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# *A Simulation Approach for Predicting the Effect of Douglas-Fir Tussock Moth Defoliation on Juvenile Tree Growth and Stand Dynamics*

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ABSTRACT. A spatially dependent tree growth projection model was developed and used to simulate juvenile grand fir, *Abies grandis* (Dougl.) Lindl., Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and ponderosa pine, *Pinus ponderosa* Laws., in northern Idaho. Simulated experiments using the model examined the effects of Douglas-fir tussock moth, *Orgyia pseudotsugata* McDunnough, defoliation on stand dynamics during the first 40 years of stand development. The sequence and intensity of the defoliation episodes were varied for different combinations of age, stand density, and tree species composition at the time of the first defoliation. The results are summarized in statistical models which predict the long-term effects of tussock moth defoliation on stand dynamics. Results indicate that the insect regulates primary forest production by reducing stand biomass and by redistributing growth energy from host to nonhost trees by altering intertree competitive relationships to the advantage of nonhosts. FOREST SCI. 27:685–700.

ADDITIONAL KEY WORDS. *Pseudotsuga menziesii, Abies grandis, Pinus ponderosa, Orgyia pseudotsugata,* growth and yield.

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TO MAKE EFFECTIVE PEST MANAGEMENT DECISIONS, managers need to know the extent of pest damage. Recently developed simulation models (Stage 1973, Mitchell 1975) being used to assist forest management planning provides managers an opportunity to explore alternatives by projecting the outcomes of different stand treatment and pest management strategies.

Stand projections not accounting for losses attributable to various damaging agents will forecast stand conditions considerably different from reality. In Douglas-fir tussock moth defoliated stands, where outbreaks of varying intensity periodically recur in the same stands, overestimating stand growth and development is very likely (Stoszek and others 1977, Tunnock 1973). Repeated defoliation episodes in the same stands affect both tree growth and stand dynamics. Altering a host tree's relative competitive status by defoliation during the juvenile phase of stand growth may be especially important in mixed stands containing nonhost trees, since nonhost neighbors remain vigorous and can respond to a competitive advantage.

This study was initiated to provide insights into tussock moth-juvenile host tree

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interactions. A model was parameterized and used to simulate juvenile stand growth and development under varied management, environmental, and biological conditions, and to quantify the effects of tussock moth defoliation on juvenile stand growth and development.

## State of Knowledge

Most studies addressing the impact of insect defoliation on tree growth concentrate on stand growth losses associated with mature trees. This substantial direct influence on tree growth and mortality is well documented (Baskerville 1960, Batzer 1973, Kulman 1971, Pollard 1972, Wickman 1963). However, insect defoliators may also significantly influence the dynamics of stand development, and thereby indirectly affect tree growth and mortality as well. Smith (1977) studied several tussock moth defoliated mature stands and found that even light to moderate defoliation levels affected the dynamics of stand development by altering the competitive relationships among host and nonhost trees. Smith also suggested that differences in postdefoliation recovery rates between host species also caused long-term alterations in stand structure and composition.

Mattson and Addy (1975) and Stoszek and others (1977) discussed the possible role of defoliating insects as regulators of primary production in the forest ecosystem. Both papers indicate the importance of quantifying these regulatory effects. Mattson and Addy further state that defoliators' "feeding on and selective destruction of some plants and plant propagules, [has] a strong influence on community composition, density, and succession."

A simulation model based on the spatial distribution and growth of individual trees could be used to quantify growth losses and stand development changes resulting from tussock moth defoliation episodes. Such a model could represent defoliation-caused changes in stand development dynamics, as well as short-term growth losses. In addition, its outputs could be used to assess the effects of defoliation on competitive relationships between trees.

Mitchell's (1975) Tree and Stand Simulator (TASS) was adapted for this study to quantify growth losses and changes in stand dynamics due to defoliation. Because TASS emphasizes individual tree crown development, with height growth and radial increment being largely functions of crown characteristics, it is well suited to quantify the growth affects associated with a defoliating insect such as the tussock moth. The intertree competitive relationships in TASS allow the role of tussock moth defoliation to be explored and quantified.

## Methods

*Collection of Biological Data.*—The field portion of this study was conducted in northern Idaho on the Palouse and Clarkia districts of the St. Joe National Forest and on nearby state and private lands, an area recently subjected to a tussock moth outbreak (Tunnock 1973) resulting in a mosaic of defoliation levels. The majority of the field work was completed during 1975. To include the growth response during the postdefoliation period, measurements of defoliated trees were completed after the 1977 growing season.

To provide the desired range of tree and stand conditions, sampling strata were defined based on the following criteria: (1) tree species (Douglas-fir, grand fir, or ponderosa pine), (2) tree height (less than 10 ft, greater than or equal to 10 ft but less than 20 ft, and greater than or equal to 20 ft but less than or equal to 45 ft), (3) competitive status (open grown or nearly so, moderate competition, and heavy competition), and (4) defoliation level (light, moderate, severe, or none). Moderate competition was recorded when the subject tree was bounded on two sides by neighbors at least as large as the subject tree; heavy competition when the subject tree was bounded on four sides by neighbors at least as large as the subject tree. A neighbor was defined as a tree whose crown was touching the subject tree's crown. Light defoliation was considered to be less than 40 percent removal of new foliage; moderate defoliation between 40 to 70 percent removal of new foliage; and heavy defoliation as greater than 70 percent removal of new foliage (Table 1).

Percent slope, aspect, habitat type, and the locations of each plot tree relative to the subject tree were collected on each study plot. Height in feet, diameter in inches, and species were recorded for each subject and neighboring tree, and each subject tree was felled to enable more intensive stem and crown measurements. This procedure was similar to that used and described by Mitchell (1975). All study plots and trees were located in either *Abies grandis/Pachistima myrsinites* or *Thuja plicata/Pachistima myrsinites* habitat types (Daubenmire and Daubenmire 1968).

