

Within-Stand Spatial Distribution of Tree Mortality Caused by the Douglas-Fir Beetle (Coleoptera: Scolytidae)

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ABSTRACT The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, causes considerable mortality in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, forests. Within-stand distribution of mortality was examined in affected stands using geostatistical techniques. A 10 × 10 m grid was established in two 4-ha study sites. Live and beetle-killed host basal area was measured at each node. In a 16-ha stand, a variable-resolution grid was established and the same information collected. The relationship between Douglas-fir basal area and Douglas-fir basal area killed was examined using non-spatially explicit and spatially explicit linear regression models. A positive linear relationship was observed between the variables. Significant spatially explicit models suggest that the relationship is also true at fine scales. Relative variograms were constructed for Douglas-fir basal area before and after the Douglas-fir beetle outbreaks. For the 4-ha sites, increased spatial dependency in the distribution of Douglas-fir basal area was observed as a result of the Douglas-fir beetle outbreak. For the 16-ha site, kriging was used to estimate live Douglas-fir basal area before and after the outbreak to a 10-m resolution and the stand rated for potential mortality illustrating the potential applicability of geostatistical techniques to rating a stand for potential mortality. Cross-validation analysis indicated that although the potential exists for large estimation errors, the majority of the estimates were within acceptable ranges. The study suggests that geostatistical approaches may be suitable to extend our understanding bark beetle ecology and improving the application of extent of mortality models.

KEY WORDS Douglas-fir beetle, *Dendroctonus pseudotsugae*, bark beetles, disturbance, risk classification model, hazard rating model

THE DOUGLAS-FIR BEETLE, *Dendroctonus pseudotsugae* Hopkins, is a bark beetle that uses Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, as its primary host. Adult beetles disperse in the spring and attack new hosts by burrowing into the bark and laying eggs in galleries constructed by the adults. Large diameter trees are preferred. Eggs hatch in 1–3 wk, the larvae develop in the bark feeding on the phloem. Pupation and transformation into the adult stage is usually complete by the fall and the brood adults overwinter under the bark and emerge the following spring (Schmitz and Gibson 1996).

In the western United States, endemic populations of the Douglas-fir beetle are commonly encountered on injured or felled Douglas-fir (McMullen and Atkins 1962, Furniss 1965, Rudinsky 1966, Wright et al. 1984). Biotic and abiotic agents such as root disease (Wright and Lauterbach 1958), defoliation (Berryman and Wright 1978, Wright et al. 1984), windthrow (Rudinsky 1966), snow breakage (McGregor et al. 1974), fire (Furniss 1965), and logging (Lejeune et al. 1961, McGregor et al. 1974) can trigger increases in population size that can cause widespread mortality. Out-

breaks of this insect most commonly last from 2 to 4 yr (Schmitz and Gibson 1996).

Furniss et al. (1979, 1981) proposed that host type proportion, tree density, and age were key factors in Douglas-fir stand susceptibility to Douglas-fir beetle. Weatherby and Thier (1993) presented a system for rating stands for susceptibility to losses to Douglas-fir beetle. The system uses stand basal area, proportion of stand basal area in Douglas-fir, average stand age, and average diameter at breast height (dbh) of all Douglas-firs larger than 22.9 cm. Shore et al. (1999) indicated that diameter at breast height, tree height, phloem thickness, aspect, and a standardized variable calculated by dividing diameter at breast height by the last 10 yr growth rate are associated with Douglas-fir beetle infestations. Negrón et al. (1999) indicated that when a stand is susceptible to a Douglas-fir beetle outbreak as indicated by the presence of large diameter trees, high stocking levels, and a high proportion of Douglas-fir, Douglas-fir basal area can be used to estimate potential mortality.

Many risk and hazard rating models have been developed to determine the degree of susceptibility of forest stands to infestation, or the amount of expected mortality, or both, caused by different bark beetle species. Bentz et al. (1993) indicated that risk classification systems developed for mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in lodgepole pine, *Pinus contorta* Dougl. ex Loud., often fail to provide the

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desired levels of accuracy. Some reasons identified as sources of error included the following: not considering beetle population phase during model development, lack of inclusion of beetle population dynamics information, and the need to include the spatial nature of beetle populations and stand conditions.

Another potential difficulty with current models is that they were developed using stand averages or are applied to a management unit regardless of the scale at which they were developed. Stand averages fail to capture the within-stand variability in stand conditions. These variations affect the spatial distribution of tree mortality caused by insects. Olsen et al. (1996) indicated that mountain pine beetle infestations in ponderosa pine, *Pinus ponderosae* Dougl. ex Laws, in the Black Hills, SD, were associated with microcosm stands, i.e., smaller stands with increased tree densities within larger stands. In a similar manner, mountain pine beetle preferentially attacks larger diameter trees in lodgepole pine forests (Cole and Amman 1969, Safranyik et al. 1974, Amman et al. 1977, Klein et al. 1978, Cole and Amman 1980) with colonizing populations clustering around larger diameter trees in a stand (Mitchell and Preisler 1991).

Douglas-fir beetle-caused mortality in affected stands is patchy. Although some epidemics may be extensive at the landscape level, individual stands exhibit different degrees of mortality and do not always suffer catastrophic mortality levels. To better understand the ecological role of bark beetles in forest ecosystems, it is imperative to extend our knowledge of the spatial distribution of tree mortality as influenced by the spatial distribution of forest conditions that affect bark beetle-caused mortality. The application of spatial analysis to bark beetle ecology may offer methodologies for this purpose. Geostatistics are statistical methods that focus in describing spatial patterns of processes. These techniques originated in the geological sciences but have become common in ecology.

For detailed discussions on geostatistical theory and methodology, see Isaaks and Srivastava (1989), Hohn (1988), and Cressie (1991). Schotzko and O'keeffe (1989) and Kemp et al. (1989) used geostatistical techniques in entomology; Chellemi et al. (1988) used them in plant pathology; and Robertson et al. (1988) and Jackson and Caldwell (1993) used them to evaluate the interaction between soil properties and plant communities. Few studies have applied these techniques to forestry problems (see Köhl and Gertner (1997) for some citations). Biondi et al. (1994) used this approach to model stem size and increment in a ponderosa pine forest and concluded that the understanding of spatial dependence can lead to improved performance of simulation and estimation models. Köhl and Gertner (1997) used geostatistical methods to present the spatial distribution of needle/leaf loss data from survey information. Raty et al. (1997) conducted a geostatistical analysis of pheromone trap catches of *Ips typographus* L. using spatial and temporal data in Romania. A number of studies have used the techniques to examine various ecological aspects

of the gypsy moth, *Lymantria dispar* (L.) (Liebhold et al. 1991, 1995; Hohn et al. 1993). Biondi et al. (1994) and Köhl and Gertner (1997) also provide brief descriptions of geostatistical methods, and Liebhold et al. (1993) discuss aspects of their application to insect ecology.

