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Tree Mortality and Top-kill Related To Defoliation by the Douglas-Fir Tussock Moth in the Blue Mountains Outbreak

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usda douglas-fir tussock moth research & development program

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Reference Abstract

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Tree mortality and top-kill resulting from defoliation by the Douglas-fir tussock moth in 1972 and 1973 in the Blue Mountains has been measured in the field annually since 1973 on a series of permanent plots. This paper summarizes tree mortality and top-kill through 1976. The study was designed to use defoliation intensity in 1972 and 1973 as a predictor of tree mortality and top-kill during and after the outbreak. Results of the study show that the pattern of tree mortality conforms to that of previous outbreaks studied in California white fir. Mortality increases with defoliation intensity, and most mortality occurs in trees defoliated 90 percent or more. Mortality summarized by four defoliation classes showed that areas classed as having heavy defoliation suffered 72 percent (number of trees) of the stand killed: moderate, 5.2 percent killed; light, 6.3 percent killed; and very light, 11.1 percent killed. The data indicate that Douglas-fir suffers proportionally more tree mortality than grand fir. Douglas-fir comprises about 20 percent of the stand on the plots, but the total percent stand mortality almost equals grand fir mortality.

The pattern of top-kill is similar to that of tree mortality; trees suffering most defoliation have the highest incidence and severity of top-kill. A breakdown by defoliation class in surviving trees shows that top-kill incidence was as follows: heavy defoliation class, 35.4 percent top-kill; moderate, 11.9 percent; light, 4.6 percent; and very light 5.9 percent. And Douglas-fir suffered twice as much top-kill as grand fir.

KEYWORDS: Insect damage (-forest, defoliation damage, Douglas-fir tussock moth, *Orgyia pseudotsugata*, Douglas-fir, *Pseudotsuga menziesii*, grand fir, *Abies grandis*, Oregon (Blue Mountains), Washington (Blue Mountains).

RESEARCH SUMMARY

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The data gathered in this study can be used for determining net impact on stand growth, but it is primarily meant to show the relation of insect populations (Mason 1976), through the pathway of tree defoliation, to tree mortality and top-kill. The effects of individual-tree damage on stand productivity through a rotation period is a study in itself and will be reported elsewhere.

Tree mortality was related to degree of defoliation, with 90 percent or more of the mortality occurring in trees 90-percent or more defoliated. Mortality caused by secondary attacks of bark beetles was concentrated in grand fir suffering 75-percent or greater defoliation; but, in Douglas-fir, mortality caused by Douglas-fir beetle was more evenly distributed in all defoliation classes. Mortality caused by bark beetles was not as high as in some past outbreaks in California (Wickman 1963). The intensive logging activity throughout the outbreak area since 1973 and 2 years of subnormal precipitation are thought to have contributed to increases in Douglas-fir beetle populations. Tree mortality was fairly evenly distributed through all d.b.h. classes.

Tree mortality as related to the defoliation classes mapped in 1972 showed that the heaviest mortality occurred in the areas classed as having heavy defoliation (38.6 percent). Mortality in moderately and lightly defoliated areas was lower (10.6 and 5.3 percent, respectively). Some areas with very light defoliation suffered mortality in 1973 similar to that of areas in the heavy defoliation class in 1972, but the average for the entire class (12.6 percent) was still about one-third as high as in heavy defoliation class areas. Differences were found in the calculated mortality levels for each class depending on how plots were stratified. The most accurate method was to stratify individual plots within a cluster into their respective defoliation classes: all moderate class plots in the moderate class strata, all light class in the light strata, and so on. A mapped defoliation class was often composed of a mixture of several classes. When tree mortality was related to defoliation classes composed of stratified plots, the following levels of mortality were determined: heavy defoliation class areas, 72 percent; moderate, 5.2 percent; light, 6.3 percent; and very light, 11.1 percent. The greatest discrepancies between the two summaries are in the heavy and moderate classes. Tree mortality in the heavy areas (72 percent) was similar to patches of mortality found in an earlier California outbreak (Wickman et al. 1973).

Mortality was related to year and years of defoliation (1972 and 1973). Heavy defoliation class areas suffered their most severe defoliation in 1972, and the highest mortality rates for any class during the outbreak were found in these areas. Little additional defoliation occurred on heavy class areas in 1973, so the inference is that 1972 defoliation caused some of the most severe tree mortality of the outbreak. In 1973, more acres were defoliated, and defoliation was especially intense in those areas having a high proportion of Douglas-fir in the stand. Some of these areas had patches of tree mortality similar to 1972 heavy defoliation class areas.

One significant finding of the study, as it relates to forest management practices in the Blue Mountains, was the differential mortality between grand fir and Douglas-fir. In 1972, mortality of the two species was about equal; but after 1973 defoliation, Douglas-fir suffered much higher rates. This is particularly significant because Douglas-fir averaged only 19.7 percent of the stand in our study areas, but suffered almost the same total amount of mortality as grand fir by 1976. We found that, individually, Douglas-fir trees are probably not more susceptible to mortality from a given level of defoliation. Some attribute of environmental conditions reflected by stand composition in terms of percent Douglas-fir probably contributes to this higher loss and possibly even the higher mortality of grand fir when it is associated with Douglas-fir. We explored this relation further and found that stands containing 50 percent or more Douglas-fir suffered the highest mortality rates in 1973. Regression analysis indicated that a positive and significant correlation did exist between total mortality of both host species and the percent of Douglas-fir in the stand. This relation may not be the same for other geographical areas and should be studied further, but it does have some strong implications for forest managers in the Blue Mountains.