Only Douglas-fir, grand fir, and ponderosa pine tree species were intensively sampled; however, several other tree and shrub species occurred on many of the plots and their location, size, and species were recorded. Other commonly occurring coniferous species were western redcedar, *Thuja plicata* Donn, western larch, *Larix occidentalis* Nutt., lodgepole pine, *Pinus contorta* var. *latifolia* Engelm., and western white pine, *Pinus monticola* Dougl. *Ceanothus* spp. were the most frequently occurring shrubs.

*Defoliation Data*.—The most recent tussock moth defoliation in northern Idaho occurred during 1971 through 1973, with heaviest defoliation in 1973 and lightest in 1971 (Tunnock 1973). The outbreak was controlled with DDT in spring 1974.

Defoliation estimates for all sample trees were made in 1975, at least 2 years after the actual time of defoliation. Defoliated sample trees were located in large (≥one-tenth of an acre) patches of advanced regeneration within mature stands or adjacent to mature stands and were measured in the same manner as nondefoliated trees. Defoliation was measured as the proportion of foliage removed by branch length by year from a minimum of one randomly selected branch per whorl throughout the tree's live crown. No juvenile tree mortality directly attributable to tussock moth defoliation was encountered.

Except for defoliation relationships, model structure is essentially the same as that described by Mitchell (1975); therefore, readers are directed to that paper for detailed discussion of the structural and functional features of the simulator. Defoliation relationships and important links, assumptions, and aspects of model structure are examined in the following sections.

*Model Parameterization*.—TASS, originally developed for coastal Douglas-fir, was parameterized to model interior Douglas-fir, grand fir, and ponderosa pine using information from the trees described in Table 1. The link between defoliation and height growth for each host species will be covered in some detail because height is an important determinant of system behavior. The relationship between the proportion of grand fir foliage removed by tussock moth defoliation and the proportion of height growth reduction the succeeding year is shown in Figure 1. Although not presented graphically, the relationship between defoliation and proportion height growth reduction for Douglas-fir was linear over the range of the data. The following straight line equation was fit to the data:

$$P = 1.139*D - 0.1359$$

where

$P$ = proportion height growth reduction the year after defoliation
$D$ = proportion of foliage removed.

*TABLE 1. Characteristics of trees represented in sampling strata used in the field study to provide defoliation and growth data for simulations. Information taken in St. Joe National Forest 1975–77.*

| Species | Size | Competitive status | None | Light | Mod-erate | Severe | Total |
|---|---|---|---|---|---|---|---|
| | Numbers of sample trees represented in indicated category | | | | | | |
| | | | Defoliation level | | | | |
| Grand fir (86 trees) | Ht. < 10 ft | Open grown—light | 6 | 1 | 1 | 0 | 8 |
| | | Moderate | 18 | 2 | 3 | 2 | 25 |
| | | Heavy | 10 | 1 | 1 | 2 | 14 |
| | | | | | | | 47 |
| | 10 ft ≥ ht. < 20 ft | Open—light | 5 | 1 | 0 | 1 | 7 |
| | | Moderate | 5 | 1 | 2 | 1 | 9 |
| | | Heavy | 4 | 0 | 1 | 1 | 6 |
| | | | | | | | 22 |
| | 20 ft ≥ ht. < 40 ft | Open—light | 2 | 0 | 0 | 0 | 2 |
| | | Moderate | 6 | 1 | 2 | 1 | 10 |
| | | Heavy | 3 | 0 | 1 | 1 | 5 |
| | | | | | | | 17 |
| Douglas-fir (69 trees) | Ht. < 10 ft | Open—light | 5 | 1 | 1 | 0 | 7 |
| | | Moderate | 16 | 3 | 3 | 2 | 24 |
| | | Heavy | 3 | 1 | 1 | 0 | 5 |
| | | | | | | | 36 |
| | 10 ft ≥ ht. < 20 ft | Open—light | 2 | 0 | 1 | 0 | 3 |
| | | Moderate | 6 | 1 | 1 | 2 | 10 |
| | | Heavy | 4 | 0 | 1 | 0 | 5 |
| | | | | | | | 18 |
| | 20 ft ≥ ht. < 40 ft | Open—light | 1 | 0 | 0 | 1 | 2 |
| | | Moderate | 7 | 1 | 1 | 1 | 10 |
| | | Heavy | 2 | 0 | 1 | 0 | 3 |
| | | | | | | | 15 |
| Ponderosa pine (27 trees) | Ht. < 10 ft | Open—light | 4 | 0 | 0 | 0 | 4 |
| | | Moderate | 7 | 0 | 0 | 0 | 7 |
| | | Heavy | 2 | 0 | 0 | 0 | 2 |
| | | | | | | | 13 |
| | 10 ft ≥ ht. < 20 ft | Open—light | 2 | 0 | 0 | 0 | 2 |
| | | Moderate | 6 | 0 | 0 | 0 | 6 |
| | | Heavy | 1 | 0 | 0 | 0 | 1 |
| | | | | | | | 9 |
| | 20 ft ≥ ht. < 40 ft | Open—light | 1 | 0 | 0 | 0 | 1 |
| | | Moderate | 3 | 0 | 0 | 0 | 3 |
| | | Heavy | 1 | 0 | 0 | 0 | 1 |
| | | | | | | | 5 |

