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# *Relationships of Douglas-fir Tussock Moth Defoliation to Site and Stand Characteristics in Northern Idaho*

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ABSTRACT. Relationships between intensity of defoliation caused by Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, and descriptive characteristics of forest sites and stands in an outbreak area of northern Idaho were quantified. Defoliation hazard predictive models were developed from inventory data collected in 70 stands covering a range of successional stages and site and stand conditions within the grand fir-western redcedar ecosystem. Two models are presented, each accounting for approximately 50 percent of the variation in defoliation intensity.

Defoliation was heavier on upper slope and ridgetop sites, negatively correlated with depth of volcanic ash mantle, and positively correlated with host tree age, proportion of grand fir in the stand, and the ratio of stand density or biomass to site index. A hypothesis that tussock moth outbreaks develop in response to changes in host foliage quality resulting from stresses is presented. FOREST SCI. 27:431–442.

ADDITIONAL KEY WORDS. *Orgyia pseudotsugata,* forest protection, hazard rating, host-insect interaction.

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INSECTS have repeatedly caused major disturbances in the coniferous forests of western North America. Reduction in timber values of affected stands, the usual consequence of such perturbations, is of particular concern in commercial forests. Measures to reduce damage are costly and, due in part to poor understanding of the causes of the problem, often ineffective.

This situation was apparent during the recent outbreaks of the Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough. As a result, the Expanded Douglas-fir Tussock Moth Research and Development Program was launched to comprehensively study the behavior of the insect, the damage caused, and the ways in which future damage might be reduced or prevented (Stark 1978). The study we present, a part of this program, was specifically aimed at quantifying relationships between habitat characteristics and levels of defoliation by the tussock moth. Identification of such relationships was, in our opinion, needed to allow prediction of spatial and temporal changes in tussock moth populations and resultant damage, a necessary ability in an effective forest and pest management system.

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The tussock moth is a defoliator of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and true firs (*Abies* spp.) in western North America. The insect is characterized by extreme population fluctuations with outbreaks generally lasting 3 or 4 years (Mason and Luck 1978). Outbreak populations can cause heavy defoliation and substantial tree growth reduction, top kill, and mortality (Wickman 1963).

Outbreaks tend to be synchronized over wide geographical areas (Clendenen,[1] Mason 1978) and occur with some regularity at 8- to 10-year intervals (Sudgen 1957, Tunnock 1973). Periodicity of outbreaks is thought to result from time-delay in the site-insect system's response to density-dependent feedback processes (Berryman 1978). Occurrence of outbreaks has been associated with climatic conditions (Watt 1968, Clendenen,[1] and Lessard[2]) and shifts in genetic composition of the tussock moth population (Stock[3]).

Population increase to outbreak levels develops in place due to the wingless nature of the female moth and the limited dispersal of early instar larvae. Consequently, highest defoliation levels are thought to first appear in those habitats most conducive to growth of the tussock moth population (Wickman and others 1973). By this reasoning, if we measure the level of defoliation that occurs in a forest habitat (the defoliation hazard) early in an outbreak sequence, we will also determine how conducive that habitat is to tussock moth population growth (its susceptibility to outbreak).

Quantification of associations between habitat attributes and defoliation hazard does not answer the question of what factors lead to release of tussock moth populations to outbreak levels and synchronization of release among separate populations. However, by examining the nature of factors common to high hazard habitats we should gain insight into the causes of tussock moth outbreaks.