Five top-kill classes were related to individual-tree defoliation categories. The most severe top-kill occurred in the trees suffering highest amounts of defoliation, and leader damage was the most common class of top-kill followed by the class that had 1 to 10 percent of the crown top-killed. Severe top-kill (greater than 25 percent of the crown) amounted to 2 percent of the total for both species, and most of this damage occurred in trees defoliated 75 percent or more.

Top-kill class was also related to d.b.h. class. In grand fir, 17 percent of the trees with larger than 12-inch d.b.h. suffered top-kill exclusive of leader-only damage. In Douglas-fir, 13 percent of trees with larger than 12-inch d.b.h. suffered top-kill exclusive of leader-only damage. Long-term effects of top-kill are probably more serious in trees with smaller than 12-inch d.b.h. In grand fir, 4.3 percent of the trees in the 1- to 6-inch d.b.h. class and 12.9 percent of the trees in the 7- to 11-inch d.b.h. class suffered top-kill exclusive of leader-only damage. In Douglas-fir, the concentration of top-damage in these d.b.h. classes was much higher at 14.6 and 21.1 percent, respectively.

Distribution of top-kill in the four defoliation classes was also summarized. When top-damage was stratified by the mapped defoliation class areas most of the top-kill occurred in Douglas-fir, and the top damage was fairly evenly distributed through all four classes for both species. When stratified by the individual-plot defoliation class areas, top-kill was concentrated in the heavy class for grand fir and the heavy and moderate classes for Douglas-fir.

When all grand fir and Douglas-fir top-kill are compared, the trends for each species are similar; but Douglas-fir suffered more than double the total amount of top-kill, exclusive of leader-only damage.

Top-kill was also related to mortality caused by bark beetles after the outbreak. Small sample size prevented statistical analysis, but trees of both species with more than 50 percent of the crown top-killed apparently have a high probability of being killed by bark beetles the first several years after a Douglas-fir tussock moth outbreak.

The main conclusion from the study is that defoliation intensity can be used as a predictor of tree damage, both for individual trees and defoliation class areas. Heavy defoliation in 1972 caused more severe damage than similar defoliation on some light and very light class areas in 1973, even though 1973 populations were more dense. This anomaly was most likely related to higher larval survival rates in 1972 than 1973 (Mason 1976). Defoliation in 1973 was also more intense on Douglas-fir in the light and very light defoliation class areas; and this relates to very high population levels in these areas in 1973 (Mason 1976), differential larval feeding behavior (Beckwith 1976), and probably physiographic features of the sites.

Introduction

The Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough), is a native insect and major defoliator of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, and true fir, *Abies* spp., forests in western North America. Outbreaks of this insect have periodically damaged large amounts of timber; since 1945, forest managers have been concerned enough with the damage potential of the insect to treat most major outbreaks with chemicals.

Most individual tussock moth outbreaks pass through three phases, which usually last about 1 year each. They are: a release phase, with rapid population growth; an outbreak phase, characterized by peak population densities; and a decline phase, ending in complete population collapse (Mason 1974, 1976; Wickman et al. 1973).

Several studies of tree damage have been made after past outbreaks; but all have been in California on one host, white fir, *Abies concolor* (Gord. and Glend.) Lindl., and only during or *after* the decline phase (Wickman 1963, Wert and Wickman 1970). Because most outbreaks are discovered from visible defoliation, the study of damage has usually been a postmortem tabulation after the outbreak collapses. In two California outbreaks, a study of damage was started during the decline phase, so some estimates of individual-tree defoliation were possible (Wickman 1963).

Recently a very large outbreak occurred in the Blue Mountains of northeastern Oregon and southeastern Washington. The infestation was detected and mapped during the outbreak phase and thus afforded a unique opportunity for study of the relation of this insect's population dynamics to tree damage. Life tables for declining populations of the tussock moth in this outbreak were recently published (Mason 1976). Mason determined that defoliation intensity in the first year that the outbreak was detected was a predictor of population trend the next year. An integral part of such prediction, for pest management purposes, is the relation between population level and trends, reflected in defoliation intensity. Levels of defoliation for individual trees can then be used to predict expected tree damage. Southwood (1966) points out the difficulties of determining this relation and recommends that correlation of the two variables should ideally be made in the same location. He does not have a suggestion for doing this under the outbreak conditions we encountered, however. Therefore, the objective of this companion study was to use defoliation intensity in 1972 and 1973 as a predictor of tree damage during and after the outbreak. In this paper, I summarize two important aspects of tree damage: tree mortality and top-kill as they are related to defoliation. The study is unique in that the relations are also mathematically represented elsewhere in model form.[1/] Growth reduction resulting from defoliation will be reported later.

1/ Overton, W. S., and J. J. Colbert. 1976. Tussock moth population dynamics and tree and stand interaction model. Annual Progress Report, Douglas-fir Tussock Moth Expanded Research and Development Program, Portland, Oregon.