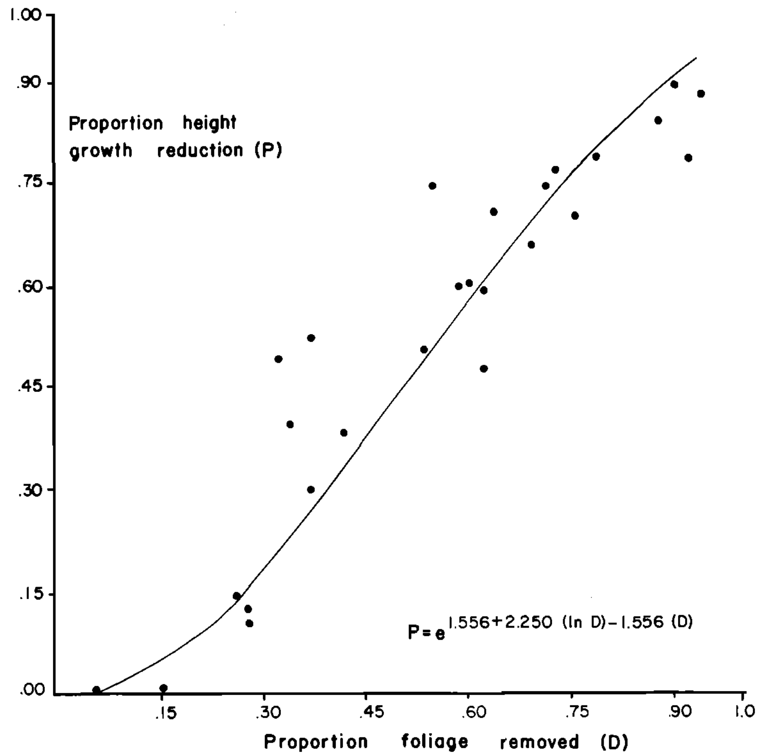


FIGURE 1. The relationship between height growth reduction (P) the following year and defoliation level (D) for grand fir. Data obtained after Douglas-fir tussock moth defoliation in St. Joe National Forest, 1975–77.

The equation produces negative height growth reduction values when the proportion of foliage removed is less than 0.12. Therefore, the curve was truncated such that 0 and 1 are the lower and upper limits for height growth reduction. Proportion of height growth reduction is actual height growth divided by expected height growth. For both species, expected height growth was calculated as the average height growth of the immediately preceding 3 years of nondefoliated sample trees.

Foliar volume is influenced by the length of time a species retains its foliage. The proportion of foliage for each species retained each year was measured by weight for the destructively sampled trees (Table 2). Grand fir had the longest period of needle retention followed by Douglas-fir and ponderosa pine. Foliar volume indexes the competitive stress a tree is under. This suppression index is FV/FVMAX, where FV is the calculated foliar volume and FVMAX is the calculated potential foliar volume with no competition.

## MODEL VALIDATION

Validating a simulation model is a difficult problem for many reasons (Naylor and others 1966). Once the model was parameterized for northern Idaho species and conditions, its outputs were matched against those of real stands. Data from three original study plots were not included in model development, and provided an independent data set to test the model outputs. These plots were chosen because they were relatively large (approximately 1/8 to 1/5 acre in size), provided the

*TABLE 2. Proportion of foliage retained by age of foliage by species. Information taken in St. Joe National Forest, 1975.*

| Age (years) | Grand fir | Douglas-fir | Ponderosa pine |
|---|---|---|---|
| 1 | 1.00 | 1.00 | 1.00 |
| 2 | 1.00 | 1.00 | 1.00 |
| 3 | 1.00 | 0.95 | 0.65 |
| 4 | 0.90 | 0.85 | 0.00 |
| 5 | 0.75 | 0.70 | 0.00 |
| 6 | 0.50 | 0.40 | 0.00 |
| 7 | 0.30 | 0.00 | 0.00 |
| 8 | 0.10 | 0.00 | 0.00 |

desired tree species composition, and were not defoliated. The actual and simulated frequency distributions of diameter and height (at actual plot age) for Douglas-fir, grand fir, and ponderosa pine on the three test plots are summarized in Table 3. Based on these comparisons, the healthy tree models were not shown to be invalid and thus adequately simulate undamaged, juvenile, grand fir, Douglas-fir, and ponderosa pine stand growth and development for the limited range of site conditions tested.

*Validation for Defoliation Effects.*—To validate defoliation effects on height growth, the sample tree data on differences in height accumulation after various defoliation levels were compared with the simulated effects of defoliation. The simulated trees represent conditions (age, size, crown position, site quality, crown volume) similar to the actual trees. The important comparison is patterns of height accumulation after defoliation. After moderate and even heavy defoliation, height accumulation has nearly returned to its original trajectory after 2 years. The model represents this pattern very well for both species (Figs. 2, 3). Although not presented graphically, there was little discernible effect of light defoliation.

## Simulated Design

*Experimental Design for the Simulation.*—By using the model to design experiments, the researcher controls all the variables in the system, and can change the level of those variables of interest in the analysis while holding external variables

*TABLE 3. Comparison of actual and simulated statistics for three plots in northern Idaho.*

| Plot number | Plot age | Kind of statistics | Diameter breast high | | | Total height | | |
|---|---|---|---|---|---|---|---|---|
| | | | $\bar{X}$ | s.d. | Range | $\bar{X}$ | s.d. | Range |
| | *Years* | | | *Inches* | | | *Feet* | |
| 1 | 18 | Actual | 1.6 | 1.1 | 0.3–5.2 | 12.5 | 6.7 | 3–32 |
| | | Simulated | 1.6 | 1.3 | 0.4–4.7 | 13.0 | 5.2 | 3–27 |
| 2 | 16 | Actual | 3.1 | 1.0 | 0.6–4.3 | 19.2 | 3.8 | 9–26 |
| | | Simulated | 3.2 | 0.8 | 1.6–4.4 | 19.9 | 3.2 | 11–25 |
| 3 | 28 | Actual | 5.9 | 1.8 | 0.8–8.3 | 28.1 | 5.6 | 18–38 |
| | | Simulated | 6.2 | 1.6 | 1.6–9.1 | 28.8 | 5.0 | 16–37 |

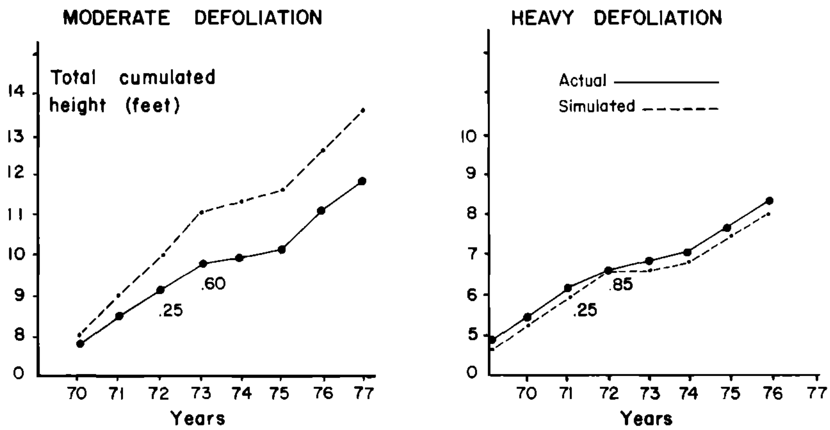


FIGURE 2. Actual and simulated height accumulation for two grand fir trees. Numbers within the figure indicate proportion of foliage removed by year.

constant. When statistical models are fit to these data, the underlying functional relationships can be more easily quantified and thus can be incorporated directly into decision-making models, allowing tussock moth defoliation impacts to be more accurately reflected.