## Methods

*Study Area.*—The study was conducted on the Palouse Ranger District of the Clearwater National Forest and adjacent federal, state, and private lands in northern Idaho. The study area, of approximately 685 $km^2$, is one of forested rolling hills, mountains, and mountainous ridges extending westward toward the Palouse Prairie. Elevations range from 750 to 1,500 m. The major underlying rock types are metasediments composed of weathered siltites and quartzites (Shively[4]). Older soils are covered or influenced by loess deposits (Richmond and others 1965). A deposit of volcanic ash of varying thickness from Mount Mazama eruptions covers portions of the forested area (Fryxell 1965). The climate is characterized by dry summers and relatively mild winters. Precipitation ranges from 560 mm on the prairie fringes to about 890 mm in the mountainous parts (National Oceanic and Atmospheric Administration 1976). Consistent with a gradient of increasing soil moisture and decreasing temperatures, the area supports climax communities of ponderosa pine (*Pinus ponderosa* Laws.), Douglas-fir, grand fir (*Abies grandis*

[1] Unpublished preliminary report by G. Clendenen. Tussock moth, *Orgyia pseudotsugata* (McD.), outbreaks and climatic factors: a correlation analysis. USDA Forest Serv Coop Aid Agreement. Coll Forest Resour, Univ Wash, Seattle. 60 p. 1975.

[2] Unpublished masters thesis by E. D. Lessard. Climatic, host tree, and site factors affecting the population dynamics of the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough). Univ Wash, Seattle. 69 p. 1974.

[3] Unpublished final report by M. W. Stock. Genetic polymorphism in the Douglas-fir tussock moth. USDA DFTM Res and Dev Program, Portland, Oreg. 31 p. 1977.

[4] Unpublished masters thesis by M. V. Shively. Reconnaissance geology and the genesis and development of soils in the Upper Palouse River Area of Idaho. Univ Idaho, Moscow. 45 p. 1977.

[Dougl.] Lindl.), western redcedar (*Thuja plicata* Donn.), western hemlock (*Tsuga heterophylla* [Raf.] Sar.), and subalpine fir (*Abies lasiocarpa* [Hook] Nutt.) (Daubenmire and Daubenmire 1968).

Tussock moth outbreaks had occurred in the area in 1945 and 1964; each outbreak was treated by aerial application of DDT (Tunnock 1973). Indications of the most recent outbreak were first gained in 1972 from egg mass surveys, although no defoliation was visible from survey aircraft that year. In 1973, aerial surveys detected varying degrees of defoliation on 70,000 acres. Stands that suffered heavy defoliation were often intermingled with stands showing little or no defoliation (Tunnock and Livingston 1974). In June 1974, the area was treated with DDT, achieving 97 percent insect mortality (Graham 1975) and stopping the outbreak at an early stage.

*Data Collection and Transformation.*—In 1975 seventy study stands were selected, without regard to the level of defoliation sustained, to cover a range of terrain physiography, aspect, stand age, and tree species composition. Three variable radius plots were systematically located from a random start in each study stand. Variables recorded on each sample plot included: aspect in degrees, percent slope, habitat type, elevation, slope position (lower, middle, upper one-third, or ridgetop relative to the major landform), and depth of the volcanic ash mantle. For all trees at least 7.6 cm diameter breast height (dbh) occurring in the variable radius plots, the species, dbh, total height, and age at breast height were recorded.

Defoliation estimates were obtained using a double-sampling procedure. In the first sample all dominant and codominant host trees in the variable radius plots were visually rated for defoliation. The crown of each tree was divided into six equal sections and, within each section, defoliation was classified into one of the following categories: none to 5 percent, 6 to 25 percent, 26 to 50 percent, 51 to 75 percent, and 76 to 100 percent.

A subset of these rated trees consisting of 40 grand fir, and 46 Douglas-fir trees from 34 stands made up the second sample. Each tree was felled, its crown was divided into six equal sections, and the branches in each section were counted. Two branches from the middle of each crown section were measured for total foliage surface area and extent of defoliation. The average foliage surface areas and extents of defoliation of the crown sections were computed and added to obtain a percent defoliation estimate for the entire tree. This information was used to develop regression estimators for total tree defoliation based on the six visual ratings for each tree. Separate estimators were developed for grand fir and Douglas-fir, each accounting for approximately 86 percent of the sample variation. These regression estimates were then applied to all visually rated trees. The results were averaged to obtain an estimate of percent defoliation per host tree for each sample stand. Defoliation intensity ranged from 2 to 49 percent and averaged 15 percent for the 70 stands.