Methods

LOCATION AND DEFOLIATION CLASSES

As reported by Mason (1976), these studies were conducted in the Blue Mountains of northeastern Oregon (some of my plots are also located in southeastern Washington). Plots were located in the Umatilla National Forest and the Wallowa-Whitman National Forest. The zone of my study covered about a 100-km transect of the tussock moth outbreak mapped by the USDA Forest Service in 1972 (fig. 1). They mapped the outbreak according

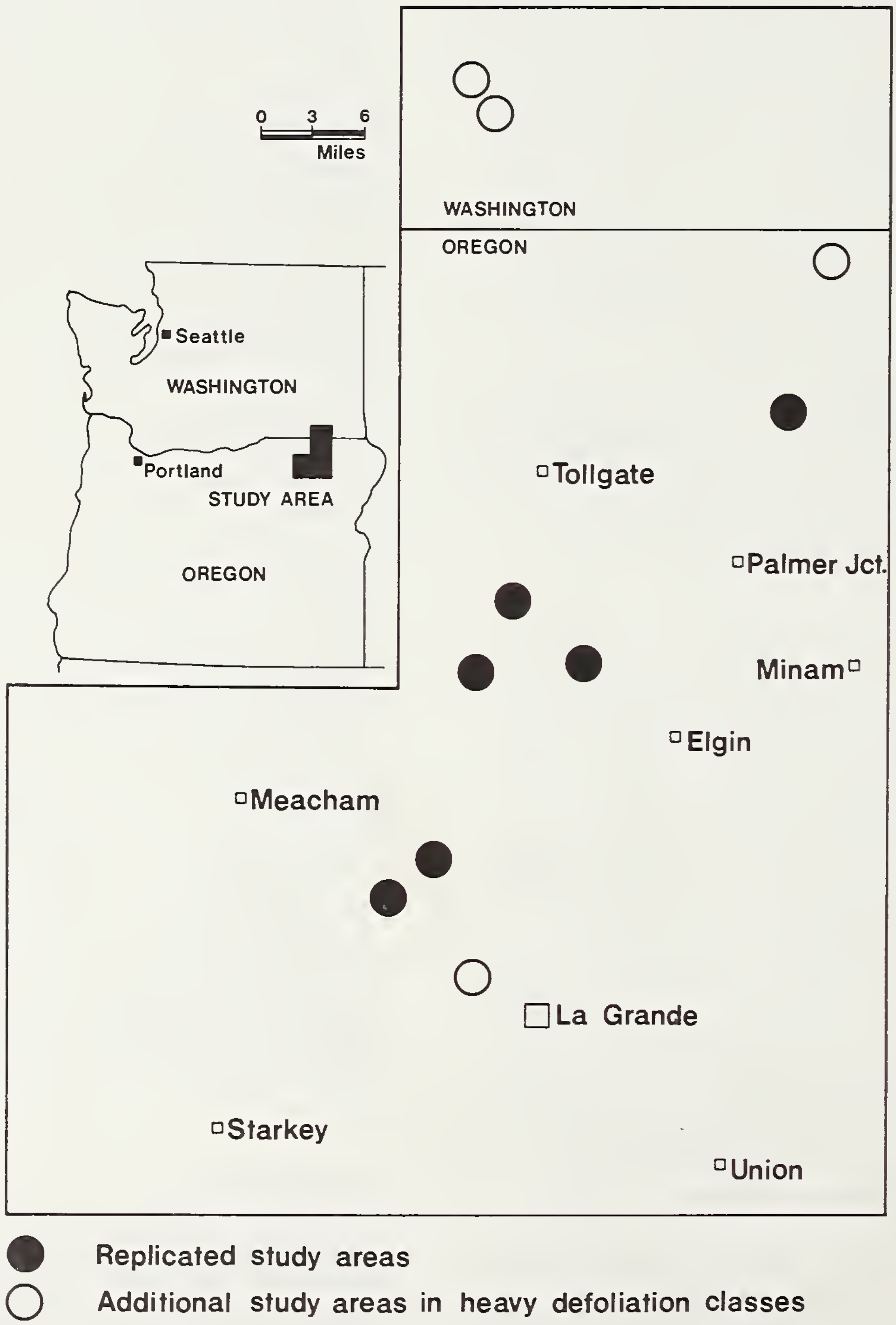


Figure 1.--Map showing location of tree-damage plot clusters in northeastern Oregon.

to visible defoliation from aerial and ground surveys in fall 1972 and stratified it into defoliation classes. Mason (1976) defined these classes as: *heavy*, >50 percent of trees completely defoliated; *moderate*, >50 percent of trees one-quarter defoliated; *light*, visible defoliation (from the air) only; and *very light*, no visible defoliation, but new egg masses present.

