribution of susceptible Douglas-fir stands by rock type, and was the expected distribution of Douglas-fir beetle in the absence of a rock type effect. The total beetle-infested area on each rock type was then calculated for each year during the analysis period of 1996 through 1999. These yearly distributions of beetle-infested area by rock type were considered to be the observed distributions of Douglas-fir beetle for each year studied. Chi-square analysis (Ott 1988) was used to detect significant differences between the expected and observed distributions.

Because differences in beetle infestations occurring in stands on different rock types could potentially be explained by other spatial or biophysical effects, two additional analyses were conducted. First, to determine whether stand fragmentation was contributing to the distribution of beetle infestations, various patch, edge, shape, and interspersion metrics were considered for characterizing and quantifying Douglas-fir stand spatial distribution among rock types. The Interspersion and Juxtaposition Index (IJI) was selected because this index measures the extent to which patch types are interspersed (McGarigal and Marks 1995) and is applicable for assessment of patch-type spatial distribution (Haines-Young and Chopping 1996). The IJI was computed using the formula provided by McGarigal and Marks (1995):

$$IJI = -\sum_{i=1}^{m^!}\sum_{k=i+1}^{m^!}\{[(e_{ik}/E)\cdot\ln(e_{ik}/E)]/\ln(1/2[m^!(m^!-1)])\}\cdot(100)$$

where $m^!$ is the number of patches (Douglas-fir stands) by rock type, e is length of each unique patch edge, E is total edge of patches within a rock type, and ln is natural logarithm ArcView's Patch Analyst software (Elkie et al. 1999) was used to compute the IJI for each rock type. Second, we used a biophysical classification scheme developed by the USDA Forest Service (USDA 1997) to examine whether other biological or physical landscape characteristics might explain the perceived rock type effect. The Forest Service biophysical classification divides a forested landscape into 11 possible discrete groups based on factors such as elevation, slope, aspect, temperature, wildfire history, potential tree species diversity, and soil moisture regime. This classification scheme integrates many site biophysical factors into a single variable. Six of the 11 possible biophysical classes occurred in the study area. Chi-square analysis (Ott 1988) was used to examine relationships between rock type and the biophysical classes such that the expected value

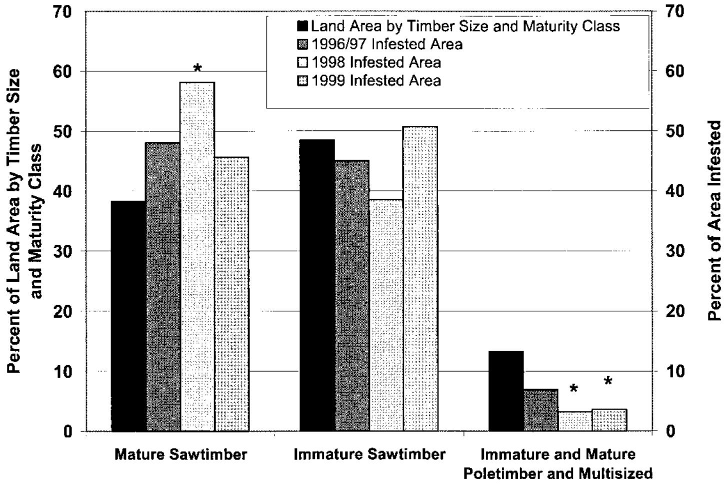

Fig. 1. Percentage of land area in various timber size and maturity classes and percentage of area affected by Douglas-fir beetle by year in the inland northwestern United States. Infestation areas that differed significantly from the expected area based on timber size and maturity class distribution are indicated with an asterisk ($P = 0.05$, chi-square test).

was the distribution of stand area by rock type, and the observed value was the distribution of stand area in each biophysical class by rock type. If rock type did not affect the occurrence or distribution of biophysical classes, then the distribution of each biophysical class by rock type should occur in the same proportion as the distribution of Douglas-fir stands by rock type.