In this study, we examined the spatial pattern of Douglas-fir basal area in Douglas-fir stands, determined if the spatial pattern of basal area influenced the spatial pattern of mortality caused by the beetle, characterized how Douglas-fir beetle changed the distribution of basal area in the stand, and pondered the potential for using geostatistical techniques to incorporate within-stand variability of basal area or other forest conditions into models to estimate potential mortality in an affected stand.

Materials and Methods

Study Sites. *Wasatch-Cache National Forest.* Two study sites were established in the Wasatch-Cache National Forest, UT, in June of 1997 in stands where a Douglas-fir beetle outbreak had collapsed and no new mortality was present. Each study site comprised a 4-ha area and was located in the Beaver Creek and the Middle Sink areas of the Logan Ranger District. At each study site, a 10 × 10 m grid was established over the 4-ha area. At each grid node a variable radius plot was established using a 20 BAF gauge in a relascope. For all sample trees in each variable radius plot, the following information was recorded: species, diameter at breast height, and whether the tree was alive, killed by Douglas-fir beetle, or dead from other causes. This information allowed examination of pre- and postoutbreak forest conditions with the same data set. Larger diameter trees are more likely to be included in variable radius plots. These larger trees contribute the most to stand basal area and are also the preferred hosts by the Douglas-fir beetle. Because plots were located in close proximity to one another, very large trees could be included in multiple adjacent plots. With this information, spatially referenced data were generated on Douglas-fir basal area, Douglas-fir basal area killed by Douglas-fir beetle, and residual Douglas-fir basal area (live Douglas-fir basal area after the Douglas-fir beetle outbreak had collapsed).

Ashley National Forest. Based on the results obtained in 1997, a 16-ha study site was established in August of 1998 at the Clements Hollow area of the Duchesne Ranger District, Ashley National Forest, UT. A sampling grid was established throughout the study site. Grid size was variable with the majority of the study site sampled using a 40 × 40 m grid. To capture small-scale variability in basal area across the study site, parts of the site were sampled in a 20 × 20 m or a 10 × 10 m grid. Areas with different sampling distances were distributed across the study site (Fig. 1). At each sample point, data were collected using the same protocol as in 1997. The objective was to examine the application of geostatistical methods over a larger area, by using ordinary kriging (Isaaks and Srivastava 1989) to estimate Douglas-fir basal area and residual

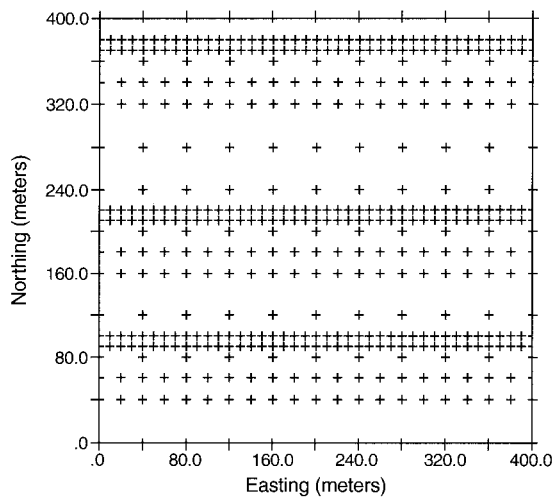


Fig. 1. Clements Hollow study area. Crosses indicate sample points. Note systematic variation in sampling distances across study site, Ashley National Forest, UT, 1998.

Douglas-fir basal area in unsampled locations, and rate the study site for potential mortality using the kriged output. In contrast to the Beaver Creek and the Middle Sink study sites, the outbreak at the Clements Hollow site had not completely collapsed. Aerial surveys of the area revealed active Douglas-fir beetle populations in the study area in 1998 and in the vicinity in 1999.

Data Analysis. Regression Analyses. The data presented here for each study site were obtained from variable radius plots in very close proximity; therefore, the presence of spatial autocorrelation was examined. The within-stand relationship between Douglas-fir basal area and basal area killed by Douglas-fir beetle was examined using linear regression with and without adjustments for spatial location. Linear regression analyses were conducted using the PROC MIXED routines in SAS (Littell et al. 1996), which incorporate spatial correlation among observations directly into the estimation process using a mixed model formulation. Instead of assuming that observations are uncorrelated, PROC MIXED estimates a covariance matrix among observations based on a spatial model. For example, consider the model $y = a + bx + e$, where y is the basal area killed by Douglas-fir beetle at n observation points, x is the initial Douglas-fir basal area at the comparable points, a and b are regression parameters, and e is the vector of model errors. If the observations are assumed to be uncorrelated, then the covariance matrix of the model errors is $\text{Cov}(e) = \sigma^2 I_n$, where I_n denotes the $n \times n$ with one on the diagonal and zero elsewhere. If instead the observations are assumed to be spatially correlated, then the covariance between e_i and e_j is estimated based on the distance (d_{ij}) between the two observations, $\text{cov}(e_i, e_j) = \sigma^2 f(d_{ij})$.

This approach reduces or removes the effects of spatial correlation among observations and produces more accurate estimates of model parameters and as-

sociated tests of hypothesis. For the regression analysis without spatial location adjustment, Douglas-fir basal area was the independent variable with basal area killed as dependent variable. For the regression analysis with spatial location adjustment, a fit-by-eye approach was used to model a variogram of the residuals from the nonspatially adjusted regression. The fit-by-eye provided starting parameters of the sill, range, and nugget describing the spatial structure of the residuals. These parameters were then incorporated into the spatially explicit model with Douglas-fir basal area as independent variable and basal area killed as the dependent variable. The spatially explicit models were compared with the nonspatial models for each study area to determine if the inclusion of spatial location information improved model fit. The -2 residual log likelihood statistic and r^2 values were used to evaluate changes in model fit. Because PROC MIXED does not calculate r^2 , the statistic was calculated from the likelihood ratios of unrestricted (no parameters applied) and restricted (with intercept and slope) models as described by Magee (1990).