The summarized field data were used to compute variables that reflect the composition and growth of the stands. Indices of stand density and tree biomass were computed from species, diameter at breast height, and the number of plot trees. Among the indices of stand density were basal area/hectare and crown competition factor (Krajicek and others 1961). Biomass estimates of various tree components were derived from Brown's (1976) equations and from data of Johnston and Bartos (1977).

Douglas-fir and grand fir site index values (SI) were calculated from Brickell's (1970) site curves and equations. Douglas-fir SI was used to represent site quality for all 70 study stands. In stands where only grand fir site trees were available, a regression equation developed from stands containing both suitable grand fir

*TABLE 1. Site and stand characteristics associated with Douglas-fir tussock moth defoliation.*

| Characteristic | Descriptive statistics | | |
|---|---|---|---|
| | Mean | Minimum | Maximum |
| Slope position (0 = lower slope, 1 = upper slope) | 0.66 | 0.00 | 1.00 |
| Depth of ash (cm) | 40.5 | 0.0 | 76.2 |
| Douglas-fir site index (m @ 50 years) [SI] | 20.3 | 15.2 | 27.4 |
| Mean host age [HA] | 62.0 | 13.0 | 121.0 |
| Coefficient of variation in stand dbh | 33.9 | 15.0 | 64.0 |
| Coefficient of variation in stand height | 24.3 | 8.0 | 60.0 |
| Stand basal area ($m^2$/ha) [BA] | 34.7 | 8.3 | 62.7 |
| Stand foliage biomass (g/ha) [FB] | 14,789.0 | 4,849.0 | 26,292.0 |
| BA/SI | 1.72 | 0.40 | 3.40 |
| FB/SI | 737.1 | 274.0 | 1,460.7 |
| 100 * grand fir BA/stand BA [$\%GF_{BA}$] | 43.2 | 0.0 | 100.0 |
| 100 * grand fir FB/stand FB [$\%GF_{FB}$] | 50.8 | 0.0 | 100.0 |

and Douglas-fir site trees was used to estimate Douglas-fir site index (Stoszek and others[5]). Ratios of density and biomass to SI were used to represent indices of site occupancy in the analysis.

Coefficients of variation of tree heights and diameters were used to express stand vertical and horizontal diversity. Preliminary inspection of the data indicated little difference in defoliation levels among some of the slope position classes. Duncan's new multiple range test revealed no statistically significant difference ($\alpha = 0.1$) in percent defoliation between upper slope and ridgetop, and between the lower and midslope stand location classes. Therefore, the four initial classes were combined into an upper slope class and a lower slope class.

Descriptive statistics for the site and stand characteristics of importance are shown in Table 1. All variables listed showed significant correlations ($\alpha = 0.05$) with percent defoliation of host trees. The data encompass an acceptable range of site and stand conditions.

## Analysis and Results

Many single independent variables exhibited statistically significant relationships with tussock moth defoliation but were often correlated with each other as well. This was not unexpected since many of these variables were merely different expressions of the same basic characteristics (e.g., tree density or volume, species composition). However, when using ordinary least squares regression analysis for variable selection and parameterization, high correlation among the independent variables can result in parameter estimates sensitive to small changes in the data (Marquardt and Snee 1975). To minimize this potential problem we used the ridge regression technique of Hoerl and Kennard (1970) to screen the various groups of candidate predictor variables. Standard multiple regression techniques were then used to estimate parameters for the final set of variables and provide the appropriate test statistics.

[5] Unpublished final report by K. J. Stoszek, H. L. Osborne, P. G. Mika, and J. A. Moore. The relationship of site and stand attributes and management practices to Douglas-fir tussock moth epidemics. USDA DFTM Res and Dev Program, Portland, Oreg. 1977.