Results

Size and Maturity Class Analysis. The majority of the analysis area contained mature (38%) and immature (49%) sawtimber (Fig. 1). In mature sawtimber, the 1998 Douglas-fir beetle infestation rate was significantly higher ($P = 0.05$, $\chi^2 = 10.34$) than the amount of stand area in that size class, indicating that beetles were attacking large-diameter, mature trees before the high 1999 infestation period. Within the immature sawtimber class, infestation rates by the beetle were about the same as the amount of land area in immature sawtimber. A small percentage of the analysis area (13%) was in multisized and mature and immature poletimber stands, therefore these three categories were combined for chi-square analysis. Infestation rates by Douglas-fir beetle were significantly lower in these stands compared with than the amount of area within these host types during 1998 ($P = 0.05$, $\chi^2 = 7.56$) and 1999 ($P = 0.05$, $\chi^2 = 7.00$). Due to the low rates of infestation in poletimber and multisized stands, the remaining analyses were performed only on mature and immature sawtimber stands.

Douglas-Fir Beetle Infestations by Rock Type. Statistical analysis of the initial eight rock categories showed that the Prichard formation had significantly higher rates of beetle infestation than expected in 1996/1997 ($P = 0.05$, $\chi^2 = 14.71$) and 1998 ($P = 0.05$, $\chi^2 = 24.61$). Other rock categories were not significant in this initial analysis and therefore were examined more closely for potential within-category relationships that might have been obscured by the initial categorization scheme or for categories that behaved similarly and could therefore be grouped.

The largest proportion of mature and immature sawtimber stands in the analysis area occurred on the Wallace formation rock type (Table 1, 30%), which was comprised of three members, including the lower, upper, and undivided (these rocks were not distinguishable as lower or upper). Chi-square analysis was performed on stands on the Wallace formation rocks to determine whether Douglas-fir beetle infestation rates varied between members. No single formation hosted infestation rates greater than expected in 1996/1997; however, both the lower and upper members showed rates of beetle infestation that were significantly different from stand distribution on those members in 1998 (Table 2). Proportionately more beetle infestation ($P = 0.05$, $\chi^2 = 7.54$) occurred on the lower Wallace (81%) compared with stand area on lower Wallace (60%), whereas proportionately less infesta-

Table 1. Total area (hectares) of mature and immature Douglas-fir sawtimber stands on various rock types in the inland northwestern United States

Rock type	Area (ha)	
Wallace formation[a]	131,944	
Wallace, lower		79,296
Wallace, undivided		7,922
Wallace, upper		44,726
Prichard formation	83,340	
Intrusive rocks[a]	59,299	
Diabase sills and dikes		8,700
Galena Point granodiorite		5,889
Other intrusive rocks		44,711
Ravalli group	55,895	
Glacial deposits	50,023	
Striped Peak formation	42,063	
Other rocks	14,519	
Libby formation	7,758	

[a] Stand area (hectares) by rock subcategory.

Table 2. Chi-square (χ^2) test for differences between expected values (percentage Douglas-fir stand area on Wallace rocks) and observed values (percentage of Douglas-fir beetle infestation area on Wallace rocks), by year in the inland northwestern United States

Wallace formation member	1996–1997 combined infestations	1998 infestations	1999 infestations
Wallace, lower	3.36	7.54*	0.29
Wallace, undivided	3.43	2.99	0.00
Wallace, upper	2.77	8.57*	0.51
Calculated χ^2	9.56*	19.10*	0.80
Test statistic df = 2, α = 0.05	5.99	5.99	5.99

Values with an asterisk are significantly different from the expected value ($P = 0.05$, chi-square test).