Geostatistical Analyses. Relative variograms were calculated for Douglas-fir basal area and residual Douglas-fir basal area for the Beaver Creek and the Middle Sink sites to examine the spatial distribution of Douglas-fir basal area across the study sites before and after the Douglas-fir beetle outbreak. Variograms were calculated using GS+ (Gamma Design Software, Plainwell, MI). Maximum lag distance for all variograms was half of the maximum distance between two points (Hohn 1988, Isaaks and Srivastava 1989). At both sites, directional relative variograms were constructed for 0, 45, 90, and 135 angle classes with a tolerance of 22.5. No evidence of directionality was detected, therefore isotropy was assumed and omnidirectional variograms used. Spherical models were fit to the variograms using a combination of fit-by-eye and least squares approaches and values for the sill, nugget, range, degree of spatial dependency, and r^2 of the fit model obtained. The spatial statistics modules in S-Plus (Mathsoft, Seattle, WA) were also used in the fit-by-eye process of the variograms. The spherical variogram model is defined as:

$$y(h) = C_0 + C[1.5(h/A_0) - 0.5(h/A_0)^3] \text{ when } h \leq A_0$$

and

$$y(h) = C_0 + C \text{ when } h > A_0$$

where h = lag interval, C_0 = nugget, C = sill, and A_0 = range.

Variogram characteristics before and after the Douglas-fir beetle outbreaks for the Beaver Creek and the Middle Sink sites were compared.

Average Douglas-fir basal area, and average diameter at breast height of live Douglas-fir across the sites before and after the Douglas-fir beetle outbreaks were calculated and the means compared with a paired t -test. To adjust the paired t -tests for spatial autocorrelation, variograms of the paired differences in basal area and average Douglas-fir diameter at breast height before and after the Douglas-fir beetle outbreak were

Table 1. Relationship between Douglas-fir basal area (dfba) and basal area killed by Douglas-fir beetle (bak) as described with linear and spatially explicit linear regression models, Wasatch-Cache and Ashley National Forests, UT, 1997–1998

Site	Model	P	R ²	MSE	–2 residual log likelihood
Beaver Creek–linear regression	Bak = 0.11 + 0.45 (dfba)	0.0001	0.38	7.9	3077
Beaver Creek–spatial linear regression	Bak = 1.31 + 0.28 (dfba)	0.0001	0.75	10.2	2674
Middle Sink–linear regression	Bak = –0.53 + 0.15 (dfba)	0.0001	0.13	5.2	2712
Middle Sink–spatial linear regression	Bak = 0.53 + 0.07 (dfba)	0.0001	0.78	5.7	2114
Clements Hollow–linear regression	Bak = 0.17 + 0.23 (dfba)	0.0001	0.19	7.1	3115
Clements Hollow–spatial linear regression	Bak = 0.47 + 0.21 (dfba)	0.0001	0.46	6.3	2929

constructed. An intercept only model, that is, with the mean paired differences only, was formulated in PROC MIXED. The residual variance of this model and the associated test of whether the intercept was different from zero was adjusted by incorporating an exponential spatial model as described earlier for the spatial regression models. However, the sampling grid was stratified into 50 m square blocks within which the spatial parameters were estimated since PROC MIXED lacks a framework for estimating an overall spatial model in a paired design scenario. All study stands were essentially pure Douglas-fir. Percent basal area ($\pm$ SEM) in Douglas-fir was 95.0 (1.0) for Beaver Creek, 89.6 (1.1) for Middle Sink, and 92.8 (1.1) for Clements Hollow. The distribution of Douglas-fir basal area before and after the Douglas-fir beetle outbreak was mapped using potential mortality classes for Utah from a Douglas-fir beetle outbreak. Low, medium, and high mortality classes correspond with Douglas-fir basal area ≤ 26.4 m²/ha, Douglas-fir basal area between 26.5 m²/ha and 39.0 m²/ha, and >39.0 m²/ha, respectively (Negrón et al. 1999).

For the Clements Hollow site in the Ashley NF, directional relative variograms were constructed as indicated above. After no evidence of directionality was observed, omnidirectional relative variograms were calculated for Douglas-fir basal area and Douglas-fir residual basal area and the variogram characteristics compared. Ordinary kriging (Isaaks and Srivastava 1989) was then used to estimate Douglas-fir basal area and Douglas-fir residual basal area in unsampled locations to a 10 m resolution. The distribution of Douglas-fir basal area before and after the Douglas-fir beetle outbreak was then mapped using the kriged data and potential mortality classes for Utah as described above. Haining (1990) indicated that cross-validation and the examination of prediction errors can be used to assess the fit of semivariogram models. To examine estimation errors obtained, a jack-knife cross validation analysis was conducted. This was done by sequentially deleting each experimentally measured location from the data set and obtaining a kriged value for that location. The kriged estimates were then compared with the actual values obtained from sampled locations (Isaaks and Srivastava 1989). The mean, minimum, maximum, median, and interquartile range of differences between kriged and actual values for Douglas-fir basal area and residual Douglas-fir basal area were calculated. The kriging and cross validation analysis were conducted with GS+ (Gamma Design Software, Plainwell, MI).

Results and Discussion

Regression Analyses. A significant positive linear relationship was observed between Douglas-fir basal area and basal area killed at all study sites using non-spatial models (Table 1). The models indicate that increased mortality correlates with increased stocking levels. The relationship between high stocking levels and increased susceptibility to various bark beetles has been documented in other studies (Safranyik et al. 1974; Sartwell and Stevens 1975; McCambridge et al. 1982; Reynolds and Holsten 1994, 1996; Negrón 1997, 1998; Negrón et al. 1999). In contrast to the current study, the previously mentioned studies examined the relationship using data from different stands and autocorrelation was not a factor. Spatial adjustment of our linear models resulted in a considerable increase in model fit as indicated by the increase in r^2 and the decrease in the –2 residual log likelihood statistics.

The significance of the spatially adjusted models suggests that the relationship between Douglas-fir basal area and basal area killed by the Douglas-fir beetle holds true at fine scales within the stand. This agrees with the concept of microcosm stands proposed by Olsen et al. (1996), where there are small stands within larger stands where forest conditions are more suitable for the development of bark beetle infestations. This stresses the importance of considering the within stand variability of forest conditions when evaluating the potential impacts of a Douglas-fir beetle outbreak in a stand. The clumped nature of Douglas-fir beetle-caused mortality may be explained by the presence of clumps of high basal area in the stand. Furniss et al. (1979, 1981) and Weatherby and Thier (1993) indicated increased susceptibility to Douglas-fir beetle in stands with high stocking levels. Negrón (1998) indicated that Douglas-fir beetle exhibited preference for slow growing trees growing under high stocking conditions and Lessard and Schmid (1990) also indicated preference for slow growing trees by Douglas-fir beetle.