EXPERIMENTAL DESIGN

The study was designed to use plots established for population studies by Mason as follows (from Mason 1976): "Six replications were established over the zone of study. Four replications contained study plots in each of the four defoliation classes. The remaining two replications contained only three study areas each because areas of heavy defoliation could not be located. Thus, 22 study plots were involved in the investigation. All plots in a replication were located approximately within the same square mile. They were established between 1 219- and 1 524-m elevation either in pure forest stands of grand fir, *Abies grandis* (Dougl.) Lindl., or in stands with a mixture of grand fir and Douglas-fir." I expanded my plot areas to include heavy class areas at the south end of the outbreak and in the Wenaha back country of Oregon and Washington, because areas in this class were being salvaged rapidly by the Forest Service wherever roads existed. I also included one plot area of heavy defoliation class in a pure Douglas-fir stand at 850-m elevation at the south end of the transect. At this point my design differs from Mason's because of the nature of tree damage studies. Clusters of 15 trees were used for the population work; but the damage studies were conducted on clusters of 1/50th-acre, circular plots superimposed around each of Mason's (1976) plots. Each replicate contained a cluster consisting of 5 to 25 ($\overline{X}$ = 10) plots shaped as a square, U, or straight line depending on the available acres of forest type and damage. Plots were 1 chain (20.12 m) apart, center to center. Every plot was staked in the center, and every tree over 1-inch (2.54-cm) d.b.h. was tagged at breast height for future location and identity.

None of the study areas was treated by insecticide although spray tests and control operations were conducted in nearby forests in 1973 and 1974.

SAMPLING TECHNIQUES

The following information was recorded for each tree: species (for both host and nonhost), diameter at breast height (to the nearest .2 inch or .5 cm), crown class (dominant, codominant, intermediate, suppressed), percent defoliation in 1972 and 1973 (see fig. 2), percent top-kill, year of death, and cause of death. Plot establishment began in August-September 1972 and continued through May 1974 after the population plot areas were established. First, priority was given to establishing plots in heavy, moderate, and light defoliation class areas. Four plot clusters were established in fall 1972; the remainder were located and measured before bud burst in spring 1973 so that 1972 defoliation estimates could be made. Plots in very light defoliation areas were not established until fall 1973 or early spring 1974 before bud burst because defoliation was not evident until the summer of 1973. Ultimately, 342 plots con-

Figure 2.--Defoliation categories used in estimates, for individual trees, of percent of crown totally defoliated, 1972-73. Inset shows partial defoliation of lower branches.

taining 2,686 grand fir and Douglas-fir trees were established.

In other tree damage studies conducted after tussock moth outbreaks, I have noted that considerable tree mortality occurs at the height of the outbreak, but it also continues for about 4 additional years (Wickman 1963). Consequently, the plots in this study were measured twice a year for tree mortality and top-kill in the spring and fall starting in fall 1972 through 1974 to date and identify cause of mortality more precisely. Then they were measured annually each fall in 1975 and 1976.

Tussock moth feeding progresses from new to older foliage, and old foliage is usually not consumed until all new foliage has been destroyed. Partly because of a higher concentration of new foliage, defoliation occurs first on the outside of the crown and in the top of the tree and then progresses inward and downward depending on larval densities. This defoliation pattern is more pronounced in true firs than Douglas-firs but is generally similar for both species. Defoliation estimates of each plot tree were recorded as one of seven classes representative of percent of crown length totally defoliated (fig. 2).

In fall 1972 or before bud burst in 1973, individual trees on the plots were classified on the extent of defoliation caused by 1972 larval populations; again in fall 1973 or early spring 1974, they were classified for defoliation caused by 1973 larval populations. No measurable defoliation was caused by the few scattered 1974 larval populations. All estimates were made by one person, eliminating interobserver variation. The use of seven illustrated classes reduced intraobserver variation.

Cause of death during the 1972-74 examinations was assumed to be tussock moth in trees defoliated 50 percent or more if we found no evidence of bark beetles, such as larvae under the bark as high on the bole as could be reached with an axe (3 m) or woodpeckering on the upper bole, emergence holes, and pitch streaks on currently attacked trees. Cause of death in 1974 and after was easier to determine because of fading of the new growth of foliage. In both years, color of cambium was also used to help determine time of death. Brown streaks or completely brown cambium in the base indicated death, as found by Belyea (1952) in balsam fir killed by spruce budworm defoliation. In trees killed by secondary beetle attack, year of death was the year of attack.

Top-kill was estimated with the aid of binoculars each fall starting in 1974. By that time, enough foliage had recovered for us to judge whether a top was dead or just defoliated. Top-kill was assigned one of the following six classes: leader only; 1 to 10 percent; 11 to 25 percent; 26 to 50 percent; greater than 50 percent; older top-kill (this was assigned at the time of plot establishment).

ANALYSIS

The tree defoliation data were summarized by the four mapped defoliation classes and tested for significant differences, among defoliation classes for both tree species and the 2 years of defoliation by analysis of variance. A t-test was also made to compare differences of defoliation of grand fir and Douglas-fir. Tree mortality and top-kill data were summarized several ways. They were tabulated by host species and by cause of death as related to individual-tree defoliation estimates. This type of summary is useful for predictive purposes and for modeling the relation between population densities and expected branch and tree defoliation and then relating defoliation to expected damage--the ultimate goal of this study.