*TABLE 2. Predictive model for Douglas-fir tussock moth defoliation using foliage biomass estimates.*

Model: ln(% defoliation/host) = $b_0 + b_1$*SP + $b_2$*AD + $b_3$*ln(HA) + $b_4$*ln(FB/SI) + $b_5$*ln(%GF)

where SP = slope position = 0 if lower slope, 1 if upper slope
AD = depth of ash mantle (cm)
HA = age at breast height averaged over all host trees
FB = total tree foliage biomass (g/ha)
SI = Douglas-fir site index (m @ 50 years)
%GF = 100 * grand fir FB/Total FB

| Parameter | Estimate | Standard deviation | Standardized coefficient | VIF[1] |
|---|---|---|---|---|
| $b_0$ | −5.018 | | | |
| $b_1$ | 0.422 | 0.194 | 0.199 | 1.138 |
| $b_2$ | −0.012 | 0.005 | −0.240 | 1.222 |
| $b_3$ | 0.672 | 0.224 | 0.304 | 1.398 |
| $b_4$ | 0.611 | 0.259 | 0.215 | 1.160 |
| $b_5$ | 0.222 | 0.069 | 0.310 | 1.315 |

$R^2$ = 53.2%  SEE[2] = 0.721 = 31.9% of the mean
$F$ = 14.53  $P\{F \geq 14.53\} < 0.0001$

[1] Variance inflation factor (Marquardt 1970).
[2] Standard error of the estimate = $\sqrt{\text{MSE}}$.

The model resulting from this process contained five site and stand variables: (1) the position of the stand on the slope, (2) the depth of the volcanic ash mantle at the site, (3) the average age of the host trees, (4) the level of site occupancy (represented by a ratio of total tree density to site index), and (5) the percentage of grand fir in the stand (represented by a ratio of grand fir density to total density). Two versions of this model are presented in Tables 2 and 3.

In the model shown in Table 2, tree density is estimated by biomass (g/ha) of foliage. Of all the models we examined which satisfied the ridge criterion of stability of parameter estimates, this model was "best" in that it provided the highest degree of fit ($R^2$ = 53.2 percent). The contribution of each predictor vari-

*TABLE 3. Predictive model for Douglas-fir tussock moth defoliation using basal area estimates.*

Model: ln(% defoliation/host) = $b_0 + b_1$*SP + $b_2$*AD + $b_3$*ln(HA) + $b_4$*ln(BA/SI) + $b_5$*ln(%GF)

where SP = slope position = 0 if lower slope, 1 if upper slope
AD = depth of ash mantle (cm)
HA = age at breast height averaged over all host trees
BA = total tree basal area ($m^2$/ha)
SI = Douglas-fir site index (m @ 50 years)
%GF = 100 * grand fir BA/Total BA

| Parameter | Estimate | Standard deviation | Standardized coefficient | VIF |
|---|---|---|---|---|
| $b_0$ | −0.681 | | | |
| $b_1$ | 0.447 | 0.198 | 0.211 | 1.146 |
| $b_2$ | −0.012 | 0.005 | −0.249 | 1.234 |
| $b_3$ | 0.505 | 0.268 | 0.228 | 1.936 |
| $b_4$ | 0.487 | 0.226 | 0.234 | 1.555 |
| $b_5$ | 0.274 | 0.075 | 0.387 | 1.473 |

$R^2$ = 51.5%  SEE = 0.734 = 32.5% of the mean
$F$ = 13.60  $P\{F \geq 13.60\} < 0.0001$

able to the model is indicated by the standardized coefficients shown in the table. The largest coefficient is associated with the natural logarithm of percent grand fir; thus a change of one standard deviation in this variable has a larger effect on predicted defoliation than a similar change in any other variable. However, all the standardized coefficients are roughly equal, indicating that the model behavior is about equally dependent on the level of all the predictor variables.

The success of the ridge regression screening technique is demonstrated by the variance inflation factors (VIF) shown in the table. These values are the diagonal elements of the inverse of the correlation matrix of predictor variables; each value represents the factor by which the variance of the parameter estimate for that variable is increased due to correlation among the predictor variables (Marquardt 1970). As can be seen, all values are less than 1.4, indicating that very little inflation of regression coefficient variances has occurred.