Geostatistical Analyses. *Wasatch-Cache National Forest.* Coefficients of determination for the spherical models fit to the relative variograms of Douglas-fir basal area and Douglas-fir residual basal area for the Beaver Creek and the Middle Sink study sites ranged from 0.94 to 0.99. After Douglas-fir beetle populations collapsed, the nugget was reduced at both the Beaver Creek and the Middle Sink sites, with a corresponding increase in spatial dependency (Table 2; Fig. 2). This indicates that basal area at specific points is more

Table 2. Characteristics for Douglas-fir basal area and residual Douglas-fir basal area variograms, average Douglas-fir basal area ($\pm$ SEM), average Douglas-fir dbh ($\pm$ SEM), and sample variance for Douglas-fir basal area before and after the Douglas-fir beetle outbreak at the Beaver Creek, and Middle Sink sites, Wasatch-Cache National Forest, UT, June 1997 and at the Clements Hollow site, Ashley National Forest, UT, August 1988

	Beaver Creek		Middle Sink		Clements Hollow	
	Douglas-fir Basal area	Residual Douglas-fir Basal area	Douglas-fir Basal area	Residual Douglas-fir Basal area	Douglas-fir Basal area	Residual Douglas-fir Basal area
Nugget	0.35	0.15	0.22	0.17	0.30	0.36
Sill	1.13	0.97	1.00	1.06	1.02	1.03
Range (m)	93.3	37.3	49.1	43.9	73.3	74.4
R^2	0.96	0.99	0.94	0.95	0.71	0.65
Spatial dependency ^a	76.5	86.8	82.1	86.0	77.6	74.0
Douglas-fir basal area (m ² /ha)	22.0 (0.7)a ^b	12.0 (0.5)b	16.9 (0.7)a ^c	14.8 (0.6)a	18.5 (0.7)a ^d	14.1 (0.7)b
Douglas-fir dbh, cm	62.3 (0.7)a ^e	53.6 (0.8)b	57.9 (0.8)a ^f	56.3 (0.8)b	32.8 (0.6)a ^g	26.8 (0.7)b
Douglas-fir basal area variance	193.6	121.3	190.5	163.2	247.5	197.8

Means in rows for each study site followed by the same letter are not significantly different (*t*-test as described by footnotes).

^a Spatial dependency = (sill/(nugget + sill)) $\times$ 100.

^b *t* = 5.25; *p* < 0.0001; df = 15.

^c *t* = 1.93; *p* = 0.0723; df = 15.

^d *t* = 11.0; *p* < 0.0001; df = 15.

^e *t* = 5.50; *p* < 0.0001; df = 15.

^f *t* = 2.15; *p* < 0.0484; df = 15.

^g *t* = 6.43; *p* < 0.0001; df = 15.

dependent on adjacent points after the Douglas-fir beetle outbreak than before the outbreak. Douglas-fir beetle reduced the within-stand variability of host type basal area. To phrase it differently, the stands became more continuous in terms of the distribution of Douglas-fir basal area.

The range is an indication of the scale of spatial pattern or patch size at short lag distances. The range decreased at Beaver Creek and to a lesser extent at the Middle Sink study site after the Douglas-fir beetle outbreak. This suggests that in the process of making basal area more continuous at short lag distances, the Douglas-fir beetle creates smaller basal area patches that are more similar to one another. Biondi et al. (1994) indicated that defining homogenous areas in forest ecosystems could lead to optimal sampling procedures and the effective application of silvicultural tools. In this study, preoutbreak basal area patches were 93 m at the Beaver Creek site and 49 m at the Middle Sink site (Table 2). The scale at which Douglas-fir beetle activity occurs within a stand may approximate these distances. This may be the appropriate scale for rating and managing stands with silvicultural approaches when the objective is to reduce potential mortality from Douglas-fir beetle outbreaks.

Mapping the distribution of Douglas-fir basal area of the two study areas before and after the Douglas-fir beetle outbreaks illustrates the changes in basal area continuity. It also demonstrates the correlation of Douglas-fir beetle caused mortality with higher stocking levels. In the Beaver Creek study site, the majority of the stand where Douglas-fir basal area was >39 m²/ha and to a lesser extent where Douglas-fir basal area was >26.4 m²/ha was impacted by Douglas-fir beetle (Fig. 3A). These values correspond to high and medium potential mortality categories for Utah as de-

scribed by Negrón et al. (1999). The residual basal area in the stand was more uniform following the beetle outbreak (Fig. 3B). Although the outbreak at the Middle Sink study site was less extensive than at the Beaver Creek site (Table 2), the area affected was in the southeastern corner of the stand which had a potential mortality rating of high or medium (Fig. 3C). The change was enough to increase the degree of continuity in basal area patches in the stand (Figure 3D).

Maps of residual basal area in stands after Douglas-fir beetle outbreaks demonstrate the patchy nature of Douglas-fir beetle outbreaks and how the beetle does not seem to remove all high-density pockets within a stand. This is important information for resource managers. Managing stands to reduce susceptibility to Douglas-fir beetle may or may not be compatible with other resource management objectives that require the preservation of clumps with high basal area in a stand. These clumps are the most likely to exhibit tree mortality by the Douglas-fir beetle. However, because not all high-density clumps are always attacked, management strategies can be developed that mimic the natural disturbance caused by Douglas-fir beetle.

Ashley National Forest. In contrast to the Beaver Creek and the Middle Sink sites, we did not observed changes in the nugget, range, or spatial dependency obtained for the Clements Hollow site as a result of Douglas-fir beetle activity (Table 2; Fig. 4A and B). The Clements Hollow site comprised 16 ha compared with the Beaver Creek and Middle Sink sites, which comprised four hectares each. Douglas-fir beetle outbreaks tend to be patchy and affected landscapes include unaffected areas. This is reflected in the small change in basal area observed in the Clements Hollow study site. Although part of the site was sampled at 10- and 20-m resolutions the majority of the site was sam-