The tree mortality data were also summarized by four defoliation classes aerially mapped by pest managers in 1972. Although mapped classes form a relatively low-resolution model, in practical terms this is the way most outbreaks are categorized. This analysis is useful for broad predictions of expected damage in the aerially mapped classes used by pest managers. Plots were also stratified by the four defoliation classes according to how they fell within clusters of plots. For instance, a moderate defoliation class was composed only of plots classified as moderate on the ground, even though in reality an aerially mapped moderate class may have been a mosaic of heavy, moderate, and light defoliation classes. Although artificial in practice, this last method of analysis is the only way the data can be compared with earlier studies in California, and it is a more accurate record of mortality, acre by acre.

Chi-square tests were made of differential mortality between grand fir and Douglas-fir by percent tree defoliation. The possible effects of species composition in the stand contributing to these differences were explored using a regression analysis. Top-kill was tabulated and summarized in a manner similar to tree mortality.

Results and Discussion

DEFOLIATION

Average individual-tree defoliation estimates for each of the four defoliation classes for 1972 and 1973 are presented in figure 3 for both species. Heavy areas did not receive additional defoliation of other than current foliage in 1973, even though some older foliage was available. Grand fir in moderate areas received 7-percent additional 1973 defoliation, and Douglas-fir trees in the same class averaged about 20-percent additional defoliation. Higher defoliation in 1973 was particularly noticeable for both species in previously light and very light areas; again, Douglas-fir suffered almost double the amout of defoliation as grand fir.

The average defoliation, with standard errors of the means, for each cluster of plots in each class was plotted for 1972 and 1973 estimates to show the variation within and between classes (figs. 4 and 5). The 1972 data shown in figure 4 fall into expected patterns by defoliation class. Standard errors of the mean are 10 percent or less; little spread and no overlap of mean percent defoliation occurs for the four classes. When 1973

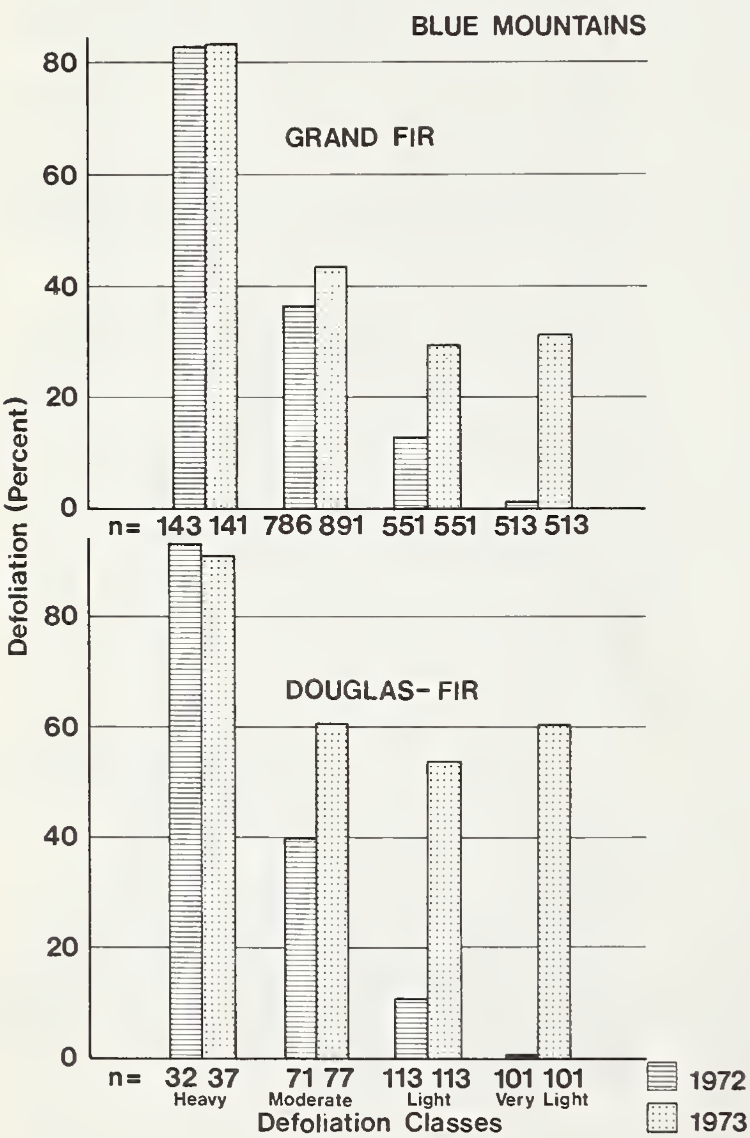


Figure 3.--Average (weighted by number of trees in each class) 1972 and 1973 defoliation of all plot trees by 1972 defoliation classes.