The model shown in Table 3 is identical to that in Table 2 except that tree density has been estimated by basal area ($m^2$/ha). Although this model did not provide quite as good a fit of the data ($R^2$ = 51.5 percent), the basal area estimates can be more readily obtained from stand inventory data than estimates of foliage biomass. Thus, this model may be more useful to forest managers in quantifying stand susceptibility to defoliation in the 1973 tussock moth outbreak area of northern Idaho and, upon reparameterization, in other areas. We feel that the small loss in predictive ability would be of little practical significance.

Model residuals were examined for violations of analysis of variance assumptions but none could be detected. Residuals appeared to be normally distributed, indicating that the choice of a log-normal model was appropriate.

Predicted percent defoliation values obtained from the "foliar biomass" equation (Table 2) are shown in Figure 1. As the model predicted defoliation in logarithmic units, a bias correction term was added to obtain predictions in original units; a second order bias approximation suggested by Beauchamp and Olson (1973) was used for this purpose. Ash depth and percent grand fir vary across the observed range of the data for each panel in the figure. The effect of the remaining predictor variables (slope position, host tree age, and site occupancy) on defoliation is illustrated by contrasts between the panels. The influence of lower vs. upper slope is illustrated in Figures 1a and 1c where average host age and site occupancy index are held constant; upper slopes are seen to have substantially higher predicted defoliation than lower slopes.

The effect of increasing site occupancy while holding slope position and host age constant is shown by comparing Figures 1c with 1d and 1e with 1f. Similarly, the influence of host age is represented in the contrast between Figures 1c and 1e, and between 1d and 1f. An increase in either of these variables results in higher predicted defoliation. In terms of defoliation levels, Figures 1b and 1f show the "best" and "worst" combination of predictor variables, respectively. The conditions portrayed in Figure 1 are within the range of the observed data (Table 1), although all combinations of predictor variables are not represented by actual stands.

The predicted values are not mathematically bounded by 0 and 100 percent; however, if the combinations of minima and maxima given for the independent variables in Table 1 are used, the minimum predicted defoliation obtained from the equation in Table 2 is 0.5 percent and the maximum is 76 percent. Within the range of the observed data the predicted defoliation levels seem reasonable.

## Discussion

Good predictive ability is a major criterion for selecting variables to formulate a hazard rating model; however, other considerations may also be important. We