Stand conditions such as density, age, and tree species composition were state variables because the level of these variables should influence system behavior subsequent to defoliation episodes. Also, forest managers can alter these variables through silvicultural treatments. Defoliation episodes of varying levels, duration, and periodicity were treated as external variables.

Table 4 gives the qualitative level of these variables and the experimental design. Three hundred separate simulations were required to complete this experiment. The levels given for each state variable in Table 5 approximate the actual level of the variable in the simulation.

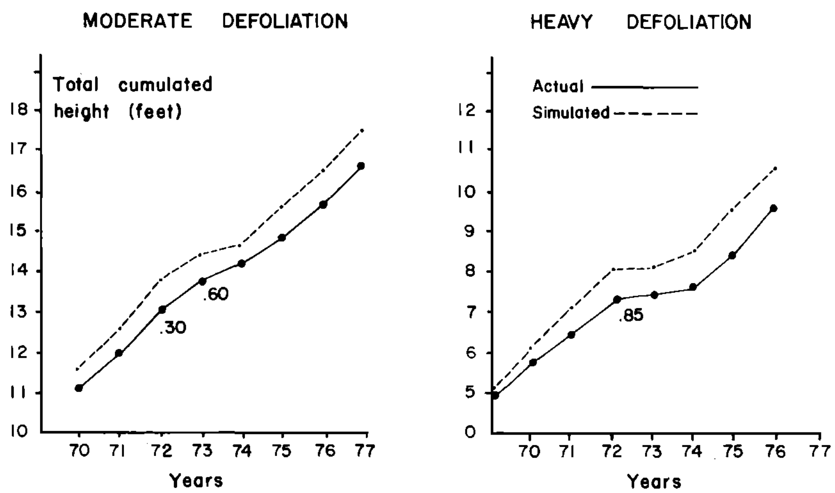


FIGURE 3. Actual and simulated height accumulation for two Douglas-fir trees. Numbers within the figure indicate proportion of foliage removed by year.

TABLE 4. *Experimental design for the simulations.*

| Species composition ($i$) | Defoliation ($j$) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | $X_{11kl}$ | $X_{12kl}$ | · | · | · | · | · | · | · | $X_{110kl}$ |
| 2 | $X_{21kl}$ | $X_{22kl}$ | · | · | · | · | · | · | · | $X_{210kl}$ |
| 3 | · | · | · | · | · | · | · | · | · | · |
| 4 | · | · | · | · | · | · | · | · | · | · |
| 5 | $X_{51kl}$ | $X_{52kl}$ | · | · | · | · | · | · | · | $X_{510kl}$ |

This design is overlaid with density ($k$) treatments and 3 replicates ($l$), where:

| | |
|---|---|
| $i = 1$ | Majority grand fir |
| $i = 2$ | Plurality grand fir |
| $i = 3$ | Majority Douglas-fir |
| $i = 4$ | Plurality Douglas-fir |
| $i = 5$ | Plurality ponderosa pine |
| $j = 1$ | No defoliation |
| $j = 2$ | Light defoliation at age 18 |
| $j = 3$ | Light defoliation at ages 18 and 28 |
| $j = 4$ | Light defoliation at age 28 |
| $j = 5$ | Moderate defoliation at age 18 |
| $j = 6$ | Moderate defoliation at ages 18 and 28 |
| $j = 7$ | Moderate defoliation at age 28 |
| $j = 8$ | Heavy defoliation at age 18 |
| $j = 9$ | Heavy defoliation at ages 18 and 28 |
| $j = 10$ | Heavy defoliation at age 28 |
| $k = 1$ | Dense stand (initial stocking 643 TPA) |
| $k = 2$ | Less dense stand (initial stocking 416 TPA) |
| $l = 1,2,3$ | 3 replicates of each treatment. |

*Other Simulation Conditions.*—The time frame for each simulation was 40 years. Site quality was held constant for all runs and approximated an *Abies/Pachistima* habitat type in terms of productivity.

Two approximate levels of stand density were achieved in the simulations by changing the initial stocking levels; the dense stand had 643 trees per acre and the sparse stand had 416 trees per acre. Even though only two initial stocking

TABLE 5. *Approximate level of each state variable in the simulated experiments.*

| State variable | Species composition (proportion by basal area at age 28) | | |
|---|---|---|---|
| | Grand fir | Douglas-fir | Ponderosa pine |
| $i = 1$ | 0.75 | 0.05 | 0.20 |
| $i = 2$ | .50 | .30 | .20 |
| $i = 3$ | .05 | .75 | .20 |
| $i = 4$ | .40 | .40 | .20 |
| $i = 5$ | .30 | .30 | .40 |

At stand age 28 each of the above species mixtures occurred under the following approximate density levels: CCF of 140 and 200 derived from initial stockings of 416 and 643 trees per acre, respectively.