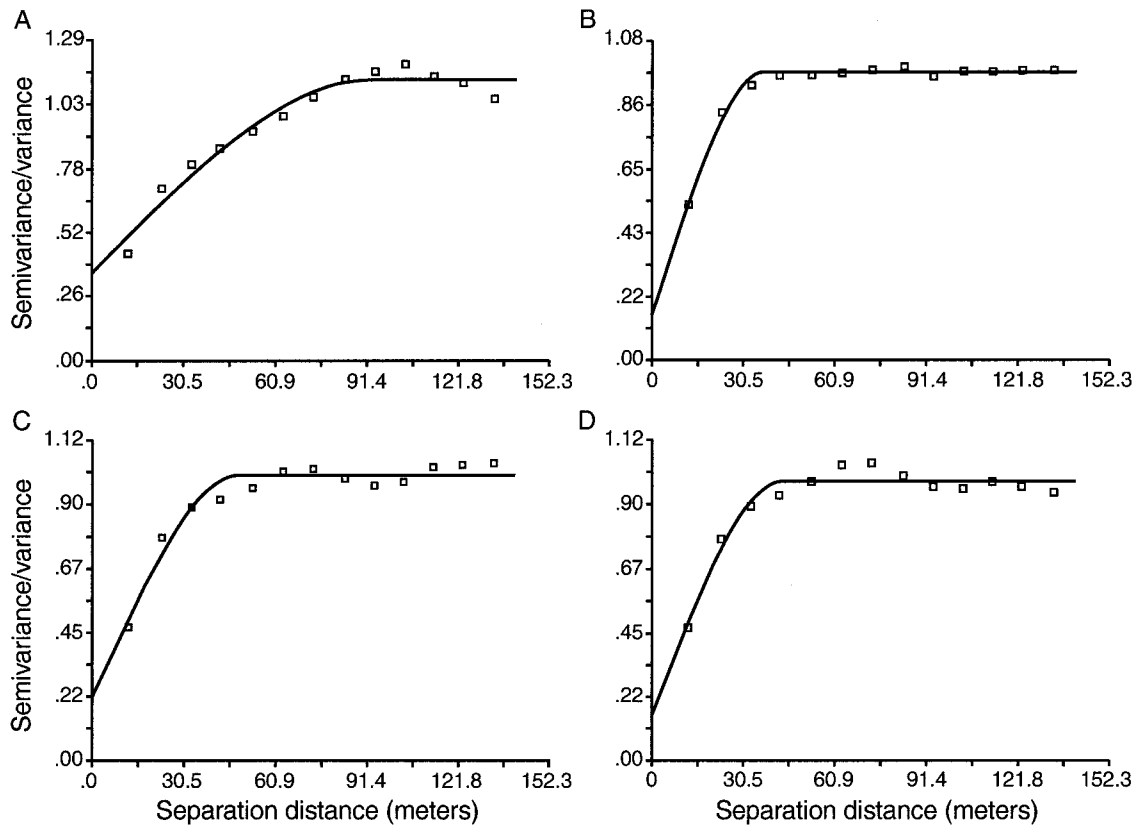


Fig. 2. Variograms for the Beaver Creek study area (A) Douglas-fir basal area; (B) Douglas-fir residual basal area; and the Middle Sink study area (C) Douglas-fir basal area; (D) Douglas-fir residual basal area. Wasatch-Cache National Forest, UT, 1997.

pled at a 40-m resolution. It is likely that increase in sampling distance coupled with sampling a stand where the outbreak had not completely collapsed made it difficult to capture changes in spatial patterning caused by the Douglas-fir beetle outbreak. The sample area was much larger, but with the compromise of reducing the number of pairs of observations available to calculate the variogram at each lag distance. This reduction in the number of pairs is probably reflected in the accuracy of the variogram characteristics. Ultimately, evaluation of these techniques at multiple scales, outbreak intensities, and different forest conditions will add to our understanding of the interplay of these factors.

Kriging output was used to map the distribution of live basal area before and after the Douglas-fir beetle outbreak using potential mortality classes to a 10-m resolution by estimating the basal area at the unsampled locations (Fig. 4C and Fig. 4D). From the maps, it can be seen, that reductions in live basal area caused by Douglas-fir beetle activity were more prevalent in the high and medium potential mortality classes located in the west side and the southeastern corner of the stand. This is in agreement with the results from the spatially referenced regression analysis.

The results illustrate how kriging can be used to incorporate within-stand variability of Douglas-fir basal area into the process of rating a stand for potential mortality. Maps of the distribution of Douglas-fir basal area in a stand can be produced using kriging techniques. Rating models can then be applied to the maps to depict areas with different potential mortality classes. Again, not all high-density clumps were removed by the beetle, which suggests that parts of the stand may still be susceptible to additional Douglas-fir beetle mortality should another outbreak develop.

Results from the cross validation analysis indicate that for estimation of Douglas-fir basal area the mean difference between kriged and actual values was $-0.08 \text{ m}^2/\text{ha}$ with a median of -0.5 . The minimum and maximum differences were $-42.1 \text{ m}^2/\text{ha}$ and $52.9 \text{ m}^2/\text{ha}$, respectively. The 25th and 75th percentiles were -6.9 and 5.3 , respectively, for an interquartile range of 12.2 . Based on an average Douglas-fir stand basal area of $18.5 \text{ m}^2/\text{ha}$ (Table 2), half of the kriged estimates were within 29% and 37% of the observed basal area. For Douglas-fir residual basal area the mean difference between kriged and actual values was $0.05 \text{ m}^2/\text{ha}$ with a median of -1.0 . The minimum and maximum differences were $-41.6 \text{ m}^2/\text{ha}$ and $45.9 \text{ m}^2/\text{ha}$, respectively. The 25th and 75th percentiles were -6.5 and