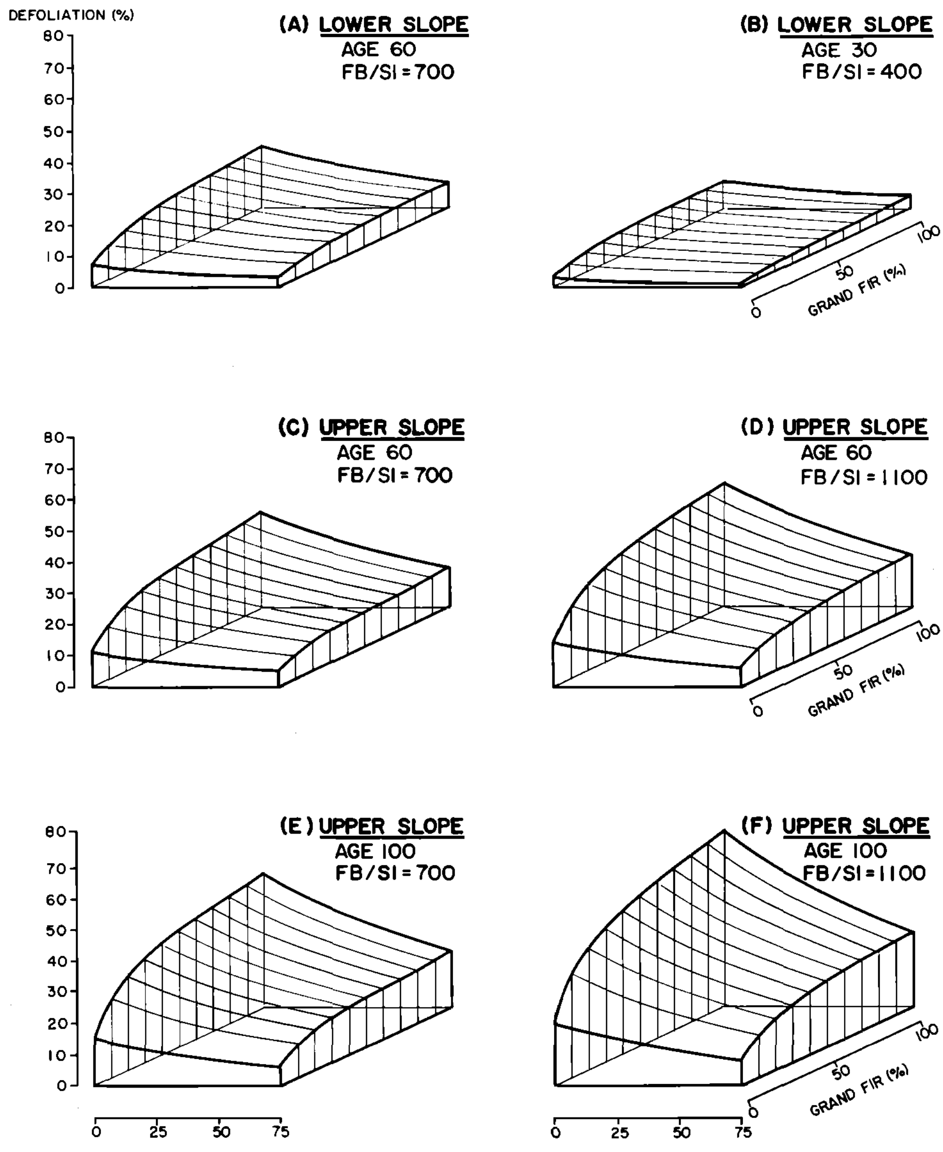


FIGURE 1. Predicted Douglas-fir tussock moth defoliation (percent per host tree) and forest site and stand characteristics in northern Idaho.

felt that (1) information required to apply the model should be available from forest resource inventories; (2) predictor variable should express factors managers can alter through silvicultural treatments; (3) the model should be compatible with current stand projection techniques to enable the use of simulation approaches in exploring alternative tussock moth hazard reducing silvicultural strategies; and (4) the predictor variables should be biologically meaningful.

*Model Interpretation.*—The models in Tables 2 and 3 portray empirical relationships between tussock moth defoliation levels and descriptive characteristics of sites and stands. These models can be directly used to rate stand defoliation hazard in northern Idaho. However, the models may also provide, upon interpretation of predictor variables, a hypothetical basis for defining the operational environment (*sensu* Mason and Langenheim 1957) of habitats susceptible to tussock moth outbreaks, and thus help in the search for factors important to dynamics of tussock moth populations. Studies conducted in other areas have found similar associations between tussock moth activity and characteristics of sites and stands. Outbreaks were shown to be more prevalent on ridgetops and upper slopes, on low productivity sites, and in mature and overmature stands with a high component of host trees in an advanced stage of succession (C. B. Williams, Jr., and others 1979, J. T. Williams and others 1980, Heller and Sader 1980). Thus interpretations based on results from northern Idaho may be applicable over most of the insect's range.

*Physiographic Location.*—Stands in midslope and lower slope locations sustained less defoliation than stands on or near ridges. Correlation between slope position and stand structure and composition was low; thus, the topographic location of a stand appears to represent factors important to tussock moth dynamics but unrelated to the physical nature of the stand.

This could be tied to the dispersal mechanism of the insect. In studies of the gypsy moth, *Lymantria dispar* (L.), which has a passive windborne mode of dispersal similar to that of the tussock moth, ridgetops were shown to favor immigration. Simulation of newly hatched gypsy moth larval dispersal showed that only those larvae that are lifted above the canopy or blown from the forest edge can be dispersed for long distances. Due to wind patterns in hilly terrain, larval dispersion "hops" from ridgetop to ridgetop (McManus 1973).