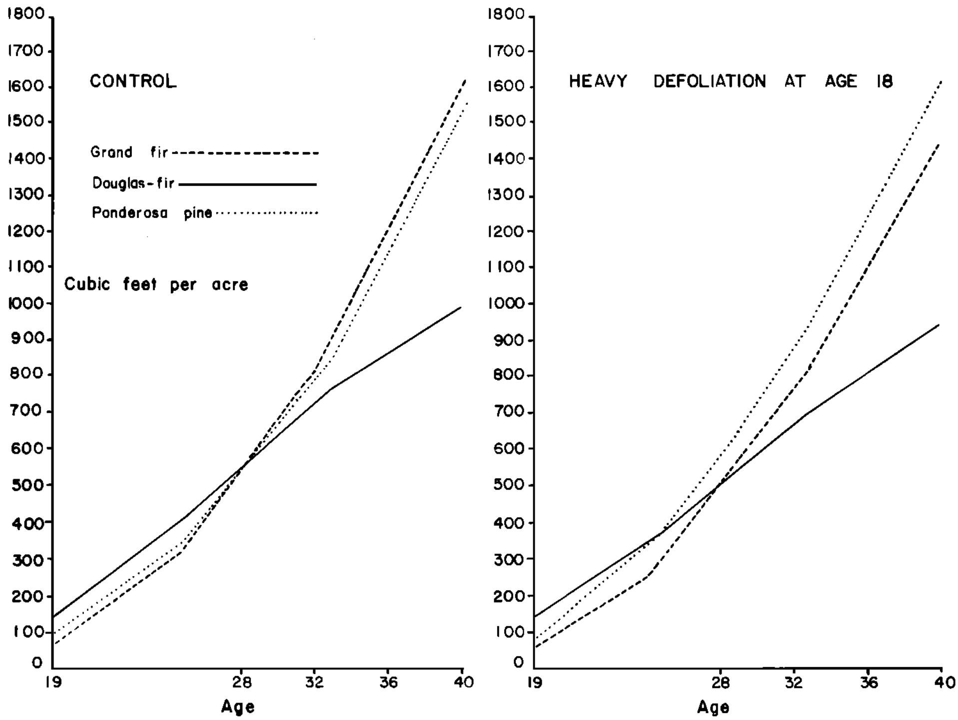


FIGURE 4. A comparison of cubic-foot volumes after the simulated effects of one Douglas-fir tussock moth defoliation episode in a mixed species stand. Stand density (CCF) is 198 (initial stocking = 643 trees per acre).

levels were used, the desired range of stand densities was produced at subsequent stand ages, rather than two identical levels, because species composition changed between individual simulations. Each tree species has different growth functions and this accounts for the majority of the differences in stand density given the same initial stocking. Stand density was expressed as Crown Competition Factor (CCF) (Krajicek and others 1961). The general defoliation patterns observed in the field were used in the model. The periodicity of simulated outbreaks was 10 years. No fertilization effect for nonhosts resulting from insect frass or bodies and increased needle fall was assumed.

*TABLE 6. The simulated effects of defoliation on two mixed species stands of different densities measured at age 40.*

| Heavy defoliation at age(s) | Stand density control at age 28 (CCF) | Volume reduction, host | Volume increase, nonhost | Volume reduction, stand |
|---|---|---|---|---|
| | | *cu ft/acre* | | |
| Control | 198 | — | — | — |
| 18 | — | 170 | 100 | 70 |
| 18 and 28 | — | 720 | 245 | 475 |
| Control | 158 | — | — | — |
| 18 | — | 132 | 65 | 67 |
| 18 and 28 | — | 589 | 146 | 443 |

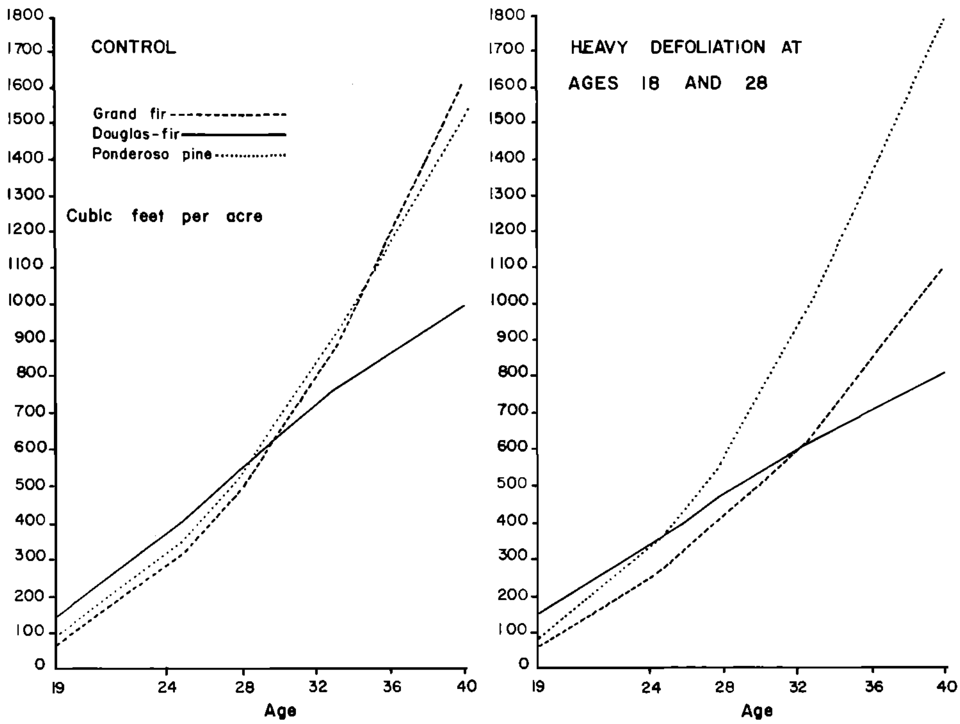


FIGURE 5. A comparison of cubic-foot volumes after the simulated effects of two Douglas-fir tussock moth defoliation episodes in a mixed species stand. Stand density (CCF) is 198 (initial stocking = 643 trees per acre).

## RESULTS OF THE SIMULATION

The simulated effects of defoliation on the growth and development of juvenile stands provide insights into the behavior of the system as well as into the tussock moth's role in influencing the stand dynamics of the system. The dynamic interaction of species composition, stand density, age of the stand at defoliation, and the number and intensity of the defoliation episodes is illustrated in selected figures.