Table 3. Chi-square (χ^2) test for differences between expected values (percentage of Douglas-fir stand area on intrusive rocks) and observed values (percentage of Douglas-fir beetle infestation area on intrusive rocks), by year in the inland northwestern United States

Intrusive rock type	1996–1997 combined infestations	1998 infestations	1999 infestations
Diabase sills and dikes	97.08*	152.54*	2.73
Galena Point granodiorite	0.96	3.36	109.65*
Other intrusive rocks	15.93*	22.87*	20.52*
Calculated χ^2	113.96*	178.78*	132.90*
Test statistic df = 3, α = 0.05	5.99	5.99	5.99

Values with an asterisk are significantly different from the expected value ($P = 0.05$, chi-square test).

tion ($P = 0.05$, $\chi^2 = 8.57$) occurred on the upper Wallace (17%) compared with that stand area (Fig. 2, 34%). In 1999, Douglas-fir beetle infestation areas were distributed in the same proportion as Douglas-fir stand area on all members of the Wallace formation. The lower member of the Wallace formation was retained as a separate category for subsequent areawide analysis. Because the upper and undivided members of the Wallace formation comprised relatively less stand area and were therefore of less significance in the areawide analysis, they were subsequently grouped with other Belt rocks.

Douglas-fir stands occurring on Libby and Striped Peak rock formations comprised 2 and 9%, respectively, of the stands examined (Table 1). Ravalli group rocks occurred beneath 13% of the entire analysis area, and were composed of four units (Burke, St. Regis, and Revett formations, and undivided Ravalli group). The Libby, Striped Peak, and Ravalli group rocks were individually examined by chi-square analysis. No patterns or significant differences in beetle infestation rates among these formations were evident. Therefore, the Libby, Striped Peak, and Ravalli group rocks were combined with the lower and undivided members of the Wallace formation as "other Belt rocks" for the final areawide analysis.

Thirteen percent of Douglas-fir sawtimber stands in the analysis area occurred on intrusive rocks (Table 1). The intrusive rocks category encompassed 55 individual rock units, most of which represented local intrusive structures (plutons, dikes, and sills). A chi-square analysis of Douglas-fir beetle infestation rates on intrusive rocks was performed to determine whether infestation rates varied by intrusive rock unit. Two intrusive rock units showed significantly higher infestation rates than expected based on the amount of stand area on those rock types (Table 3). Diabase sills and dikes in the Sandpoint, Bonner's Ferry, and St. Joe Districts hosted 52% of the 1996/1997 infestations ($P = 0.05$, $\chi^2 = 97.08$) and 62% of the 1998 infestations ($P = 0.05$, $\chi^2 = 152.54$), compared with 15% of sawtimber stand area on that rock unit (Fig. 3).

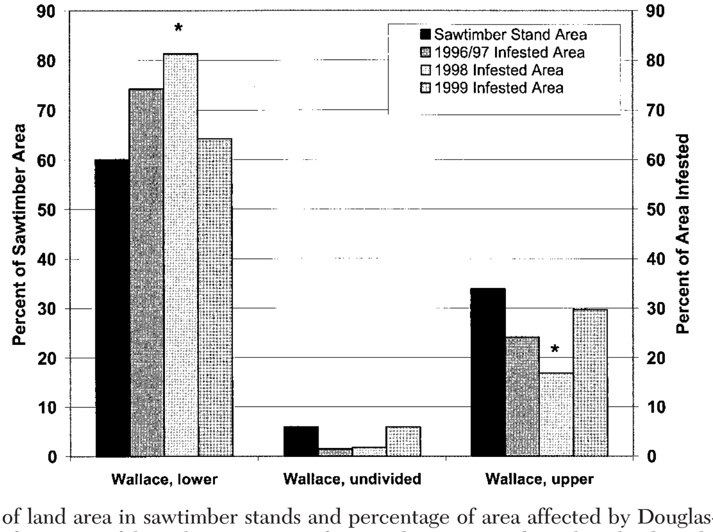

Fig. 2. Percentage of land area in sawtimber stands and percentage of area affected by Douglas-fir beetle by year for members of the Wallace formation of the Belt Supergroup of metasedimentary rocks in the inland northwestern United States. Infestation areas that differed significantly from the expected area based on rock type distribution are indicated with an asterisk ($P = 0.05$, chi-square test).