However, though tussock moth larvae dispersed from the population centers may enrich nearby populations, research indicates they are unlikely to invade new habitats in concentrations needed to develop new outbreak centers. Mitchell (1979), studying early instar dispersal in Oregon and British Columbia, concluded that most larvae would disperse no farther than 200 meters and that the chance of dispersal leading to significant damage in a new habitat was small. And since outbreaks collapse within 3 to 4 years of their inception, there is little chance for dispersed larvae to build to outbreak levels (Wickman and others 1973).

Another possible interpretation relates to the soil characteristics of such sites. Upper slope sites typically have shallower, better drained and less fertile soils than lower slope sites (Ralston 1964, Carmean 1975). Thus, trees in such conditions are more likely subject to stresses caused by water and nutrient deficiencies or imbalances.

As a result of such stress factors, the nutritional quality of host foliage may change to one that favors tussock moth population increase. Water stress of plants is known to result in marked increase in total nitrogen and the proportion of soluble protein nitrogen in the foliage (White 1974, 1978). White hypothesized, based on numerous examples, that many more young insects survive on plants with a richer, stress related, source of nitrogen.

*Depth of Volcanic Ash.*—Defoliation was inversely correlated with depth of the volcanic ash mantle. This term was also found to be independent of stand characteristics. Soils formed from this relatively recent ash deposit have, compared to the underlying soils, a higher moisture holding capacity, higher content of available moisture, lower bulk density, and higher cation exchange capacity, even though they are less fertile (Fosberg and others 1979). Tiedeman and Klock (1977), examining similar volcanic ash soil, concluded that total moisture holding capacity increased with increasing ash content. Thus, as ash depth increased, water availability could increase, promoting nutrient uptake and tree vigor and possibly changing the quality of host foliage in a manner deleterious to larval feeding.

*Age of Host Trees.*—Defoliation was positively correlated with mean age of grand fir and Douglas-fir trees in the stand. Stands less than 50 years old sustained little defoliation, regardless of species composition and physiographic location. Young stands were found to be defoliated only when adjacent to heavily defoliated mature and overmature stands, with defoliation confined to the boundary zone between the two types.

Maturation and senescence phenomena are prominently associated with age. Flowering is one such process. Grand fir and Douglas-fir initiate flowering at 20–40 years and 10–20 years, respectively (Eis 1973). Flowering can be induced in both tree species by climatic stress or reduced tree vigor (Puritch 1972) and occurs, according to Eis (1973), one year after a dry, warm summer follows a moist and cool one. Due to higher solar radiation, flowering is more abundant on trees with free standing crowns and on southerly slopes or ridgetops (Puritch 1972). Pollen and cone production drains carbohydrate and nitrogen reserves at the expense of vegetative structures (Dickman and Kozlowski 1968, Rook and Sweet 1971). Thus it is possible that such a stress increases tree predisposition to the tussock moth. Our records show 1971 as a year with heavy pollen production in grand fir in northern Idaho and in the Blue Mountains of Oregon; both areas were subject to tussock moth outbreaks from 1972 to 1974.

*Proportion of Grand Fir.*—Defoliation increased as the proportion of the total foliage biomass represented by grand fir increased. This, together with our observation that grand fir sustained significantly higher defoliation ($T$ test, $\alpha = 0.01$) than Douglas-fir when growing in the same stand, indicates the importance of grand fir foliage in tussock moth dynamics in northern Idaho.

Moisture requirements of grand fir are higher than the requirements of Douglas-fir (Lopushinsky 1969), and establishment and growth of grand fir is limited to sites that are higher on the soil moisture gradient than sites supporting Douglas-fir climax communities (Daubenmire and Daubenmire 1968). Thus the preferred host status of grand fir may reflect its greater tendency for developing moisture stress than would Douglas-fir under similar moisture regimes.