*Frequency of Defoliation.*—Figure 4 contrasts the growth of a dense stand (initial stocking of 643 TPA) of nondefoliated mixed species composition with the same stand sustaining one heavy defoliation episode at ages 18 and 19. The nondefoliated stand exhibited the dynamic behavior characteristics of mixed species stands. The heavy defoliation episode beginning at age 18 somewhat alters stand development. The net effect measured at age 40 is summarized in Table 6.

Two defoliation episodes affect stand growth and development substantially more than a single outbreak (Figs. 4 and 5 and Table 6). Light defoliation had little impact on the volume accumulation of the stand. Volume accumulation in stands with moderate defoliation fell between the values associated with light and heavy defoliation.

*Stand Density.*—The results of a reduction in stand density, while species composition and defoliation episodes remained constant, are summarized in Table 6. One and two defoliation episodes showed progressively greater reductions in host volume with a concurrent increase in nonhost volume. However, these changes

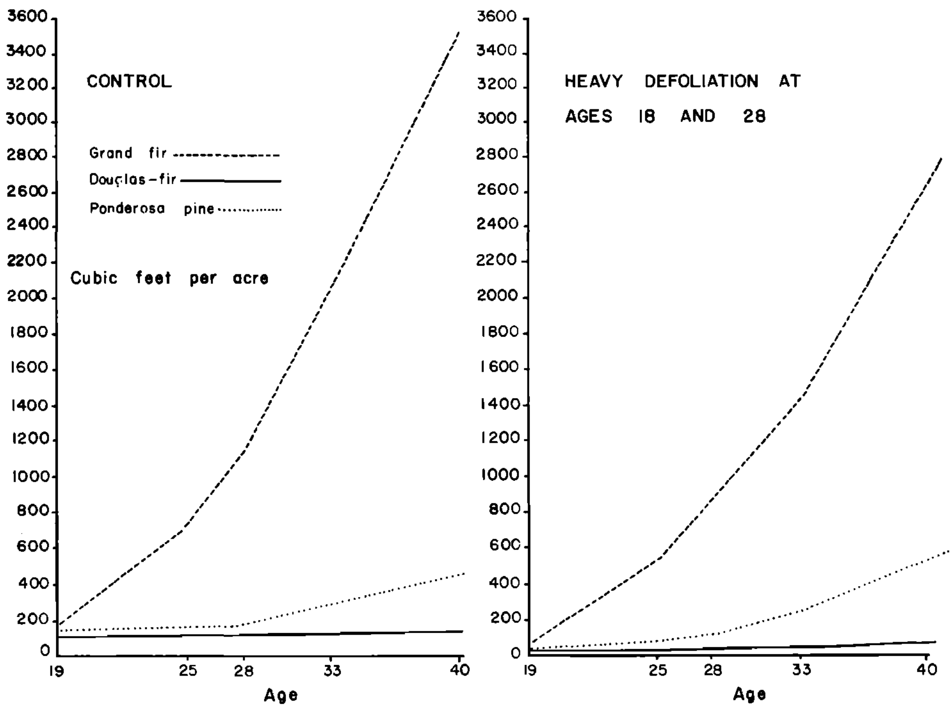


FIGURE 6. A comparison of cubic-foot volumes after the simulated effects of two Douglas-fir tussock moth defoliation episodes in a grand fir dominated stand. Stand density (CCF) is 203 (initial stocking = 643 trees per acre).

were slightly smaller in the less dense stands (Table 6). Based on the level of difference in density between the two case study stands, stand density has a small but discernible influence on stand behavior subsequent to tussock moth defoliation.

*Species Composition of the Stand.*—Species composition was also varied in the simulations. Although one defoliation episode caused relatively minor changes in the behavior of grand fir dominated stands, the effect of two episodes was substantial, as illustrated in Figure 6, and summarized in Table 7.

*TABLE 7. The simulated effects of defoliation on two stands of the same density and different species composition measured at age 40.*

| Heavy defoliation at age(s) | Control species compositon (percent basal area, age 28)[a] | Volume reduction, host | Volume increase, nonhost | Volume reduction, stand |
|---|---|---|---|---|
| | | cu ft/acre | | |
| Control | 30 GF; 30 DF; 40 PP | — | — | — |
| 18 | — | 170 | 100 | 70 |
| 18 and 28 | — | 720 | 245 | 475 |
| Control | 75 GF; 5 DF; 20 PP | — | — | — |
| 18 | — | 151 | 55 | 96 |
| 18 and 28 | — | 822 | 136 | 686 |

[a] CCF for both control stands is approximately 200 measured at age 28. Produced from an initial stocking of 643 trees per acre. GF = grand fir; DF = Douglas-fir; PP = ponderosa pine.

*TABLE 8. Alternative statistical models for predicting the long-term effect of tussock moth defoliation on juvenile stand growth and development.*

| Model | $R^2$ | Standard error of estimate as a percent of the mean |
|---|---|---|
| [1] $\ln(VRS) = 2.9924 + 1.1578*DS + 0.2618*DI - 0.00013*PH^2 + 0.00001*CCF^2 + 0.02664*PGF$ | 0.78 | 27.8 |
| [2] $\ln(1/PVR - 1) = 5.0954 - 1.1974*DS - 0.2774*DI - 0.00001*CCF^2 - 0.0268*PGF + 0.00013*PH^2$ | .79 | 25.0 |
| [3] $\ln(1/CPH - 1) = 9.0849 - 0.5739*DS - 0.4829*DI - 0.0477*PH + 0.0331*CCF - 2.2732*\ln(CCF) - 0.0002*INT^{a}$ | .88 | 19.0 |
| [4] $\ln(VRH) = 2.0898 + 0.8049*DS + 0.3629*DI + 0.1528*\ln(CCF) + 0.4066*\ln(PGF)$ | .82 | 21.4 |
| [5] $\ln(1/PHR - 1) = 5.2143 - 1.0029*DS - 0.4718*DI + 0.0002*PH^2 - 0.00001*CCF^2 - 0.6104*\ln(PGF)$ | .70 | 39.6 |

where:

VRS = cubic-foot volume reduction per acre for the stand at age 40
PVR = proportion of cubic-foot volume reduction for the stand at age 40
CPH = change in proportion host at age 40
VRH = cubic-foot volume reduction per acre for the host species at age 40
PHR = proportion of cubic-foot volume reduction for the host species at age 40
DS = defoliation sequence:
= −2 if control (no defoliation)
= −1 if defoliated at age 18
= 1 if defoliated at age 28
= 2 if defoliated at both age 18 and 28
DI = defoliation intensity:
= −2 if control (no defoliation)
= −1 if light defoliation
= 1 if moderate defoliation
= 2 if heavy defoliation
PH = percent host species by basal area at beginning of first defoliation episode
= 1 if nondefoliated (control)
CCF = crown competition factor at the time of first defoliation episode
= 1 if nondefoliated (control)
PGF = percent grand fir by basal area at the time of first defoliation episode
= 1 if nondefoliated (control)
INT = an interaction term = PH*CCF

[a] All variables, except this term, are significant at an $\alpha$ of 0.01. The interaction is significant at an $\alpha$ level of 0.16.

*Predictive Equations.*—Although graphical representations of case study stands are useful for understanding the general behavior of the simulated system, only a limited number of the 300 required for this study are practical. Thus, the results of all simulations are summarized in Table 8.

The effect of defoliation on stand growth and development can be expressed in various ways; therefore, five different equations are given in Table 8. The dependent variables were selected because they are good indicators of defoliation effects and are helpful in summary analysis of the simulations. The independent variables in these equations were chosen because the simulated experiments, outlined in Table 4, were designed to provide an acceptable range of these variables. The parameters were estimated using least squares regression analysis. The dependent variables in Equations 2, 3, and 5 were transformed such that the derived predicted values are mathematically bounded by 0 and 1.

## Discussion

Defoliation-induced changes varied according to stand conditions at the time of defoliation. Increased growth of the nonhost ponderosa pine partially compensated for the reduced host species volume. The intertree competitive relationships were altered to the advantage of nonhost trees.

Defoliation effects are cumulative; that is, the effect of two episodes is not simply twice that of one outbreak. Rather, the vigor and position of the host trees were reduced by the first defoliation; this change is reflected when the second outbreak is applied. This important feature identified by simulation of defoliation impacts is generally not considered in more common statistical approaches which predict impacts as a function of various defoliation and stand variables, and ignore the changing behavior of the stand.

Stand density also discernibly influences stand behavior subsequent to tussock moth defoliation, especially when the stand is defoliated twice. Because defoliation speeds up vertical differentiation of the stand, host trees occupying lower crown positions fall farther behind their larger neighbors. In dense stands, more of these small trees died from suppression. While their loss reduces total volume, merchantable volumes are not reduced correspondingly.

Change in proportion host volume at age 40 is perhaps the dependent variable that best expresses defoliation-induced changes in stand dynamics (Equation 3, Table 8). Change in proportion host is simply the difference in the proportion host volume in the control (nondefoliated) and the defoliated stand.

Stands containing a large proportion of nonhosts at the first defoliation episode show the greatest change in proportion host at age 40 because relatively more ponderosa pine were available to respond to a temporary competitive advantage (Fig. 7). Thus, not only was host volume directly reduced by defoliation, it was further reduced by a lessened competitive situation for hosts and a corresponding improvement for nonhosts.

Stand density at the first defoliation also influenced the response of the stand to defoliation (Fig. 8). The change in proportion host increases until just after crown closure (a CCF value of approximately 125), and then decreases. In open stands, competition is not significant and ponderosa pine does not benefit from a "defoliation thinning effect"; therefore, the change in proportion host derives primarily from defoliation-caused reductions in host volume. As stand density increases, competition begins to affect ponderosa pine growth and it increasingly responds to an improved competitive status, up to a point. After crown closure, stand density increases and ponderosa pine loses live crown and thus its ability to respond to a temporary competitive advantage. At high stand density there is little increase in nonhost volume, and the change in proportion host again results from defoliation-caused volume reductions.

The interaction between stand density and species composition and the resulting influence on change in proportion host is shown in Figure 9. One can visualize the probable interaction by inspecting the separate relationships between change in proportion host and species composition and stand density shown in Figures 7 and 8. An increase in nonhost, the upper curve in Figure 9, causes change in host volume to be greater on a proportional basis and shifts the inflection point to the left. The difference in area under the two curves is attributed to increased

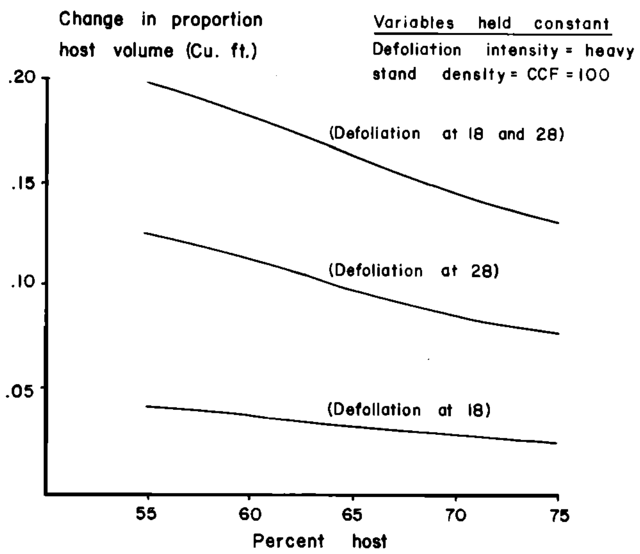


FIGURE 7. Predicted change in the proportion of host volume at age 40 for different tree species composition and defoliation sequence.

volume growth for the more abundant ponderosa pine and a resulting competition-caused reduction in host volume. The inflection point shift toward less dense stands in the mixed species stand is caused by species dependent differences in tolerance to shading and by changes in individual tree spatial arrangements. Ponderosa pine loses live crown faster than the host species as stand density increases. This, and the fact that in mixed stands an individual ponderosa pine is more likely to compete with another ponderosa as well as with hosts, shifts the inflection point.