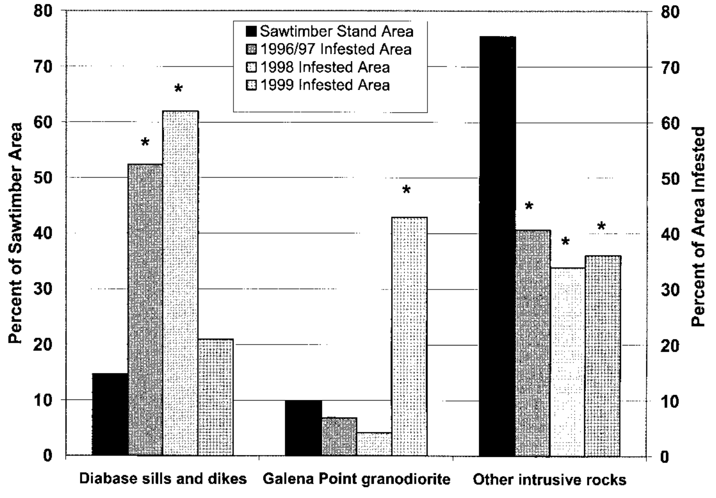

Fig. 3. Percentage of land area in sawtimber stands and percentage of area affected by Douglas-fir beetle by year for three categories of intrusive rocks in the inland northwestern United States. Infestation areas that differed significantly from the expected area based on rock type distribution are indicated with an asterisk ($P = 0.05$, chi-square test).

Galena Point granodiorite, a pluton on the Priest Lake Ranger District, hosted 43% of the 1999 infestation area ($P = 0.05$, $\chi^2 = 109.65$), compared with 10% of Douglas-fir stands on that rock unit. The remaining 75% of Douglas-fir sawtimber stands on other intrusive rocks had significantly lower infestations of Douglas-fir beetles during all years of the study ($P = 0.05$; 1996/1997, $\chi^2 = 15.93$; 1998, $\chi^2 = 22.87$; 1999, $\chi^2 = 20.52$). Even during the peak year of the outbreak (1999), stands growing on these other intrusive rocks had significantly lower rates of beetle infestations than expected compared with the amount of Douglas-fir stand area they contained. Approximately 11% of the Douglas-fir stands in the entire study area occurred on glacial deposits, whereas other rock types (carbonate rocks, metamorphic rocks, other [nonglacial] deposits, extrusive rocks, and sedimentary rocks) occurred under ≈3% of the analysis area. These rock types were uncommon in the study area and a more detailed analysis was not possible. Among the intrusive rocks, diabase sills and dikes were retained as a separate category for subsequent analysis. All other intrusive rocks, including Galena Point granodiorite, which occupied too small of a land area to be of significance in the areawide analysis, were grouped with glacial deposits and other rocks for subsequent analysis.

The final, areawide chi-square analysis was performed for all mature and immature sawtimber-sized Douglas-fir stands in the analysis area, for five rock categories, including the Prichard formation, the lower member of the Wallace formation, other Belt rocks, diabase sills and dikes, and glacial deposits and other rocks (Table 4). In the nonoutbreak years of 1996/1997, significantly greater areas of Douglas-fir beetle infestations occurred on the Prichard formation (35%; $P = 0.05$, $\chi^2 = 14.71$) and on diabase sills and dikes (11%; $P = 0.05$, $\chi^2 = 43.64$) than the amount of Douglas-fir stands on those rock types (19 and 2%, respectively; Fig. 4). In contrast, significantly less infestation area occurred on other Belt rocks (10%; $P = 0.05$, $\chi^2 = 17.86$) compared with Douglas-fir stand area on other Belt rocks (36%) during those years. During the first year in which beetle populations began increasing (1998), significantly higher areas of beetle infestation again occurred on Prichard formation (40%; $P = 0.05$, $\chi^2 = 24.61$), and also occurred on the

Table 4. Chi-square (χ^2) test for differences between expected values (percentage stand area in each rock type) and observed values (percentage of Douglas-fir beetle infestation area on each rock type) by year in Douglas-fir stands in the inland northwestern United States, and Interspersion and Juxtaposition Index IJI for each rock type