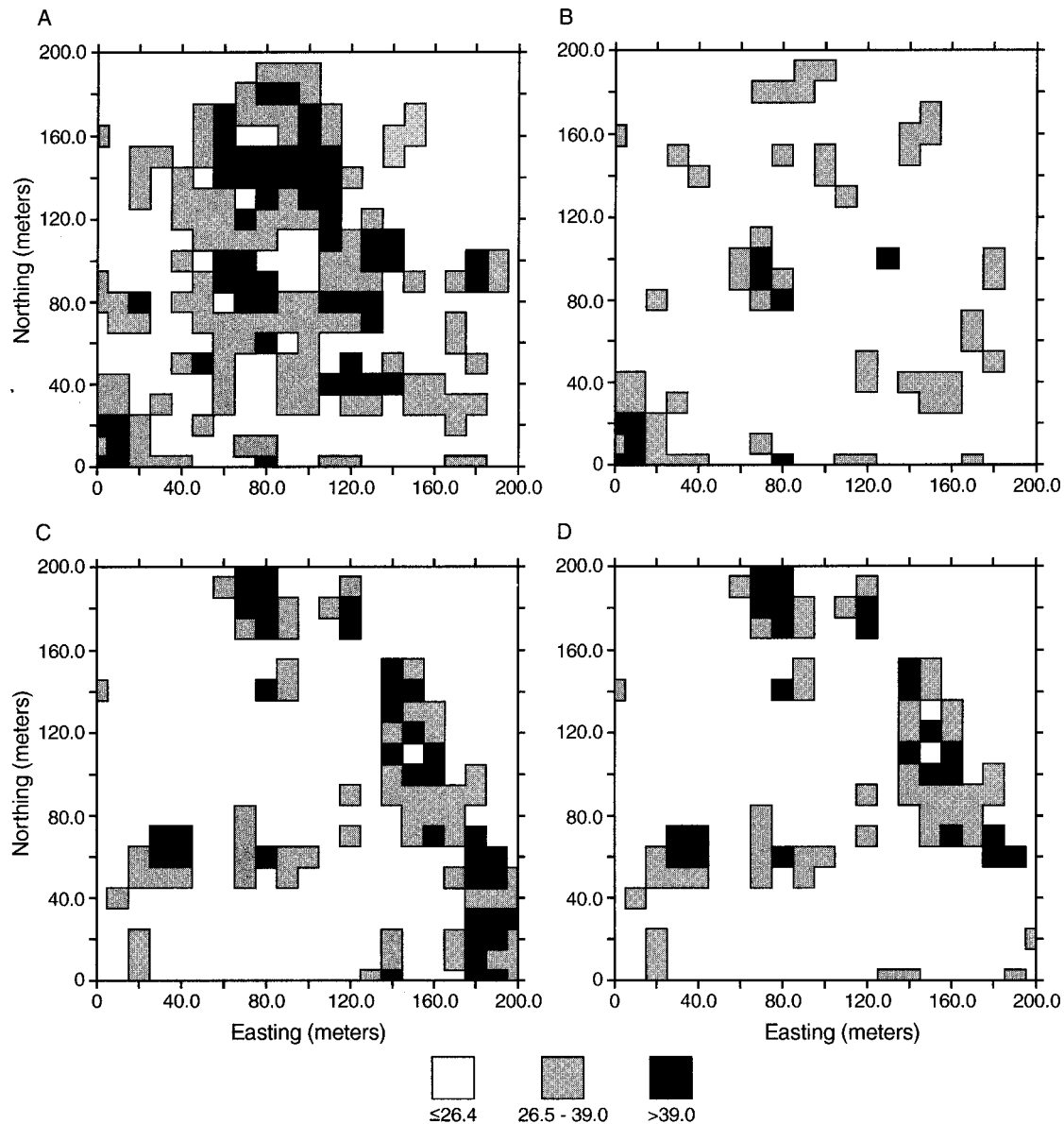


Fig. 3. Distribution of (A) Douglas-fir basal area; (B) Douglas-fir residual basal area for the Beaver Creek study area; (C) Douglas-fir basal area; (D) Douglas-fir residual basal area for the Middle Sink study area. Stocking levels (m^2/ha) portrayed correspond to high, medium, and low potential mortality classes for Utah as described in text. Wasatch-Cache National Forest, UT, 1997.

4.8, respectively, with an interquartile range of 11.3. Based on an average residual Douglas-fir stand basal area of $14.1 \text{ m}^2/\text{ha}$ (Table 2), half of the kriged estimates were within 34 and 46% of the observed residual Douglas-fir basal area. Isaaks and Srivastava (1989) indicated that examination of the spatial arrangement of the residuals can help in the process of improving the estimation process by suggesting changes in direction and distance of neighbors to be used in kriging. In addition, cross-validation estimates can be affected by clustering in the data set. Clustering was not of concern in our study because our sampling points

were regularly distributed across the study site. In our study, cross-validation estimates for Douglas-fir basal area before and after the Douglas-fir beetle outbreak were generally overestimated for areas of lower basal area and underestimated for areas of higher basal area. This is likely to be caused by the smoothing nature of estimation through kriging. Liebhold et al. (1991) indicates that although the kriged estimates minimize residual variance, substantial error can be present in the estimates. The majority of our estimates were within acceptable ranges but we also observed the potential for large estimation errors in our cross val-