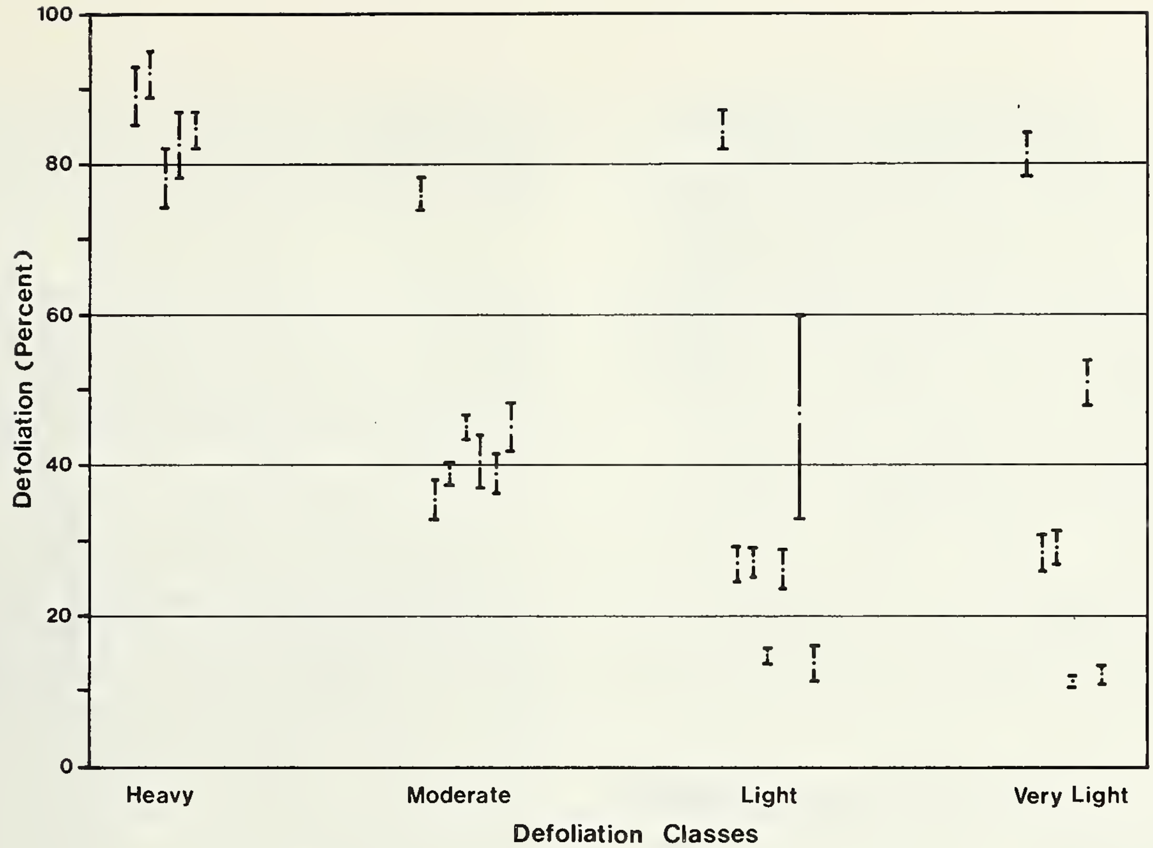


Figure 4.--Average percent defoliation, 1972 (S.E. of replicated plot clusters).

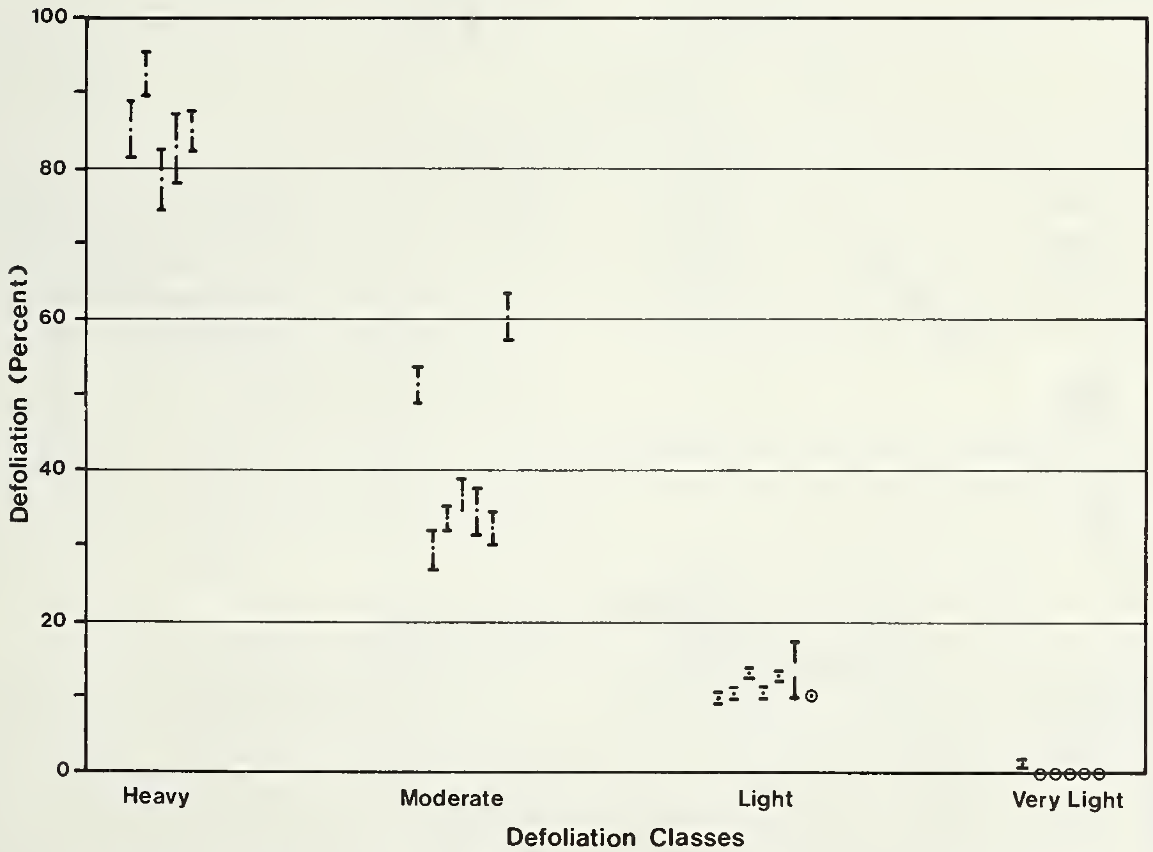


Figure 5.--Average percent defoliation, 1973 (S.E. of replicated plot clusters).