Rock type	1996–1997 average infestations	1998 infestations	1999 infestations	IJI
Prichard formation	14.71*	24.61*	7.74	59
Wallace formation, lower	0.38	24.04*	0.14	58
Other Belt rocks	17.86*	17.70*	0.15	61
Diabase sills and dikes	43.64*	0.18	0.00	53
Glacial deposits and other rocks	0.40	12.06*	9.70*	72
Calculated χ^2	77.00*	78.59*	17.73*	
Test statistic df = 4, α = 0.05	9.49	9.49	9.49	

Values with an asterisk are significantly different from the expected value ($P = 0.05$, chi-square test).

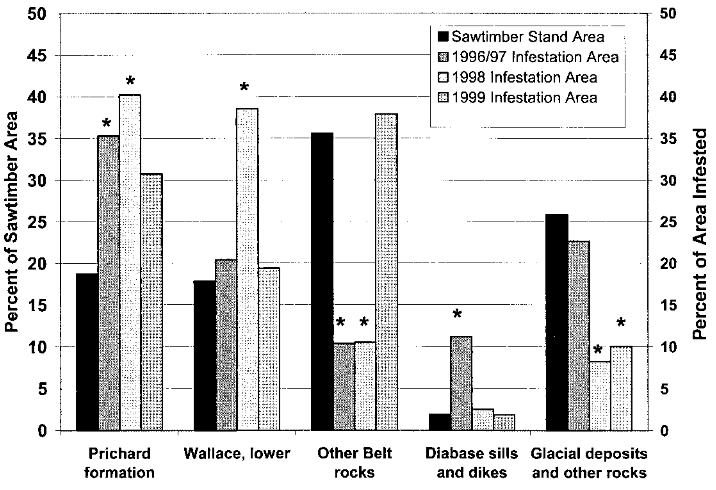

Fig. 4. Percentage of land area in sawtimber stands and percentage of area affected by Douglas-fir beetle by year for five rock type categories in the inland northwestern United States. Infestation areas that differed significantly from the expected area based on rock type distribution are indicated with an asterisk ($P = 0.05$, chi-square test).

lower Wallace formation rock type (39%; $P = 0.05$, $\chi^2 = 24.04$), which occurred under 18% of the Douglas-fir sawtimber stand area. As in 1996/1997, other Belt rocks were again affected at a rate significantly lower than expected in 1998 (10%; $P = 0.05$, $\chi^2 = 17.70$), and glacial deposits and other rocks were also affected at rates significantly lower than expected in 1998 (8%; $P = 0.05$, $\chi^2 = 12.06$) based on the amount of stand area (26%) on other rocks. By 1999, the proportion of infestation areas by rock type did not differ from the proportion of stand area by rock type for most of the analysis area. The exception was the beetle infestation rate on glacial deposits and other rocks, which at 10% was significantly lower ($P = 0.05$, $\chi^2 = 9.70$) than the amount of stand area (26%) on that rock type. The Galena Point granodiorite, which had been significant within the intrusive rock category in 1999, occupied too small of an area (1%) to be of significance in the areawide analysis.

Interspersion and Juxtaposition Index and Biophysical Class Analyses. IJI values measured the extent that Douglas-fir stands on the various rocks were interspersed. Values ranged from 53 for diabase sills and dikes to 72 for glacial deposits and other rocks (Table 4). All other rock types showed similar IJI values, ranging from 58 to 61. The IJI approaches zero when the distribution of stands is uneven and approaches 100 when stands are equally adjacent. Thus, Douglas-fir stands growing on diabase sills and dikes were somewhat clumped in their distribution relative to stands on glacial deposits and other rocks, with stands on all other rock types falling somewhere in between.