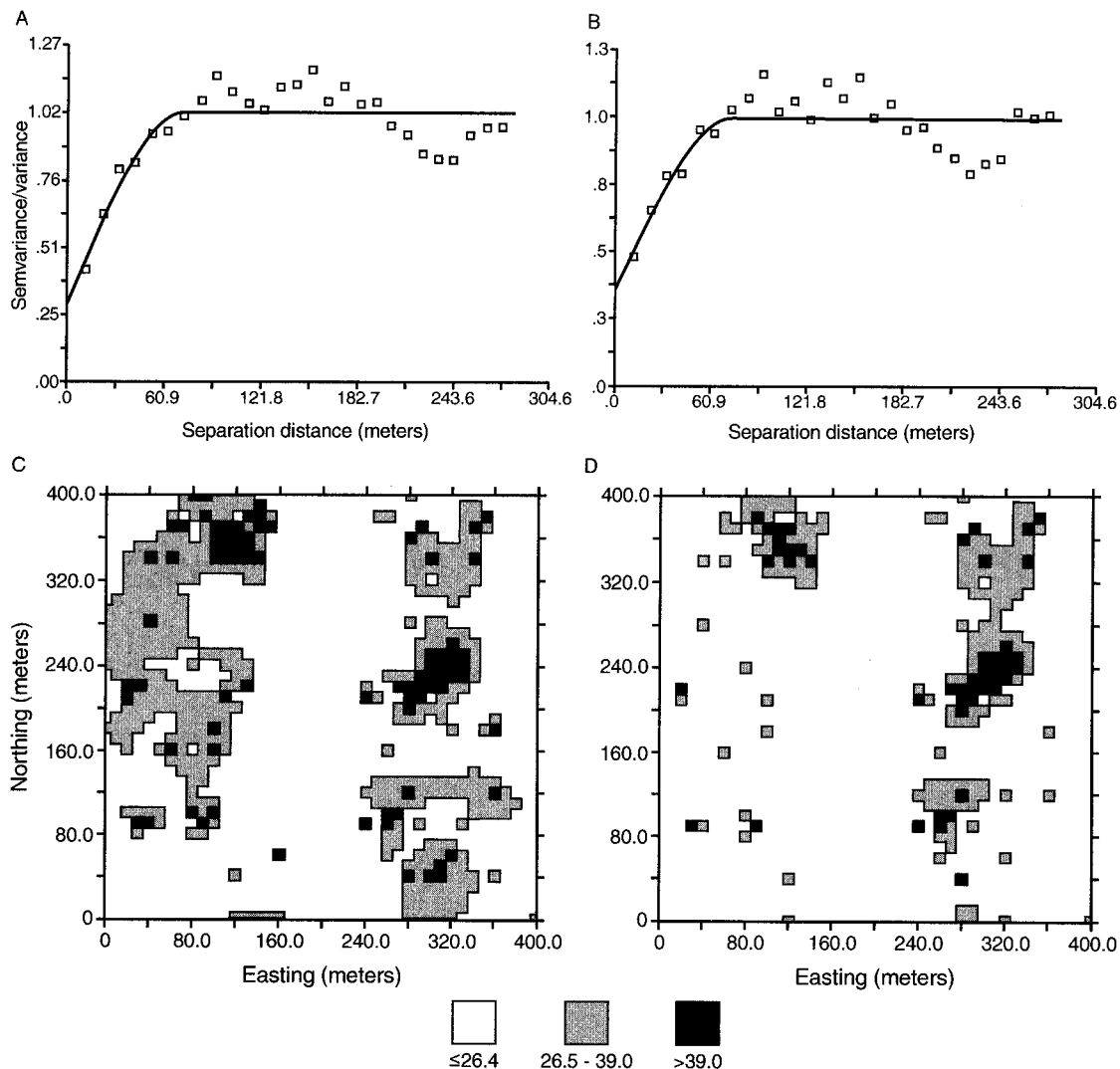


Fig. 4. Variograms for the Clements Hollow study area (A) Douglas-fir basal area; (B) Douglas-fir residual basal area. Distribution based on kriged estimates to a 10×10 -m resolution of (C) Douglas-fir basal area; (D) Douglas-fir residual basal area for the Clements Hollow study area. Stocking levels (m^2/ha) portrayed correspond to high, medium, and low potential mortality classes for Utah as described in text. Ashley National Forest, UT, 1998.

idation analysis. Kriged output examination needs to be made with an awareness of estimation errors so that outputs generated are adequately interpreted by the users. This is particularly true in areas exhibiting extreme variability or areas with few data points on which to base estimation (Köhl and Gertner 1997). Capturing the variability at a small scale may be crucial in the process of adequately measuring the variability across the stand, accurately describing the spatial variability in a functional model, and obtaining kriged estimates with minimal variance. Accuracy of kriging estimates is dependent on the nugget, the range, and the number of neighbors used to estimate values at unsampled locations.

In their geostatistical analysis of needle/leaf loss survey data, Köhl and Gertner (1997) concluded that

these techniques are suitable for describing the spatial distribution of forest damage, particularly for comparing results of survey data from different years. Coulson et al. (1999) working with southern pine beetle, *Dendroctonus frontalis* Zimmermann, populations at the mesoscale in east Texas examined landscape heterogeneity using moment of inertia analysis. That study evaluated the influence the spatial arrangement of suitable southern pine beetle habitat on the distribution and abundance of infestations. Suitable habitat was determined by stand hazard and behavioral traits of the insect. Our study and the study by Coulson et al. (1999) examined different spatial scales. The studies indicate that bark beetles exhibit spatial patterning at both the landscape and within-stand scales. Developing an understanding of the different spatial scales

at which bark beetles operate can help in refining management approaches and explaining their role as disturbance agents.

Our results suggest that geostatistical approaches have potential for use in measuring and characterizing changes in forest conditions resulting from bark beetle outbreaks. Douglas-fir beetle-caused mortality resulted in a more continuous stand in terms of basal area by removing high-density clumps. In addition, geostatistical approaches may offer adequate methodologies that incorporate the influence of variability in stand conditions into models to estimate potential mortality. Based on this study, an approach may be to sample the distribution of basal area or other important metric at a small-scale where spatial autocorrelation is present using sample points in a grid system. Variogram models can be constructed and kriging techniques used to develop a small-scale map of potential mortality classes based on the selected metric.

The geostatistical analysis conducted in this study has allowed us to begin exploring how within-stand basal area distribution influences the activity of Douglas-fir beetle within a stand; how the Douglas-fir beetle changes the distribution of basal area in the stand; and the potential application of these techniques to bark beetle management. We acknowledge that more replication and additional research are required in this arena. Nevertheless, we conclude that geostatistical approaches offer valuable tools for extending our knowledge of bark beetle ecology and developing improved management strategies.

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References Cited

- Amman, G. D., M. D. McGregor, D. B. Cahill, and W. H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. General Technical Report, INT-GTR-36. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Bentz, B. J., G. D. Amman, and J. A. Logan. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *For. Ecol. Manage.* 61: 349–366.
- Berryman, A. A., and L. C. Wright. 1978. Defoliation, tree condition, and bark beetles. In M. H. Brookes, R. W. Stark, and R. W. Campbell [eds.], *The Douglas-fir tussock moth: a synthesis*. USDA For. Serv. Tech. Bull. 1583: 81–87.
- Biondi, F., D. E. Myers, and C. C. Avery. 1994. Geostatistically modeling stem size and increment in an old-growth forest. *Can. J. For. Res.* 24: 1354–1368.
- Chellemi, D. O., K. G. Rohrbach, R. S. Yost, and R. M. Sonoda. 1988. Analysis of the spatial pattern of plant pathogens and diseased plants using geostatistics. *Phytopathology* 78: 221–226.
- Cole, W. E., and G. D. Amman. 1969. Mountain pine beetle infestations in relation to lodgepole pine diameters. Research Note, RN-INT-95. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Cole, W. E., and G. D. Amman. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: course of an infestation. General Technical Report, INT-GTR-89. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Coulson, R. N., McFadden, B. A., Pulley, P. E., Lovelady, C. N., Fitzgerald, J. W., and S. B. Jack. 1999. Heterogeneity of forest landscapes and the distribution and abundance of the southern pine beetle. *For. Ecol. Manage.* 114: 471–485.
- Cressie, N.A.C. 1991. *Statistics for spatial data*. Wiley, New York.
- 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., R. L. Livingston, and M. D. McGregor. 1981. Development of a stand susceptibility classification for Douglas-fir beetle, pp. 115–128. In R. L. Hedden, S. J. Barras, and J. E. Coster [technical coordinators.], *Hazard-Rating Systems in Forest Insect Pest Management: Symposium Proceedings*. 31 July–1 August 1980, Athens, GA. Society of American Foresters, Entomology Working Group, and USDA Forest Service, and The University of Georgia, Department of Entomology. 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-GTR-59. USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, UT.
- Haining, R. 1990. *Spatial data analysis in the social and environmental sciences*. Cambridge University Press, Cambridge.
- Hohn, M. E. 1988. *Geostatistics and petroleum geology*. Van Nostrand Reinhold, New York.
- Hohn, M. E., A. M. Liebhold, and L. Gribko. 1993. Geostatistical model for forecasting the spatial dynamics of defoliation caused by the gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae). *Environ. Entomol.* 22: 1066–1075.
- Isaaks, E. H., and R. M. Srivastava. 1989. *An introduction to applied geostatistics*. Oxford University Press, New York.
- Jackson, R. B., and M. M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. *J. Ecol.* 81: 683–692.
- Kemp, W. P., T. M. Kalaris, and W. F. Quimby. 1989. Rangeland grasshopper (Orthoptera: Acrididae) spatial variability: macroscale population assessment. *J. Econ. Entomol.* 82: 1270–1276.
- Klein, W. H., D. L. Parker, and C. E. Jensen. 1978. Attack, emergence, and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. *Environ. Entomol.* 7: 732–737.
- Köhl, M., and G. Gertner. 1997. Geostatistics in evaluating forest damage surveys: considerations on methods for