*Site Occupancy.*—The ratio of biomass levels to site productivity, in our case represented by estimates of total foliage biomass or basal area per hectare and site index for Douglas-fir, represents an index of occupancy of the site. The positive relationship between increasing site occupancy and defoliation suggests that density dependent factors are causally implicated in the interactions between the host tree and the tussock moth. With increasing stand density the amount of photosynthetically active tissue (needles) relative to the amount of inactive tissue (flower, twig, branch, stem, and root surfaces) decreases, therefore lowering primary production and vigor.

In addition, as total biomass on a particular site increases, the demands for water, nutrients, or both, may reach levels at which the ability of the site to support further growth decreases. This effect is compounded by the tie-up of nutrients, particularly phloem-immobile elements, in the standing biomass. Any sudden strain on the plant-site system, such as that caused by drought, heavy flowering, etc., could change foliage biochemistry of host trees in a manner benefiting the Douglas-fir tussock moth population.

*Conceptualization.*—The biological interpretations offer a consistent association of high tussock moth defoliation levels with habitats where host trees are likely to be under stress. This suggests that tussock moth outbreaks may develop in response to host foliage quality changes resulting from moisture and nutritional stresses. Sites with potential for moisture or nutrient deficiencies or where standing biomass levels may have exceeded the long-term carrying capacity for the host species appear to be prime candidates for heavy tussock moth defoliation.

Other observations seem to support this hypothesis. Cates,[6] working with white fir (*Abies concolor* [Gord. and Glend.] Lindl.), found that tussock moth larvae feeding on foliage of moisture stressed trees gained weight faster than larvae feeding on foliage of trees which grew under better moisture conditions. Laboratory tests implicated two monoterpenes, camphene and isobornyl acetate, as deterrents to larval feeding; moisture stress was found to decrease foliar concentrations of these two compounds. Stoszek and others,[7] studying a subsample of stands from the present study, found that increasing tussock moth defoliation in grand fir was associated with decreasing foliage concentrations of boron and calcium. Reviews by Mattson and Addy (1975 ), Kulman (1971), and Stark (1965), among other works, show the importance of food quality on the population dynamics of phytophagous insects. Development rates, fecundity, and survival of defoliating insects are directly affected by the chemical composition and nutritional quality of the foliage (White 1978). The mineral nutrient composition of the foliage even affects larval resistance to virus disease (Smirnoff and Bernier 1973).

In the case of the Douglas-fir tussock moth, the specific nature of the population release mechanism(s), including the trigger factor(s), remain unidentified. We suggest that these mechanisms include the quality of host tree foliage grown under conditions associated with high defoliation hazard, and the chemical changes within the foliage resulting from extrinsic stress.

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## *Organic Reserves: Importance to Ectomycorrhizae in Forest Soils of Western Montana*

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ABSTRACT. The important attributes contributed to forest soils by organic matter make it imperative to determine the quantity and type required to sustain good forest tree growth. Quantitative measurement of soil humus, decayed wood, and charcoal as related to numbers of active ectomycorrhizal root tips (in random soil cores from old-growth sites in western Montana) showed both positive and negative relationships with organic matter. Increased quantities of organic material, to 45 percent by volume of the top 30 cm of soil, were associated with increased numbers of ectomycorrhizae. At 45 percent organic matter or above, numbers of ectomycorrhizae decreased. Study results also showed association with soil organic matter had a relatively greater positive effect on ectomycorrhizae of the dry site than the moist sites. FOREST SCI. 27:442–445.

ADDITIONAL KEY WORDS. Woody residues, fuels, forest fire, soil quality, fungi, decomposition products, soil organic matter.

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NATIONAL WOOD FIBER NEEDS indicate substantial increases in demand for wood fiber-based products. This demand has resulted in increased efforts to remove all available fiber at harvesting sites. Intensive fiber removal or intense wildfire potentially reduces the parent materials (litter and wood residues) available for the production of organic reserves in forest soils. This reserve, primarily in the form of humus, decayed wood, and charcoal, has been shown critical to the support of both nonsymbiotic nitrogen fixing and ectomycorrhizal activities in forest soils of western Montana (Harvey and others 1976, 1978, 1979; Larsen and others 1978). Harvest and fire-caused reductions of organic materials on and

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