Biophysical class (USDA 1997) distributions by rock type showed significant differences from the expected distributions (Table 5). The lower Wallace rock type was less likely to contain warm and dry habitat than expected ($P = 0.05$, $\chi^2 = 25.62$), whereas diabase sills and dikes were more likely to contain cool and moist habitat ($P = 0.05$, $\chi^2 = 10.34$). Other Belt rocks (besides Prichard and lower Wallace) were more likely to contain warm and dry habitat ($P = 0.05$, $\chi^2 = 15.07$), and glacial deposits and other rocks were less likely to occur on warm and dry ($P = 0.05$, $\chi^2 = 43.22$), moderately warm and moderately dry ($P = 0.05$, $\chi^2 = 11.92$), and moderately warm and moist ($P = 0.05$, $\chi^2 = 15.05$) conditions. Prichard formation rocks

Table 5. Chi-square (χ^2) test for differences between expected values (percentage stand area in each rock type) and observed values (percentage biophysical class area on each rock type), in Douglas-fir stands in the inland northwestern United States

Rock type	Class 1[a]	Class 2[a]	Class 3[a]	Class 4[a]	Class 5[a]	Class 6[a]
Prichard formation	0.01	7.77	1.55	0.07	0.24	2.67
Wallace formation, lower	25.62*	5.34	3.89	2.53	0.00	0.72
Other Belt rocks	15.07*	0.01	6.73	4.86*	0.39	1.26
Diabase sills and dikes	2.06	1.42	0.37	0.84	0.00	10.34*
Glacial deposits and other rocks	43.22*	0.83	11.92*	15.05*	1.41	0.06
Calculated χ^2 test statistic	85.97*	15.37*	24.46*	23.36*	2.04	15.05*
df = 4, $\alpha = 0.05$	9.49	9.49	9.49	9.49	9.49	9.49

Values with an asterisk are significantly different from the expected value ($P = 0.05$, Chi-square test).

[a] Biophysical class definitions: 1 = *warm and dry*; 2 = *moderately warm and dry*; 3 = *moderately warm and moderately dry*; 4 = *moderately warm and moist*; 5 = *moderately cool and moist*; 6 = *cool and moist.*

did not show any significant differences between biophysical classes.

Discussion

Significant effects of rock type on the infestation pattern of Douglas-fir beetle were found in spite of the need for broad classifications of tree size and maturity attributes (i.e., mature sawtimber and immature sawtimber). The early years (1996/1997) of the analysis period were considered nonoutbreak years, whereas in 1998 the first signs of increased beetle activity became apparent, significantly so in mature sawtimber stands. By 1999, beetle populations had increased to such high levels in mature sawtimber stands that previously less susceptible immature sawtimber stands were also attacked. Douglas-fir beetles preferentially attack mature and overmature Douglas-fir trees that are stressed before attack (Furniss et al. 1979, 1981; Negron 1998, Negron et al. 1999). The increased population of Douglas-fir beetles during the analysis period may have resulted from the severe tree damage caused by a November 1997 ice and snow storm throughout the analysis area. The broken and damaged trees would provide excellent habitat for the 1998 population of Douglas-fir beetles (Furniss et al. 1981). The increased beetle population, subsequent attacks and tree mortality would have then been evident on the 1999 aerial surveys.

Douglas-fir beetle infestations in mature and immature sawtimber stands during early years of the analysis period (1996–1998) occurred more frequently on the Prichard and lower Wallace rock formations and on diabase sills and dikes. By 1999, stands on all rock types were affected at about the same proportion as expected based on their occurrence, except for those on glacial deposits and other rocks, which were affected less frequently than expected. Among the intrusive rocks, infestations occurred at a high rate on the Galena Point granodiorite in 1999, though this rock type occupied too small of an area to be of significance in the areawide analysis. Diabase sills and dikes and the Galena Point granodiorite were both associated with and surrounded by Prichard and lower Wallace formation rocks. Stands on these relatively small sills, dikes, and plutons were likely infested with Douglas-fir beetles because of their proximity to stands on Prichard and lower Wallace rocks, which were harboring Douglas-fir beetle populations.