data are plotted in figure 5, however, the heavy and moderate class areas show practically no change from 1972 to 1973, either within replicates or between classes. Light and very light areas overlap, and both resemble the moderate defoliation class. One replicate in each of the light and very light classes reaches the moderate class, and one replicate in each class reaches the heavy defoliation class.

Next, 1972 defoliation was plotted against 1973 defoliation (fig. 6). This figure further illustrates relatively little change in the heavy and moderate classes as compared with the increased 1973 defoliation in all of the very light plot clusters and four of the light plot clusters.

These relations were explored further for the replicated plot clusters by using an analysis of variance and several t-tests on percent defoliation means to test for differences between defoliation classes and between years.[2]

[2] A similar analysis was also performed where the number of trees per plot was used as a covariate to remove the variation caused by unequal numbers of trees. In all instances, the two separate analyses concurred.

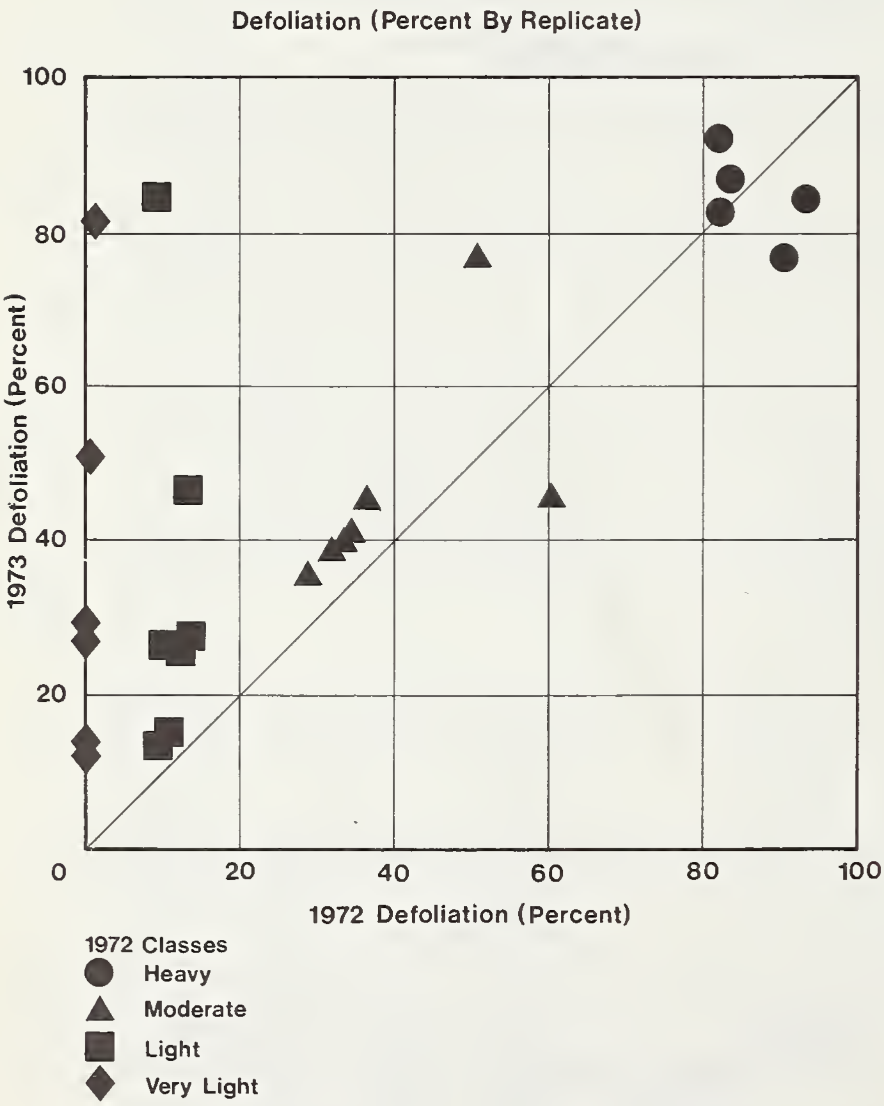


Figure 6.--Percent defoliation in 1972 and 1973 in replicated plot clusters.

The comparison of 1972 replicated plot defoliation means among classes for grand fir (F = 524) and Douglas-fir (F = 244) was highly significant at the .01 level. The F value for plot defoliation means in 1973 indicated that the differences between defoliation of grand fir (F = 50.5) and Douglas-fir (F = 6.92) were also highly significant at the .01 level.