The two curves intersect at a CCF of 240 (Fig. 9). Intersection occurs at high stand density because the ponderosa pine does not respond to a defoliation-in-

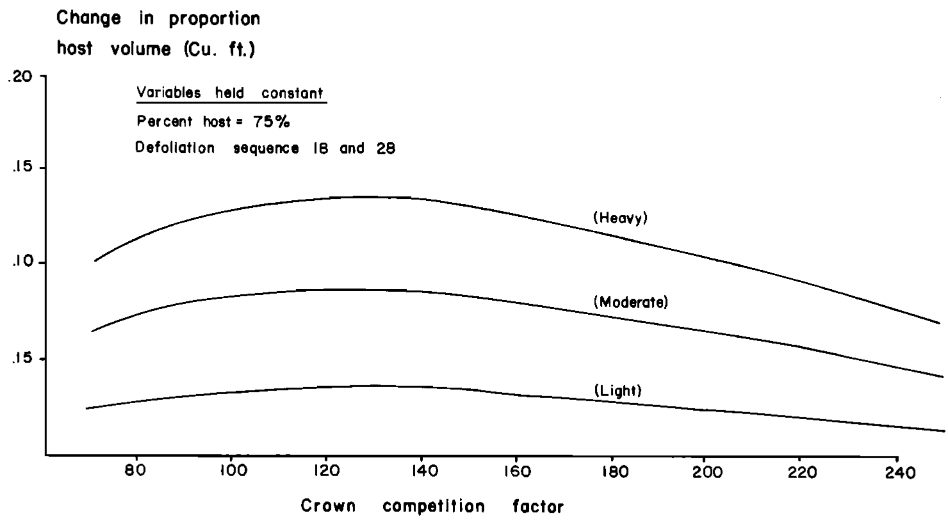


FIGURE 8. Predicted change in the proportion of host volume at age 40 for different stand densities and defoliation levels.

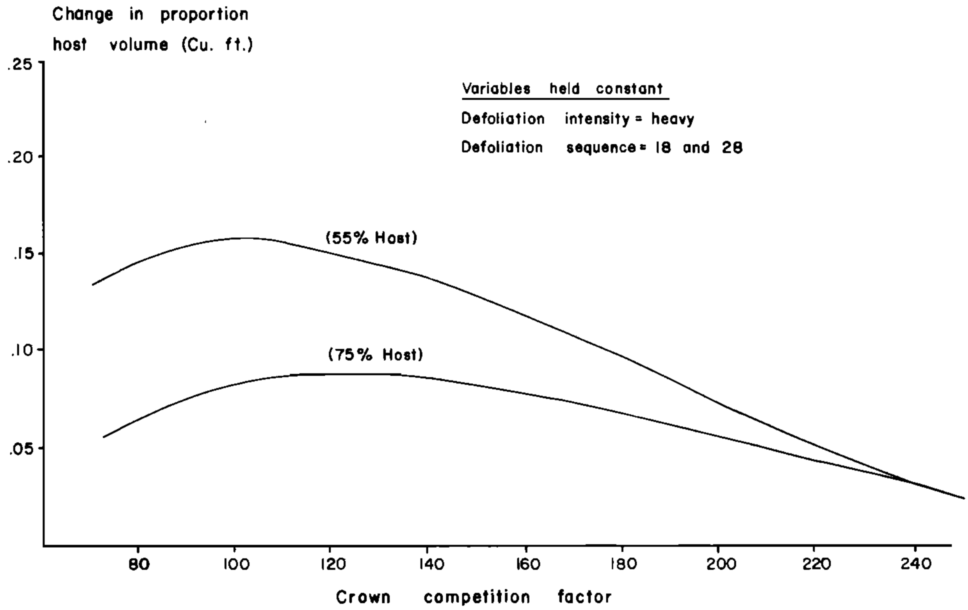


FIGURE 9. Predicted change in the proportion of host volume at age 40 for different tree species composition and stand densities.

duced temporary competitive advantage, regardless of species composition. Therefore, the change in proportion host at high stand density is due to defoliation-caused reductions in host volume, and on a proportional basis is the same for both species mixtures. The results of this study support Smith's (1977) thesis that even light to moderate defoliation levels may affect the dynamics of stand development. If tussock moth defoliation directly resulted in tree mortality, the effect of defoliation on stand dynamics would be greater than is portrayed in this study.

## SUMMARY AND CONCLUSIONS

The tussock moth regulates primary productions and biomass accumulation over time, primarily by redistributing growth energy from host to nonhost trees by altering competitive relationships to the advantage of nonhost trees. The greatest reduction in total volume occurs after two defoliation episodes. This situation requires the mature stand acting as an insect source to remain susceptible for at least one tussock moth cycle. An important management implication is apparent. Leaving susceptible mature stands untreated significantly increases defoliation-induced changes in adjacent young stands and patches of advanced regeneration. Silvicultural systems, such as group selection, that result in a mosaic of age classes should be applied cautiously on "high-risk" tussock moth sites.

The use of a high resolution simulation model to assess the growth response of individual trees to defoliation and to show how these individual responses collectively affect stand behavior over time has been demonstrated. Using the growth simulator to replicate field situations is potentially the most powerful application of the model because simulated outputs can help identify and bridge information gaps.

Although this paper has concentrated on using the model to quantify the dynamic interactions of juvenile stand growth and development under tussock moth defoliation episodes, the general approach potentially has much wider application. For example, the model may also project the effects of numerous other natural influences on stand behavior. One obvious use is in estimating the effects of other defoliating insects, such as the spruce budworm, on juvenile stand growth and development. The process would be very similar to the study here described. Furthermore, this model, calibrated to include the effects of various other forest pests (such as defoliating diseases, shoot and bud damaging insects, mechanical damage, and growth impacting fungi), can be used to explore the role of these agents in altering future dynamic behavior of the forest.

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