- describing spatial distributions. *For. Ecol. Manage.* 95: 131–140.
- Lejeune, R. R., L. H. McMullen, and M. D. Atkins. 1961. The influence of logging on Douglas-fir beetle populations. *For. Chron.* 37: 308–314.
- 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 Nat.* 50: 333–338.
- Liebholt, A. M., J. S. Elkington, G. Zhou, M. E. Hohn, R. E. Rossi, G. H. Boettner, C. W. Boettner, C. Burnham, and M. L. McManus. 1995. Regional correlation of gypsy moth (Lepidoptera: Lymantriidae) defoliation with counts of egg masses, pupae, and male moths. *Environ. Entomol.* 24: 193–203.
- Liebholt, A. M., R. E. Rossi, and W. P. Kemp. 1993. Geostatistics and geographic information systems in applied insect ecology. *Annu. Rev. Entomol.* 38: 303–327.
- Liebholt, A. M., X. Zhang, M. E. Hohn, J. S. Elkington, M. Ticehurst, G. L. Benzon, and R. W. Campbell. 1991. Geostatistical analysis of gypsy moth (Lepidoptera: Lymantriidae) egg mass populations. *Environ. Entomol.* 20: 1407–1417.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.
- Magee, L. 1990. R2 measures based on Wald and likelihood ratio joint significance tests. *Am. Stat.* 44: 250–253.
- McCambridge, F. F., F. G. Hawksworth, C. B. Edminster, and J. G. Laut. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-RP-235, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO.
- McGregor, M. D., M. M. Furniss, W. E. Bousefield, D. P. Almas, P. J. Gravelle, and R. D. Oakes. 1974. Evaluation of the Douglas-fir beetle infestation North Fork Clearwater River Drainage, Northern Idaho, 1970–73. Forest Pest Management Report 74-7. USDA Forest Service, Northern Region, Missoula, MT.
- 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.
- Mitchell, R. G., and H. K. Preisler. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *For. Sci.* 37: 1390–1408.
- Negrón, J. 1997. Estimating probabilities of infestation and extent of damage by the roundheaded pine beetle in ponderosa pine in the Sacramento Mountains, New Mexico. *Can. J. For. Res.* 27: 1936–1945.
- Negrón, J. F. 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. *For. Ecol. Manage.* 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. *West. J. Appl. For.* 14(3): 1–7.
- Olsen, W. K., J. M. Schmid, and S. A. Mata. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *For. Sci.* 42: 310–327.
- Raty, L., C. Ciornei, and V. Mihalciuc. 1997. Spatio-temporal analysis for *Ips typographus* monitoring catches in two Romanian forest districts, pp. 191–203. In J. C. Gregoire, A. M. Liebhold, F. M. Stephen, K. R. Day, and S. M. Salom [eds.], Integrating Cultural Tactics into the Management of Bark Beetle and Reforestation Pests: Proceedings. 1–3 September 1996, Vallombrosa, Italy. Sponsored by the International Union of Forest Res. Organizations, Working Parties S7.03.03 and S7.03.05. USDA For. Serv. Northeast. For. Exp. Stn. Gen. Tech. Rep. NE-236.
- Reynolds, K. M., and E. H. Holsten. 1994. Classification of spruce beetle hazard in Lutz spruce (*Picea X lutzii*) stands on the Kenai Peninsula, Alaska. *Can. J. For. Res.* 24: 1015–1021.
- Reynolds, K. M., and E. H. Holsten. 1996. Classification of spruce beetle hazard in Lutz and Sitka spruce stands on the Kenai Peninsula, Alaska. *For. Ecol. Manage.* 84: 251–262.
- Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. *Ecology* 69: 1517–1524.
- Rudinsky, J. A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. *Can. Entomol.* 98: 98–111.
- Safranyik, L., D. M. Shrimpton, and H. S. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. *Environ. Can. For. Serv. For. Tech. Rep.* 1.
- Sartwell, C., and R. E. Stevens. 1975. Mountain pine beetle in ponderosa pine, prospects for silvicultural control in second-growth stands. *J. For.* 73: 136–140.
- Schmitz, R. F., and K. E. Gibson. 1996. Douglas-fir beetle. Forest Insect and Disease Leaflet 5. USDA Forest Service, Washington, DC.
- Schotzko, D. J., and L. E. O'keeffe. 1989. Geostatistical description of the spatial distribution of *Lygus hesperus* (Heteroptera: Miridae) in lentils. *J. Econ. Entomol.* 82: 1277–1288.
- Shore, T. L., L. Safranyik, W. G. Riel, M. Ferguson, and J. Castonguay. 1999. Evaluation of factors affecting tree and stand susceptibility to the Douglas-fir beetle (Coleoptera: Scolytidae). *Can. Entomol.* 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 No. R4-93-05. USDA Forest Service, Intermountain Region, Ogden, UT.
- Wright, K. H., and P. G. Lauterbach. 1958. Ten year study of mortality in a Douglas-fir saw-timber stand in Coos and Douglas Counties, Oregon. Research Paper PNW-RP-27. USDA Forest Service, Pacific Northwest and Range Experiment Station, Portland, OR.
- Wright, L. C., A. A. Berryman, and B. E. Wickman. 1984. Abundance of the fir engraver, *Scolytus ventralis*, and the Douglas-fir beetle, *Dendroctonus pseudotsugae*, following tree defoliation by the Douglas-fir tussock moth, *Orgyia pseudotsugata*. *Can. Entomol.* 116: 293–305.

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