Douglas-fir stands growing on the Prichard and lower Wallace formations and on diabase sills and dikes had similar spatial distribution patterns as stands growing on the other rock types occupying substantial portions of the study area. Although some differences in expected distribution of rock types across biophysical classes did occur, these differences did not seem to be related to beetle infestation patterns. For example, although stands on both lower Wallace and glacial deposits and other rocks had lower than expected distributions of warm and dry habitat, the lower Wallace showed a high 1998 infestation area, whereas glacial deposits and other rocks showed a low 1998 infestation area. The similarities in spatial distributions and lack of biophysical land class effect suggest that rock types directly influence trees growing upon them, possibly through nutritional differences. Furthermore, nonoutbreak and early outbreak populations of Douglas-fir beetles such as those occurring in 1996–1998 may persist in trees growing on Prichard and lower Wallace formation rock types, and perhaps diabase sills and dikes. However, by the 1999 outbreak period, areas infested by Douglas-fir beetles were not significantly different from the distribution of stand area for any of the rock types except glacial deposits and other rocks, which were affected at rates lower than expected. It seems that by 1999, the beetle populations were so large that they were capable of successfully attacking trees growing on almost all of the rock types in the study area.

Douglas-fir stands on Prichard and lower Wallace rock formations, and perhaps diabase sills and dikes, may act as refugia for nonoutbreak populations of Douglas-fir beetle. *Armillaria ostoyae* root rot is prevalent throughout the study area and may leave the trees more susceptible to successful attack by bark beetles. Douglas-fir root biochemistry, including phenolic and sugar concentration ratio, significantly affects the incidence of *Armillaria* infection (Entry et al. 1991). Potassium nutrition affects Douglas-fir root phenolic and sugar concentration ratios (Shaw et al. 1998). Therefore, it may be that Douglas-fir trees unable to produce sufficient resins to resist root rot infection are also more susceptible to attack by Douglas-fir beetles. Additionally, root rot-infected trees are more prone to windthrow, and such downed trees provide additional suitable Douglas-fir beetle habitat (Furniss 1962). Mature, sawtimber-sized Douglas-fir trees growing on soils developed from Prichard and lower Wallace formation rocks and perhaps intrusive dikes and sills may be nutrient-stressed, thus providing susceptible trees as Douglas-fir beetle habitat. Severe nutrient stress has been suggested to limit or decrease a tree's ability to resist attack by herbivorous insects by limiting the tree's ability to produce and/or accumulate defensive compounds (Tuomi et al. 1988). Nutrient limitations for stands growing on Prichard and lower Wallace rock formations (and perhaps on diabase sills and dikes) may contribute to physiological stresses experienced by Douglas-fir growing on these sites (Mandzak and Moore 1994; Moore et al. 1998; Shen et al. 2000, 2001). Populations of Douglas-fir beetles may persist at relatively low levels in stands on these sites. After a large disturbance, such as the 1997 ice storm, these beetle populations may experience significant increases allowing subsequent infestations to expand into stands growing on a variety of rock types.

In stands of sawtimber-sized Douglas-fir, infestations of Douglas-fir beetles were larger in 1998 than in preceding years, and these infestations were more prevalent in stands growing on Wallace and Prichard rock formations than other rock types. The conditional probability of encountering Douglas-fir beetle infestations in stands growing on Prichard formation rocks was several times greater than for other rock types during the nonoutbreak years, 1996 and 1997. If rock type, and, presumably, nutrient stress are associated with subsequent Douglas-fir beetle infestation levels, then rock type could be used in quantitative hazard rating models similar to those proposed by Furniss et al. (1981), Negron (1998), and Negron et al. (1999). Furthermore, early warning systems for predicting Douglas-fir beetle outbreaks could be established in Douglas-fir stands growing on Prichard and lower Wallace rock formations and perhaps diabase sills and dikes, because beetle populations seem to first reach outbreak levels in stands growing on these rock types. Silvicultural practices aimed at reducing the amount of overmature, sawtimber-sized Douglas-fir stands growing on these susceptible rock types may also reduce the tree mortality and consequent increased wildfire danger encountered in the most recent Douglas-fir beetle epidemic.

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