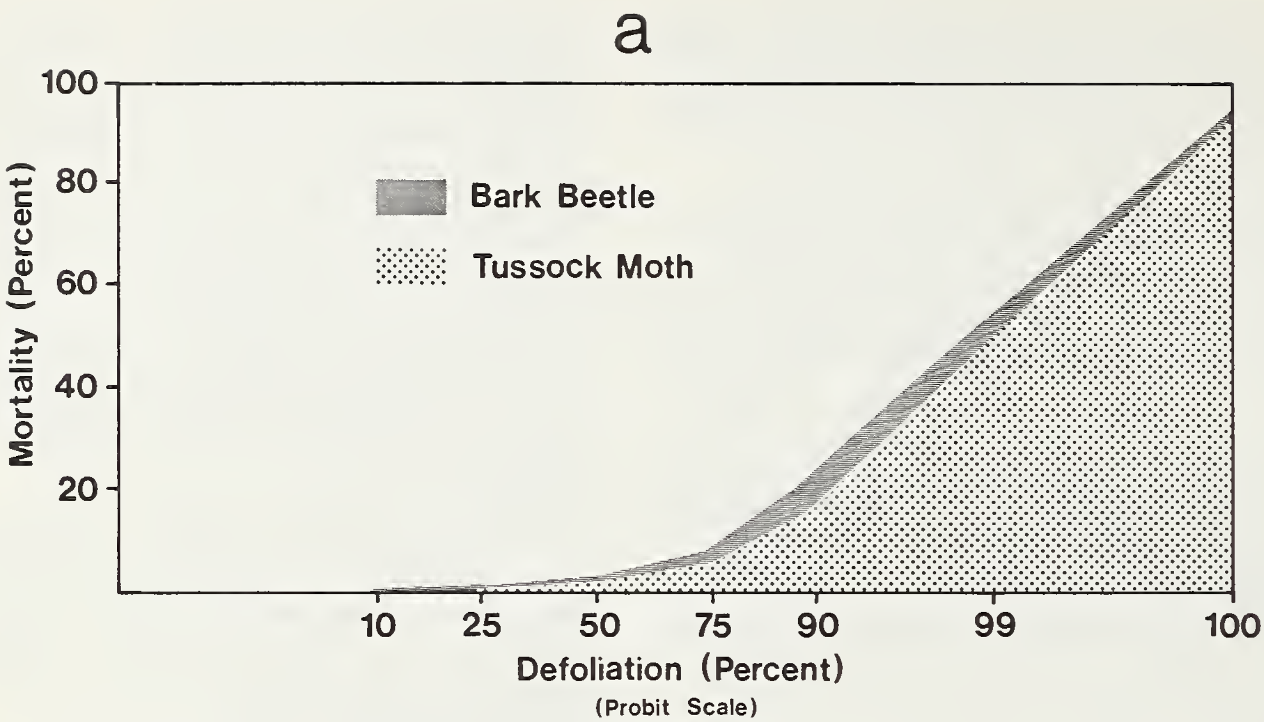
I suspected that the highly significant difference among means for the four classes for both years could be caused by the high mean in the heavy class. Therefore, an analysis of variance was made comparing means of only the moderate, light, and very light classes for grand fir--to determine if the differences among those class means were significant in 1973. The F value of 7.26 was highly significant (.01 level) indicating a difference. A multiple comparison test was conducted to find out where the differences existed and, as expected, the heavy class mean was significantly greater than the other classes, and the moderate class was significantly greater than the light class at the .01 level. No other differences were significant. The same test made on Douglas-fir for 1973 defoliation means gave an F value of 1.34 and was not significant, indicating either too small a sample or much variation within moderate, light, and very light defoliation classes for this species.

The defoliation estimates and the classifying of plot clusters by defoliation class were consistent and relatively free of variation in 1972. Heavy defoliation in 1973 in some light and very light classes, however, created enough variation to obscure the original 1972 pattern of defoliation classes. Also of interest was the small amount of foliage gain in heavy class areas in 1973 (fig. 6). No additional defoliation occurred on any of the plots in 1974, even though several had enough early instar larvae to cause potential defoliation. The populations on these plots declined so rapidly that no measurable defoliation and few survivors were found by the end of the summer (Mason 1976).

Another series of tests were made to see if significant differences occurred between defoliation of grand fir and Douglas-fir. A t-test was used to compare the replicated plot, percent-defoliation means for Douglas-fir and grand fir for 1972 and 1973 (table 10, appendix). No significant difference was found in defoliation between Douglas-fir and grand fir in 1972, nor between the two species in the heavy class areas in 1973. But in the other classes in 1973, Douglas-fir suffered significantly more severe defoliation. This defoliation differential between grand fir and Douglas-fir plays an important role in the patterns of tree mortality that will be summarized in the following sections.

TREE MORTALITY RELATED TO DEGREE OF INDIVIDUAL-TREE DEFOLIATION

Tree mortality related to degree of defoliation shown in figure 2 (the highest defoliation regardless of year) was estimated for individual trees (figs. 7a and 7b). Cause of death is graphed on a probit scale for mortality from defoliation alone and secondary attack by bark beetles after defoliation. For both grand fir and Douglas-fir mortality from



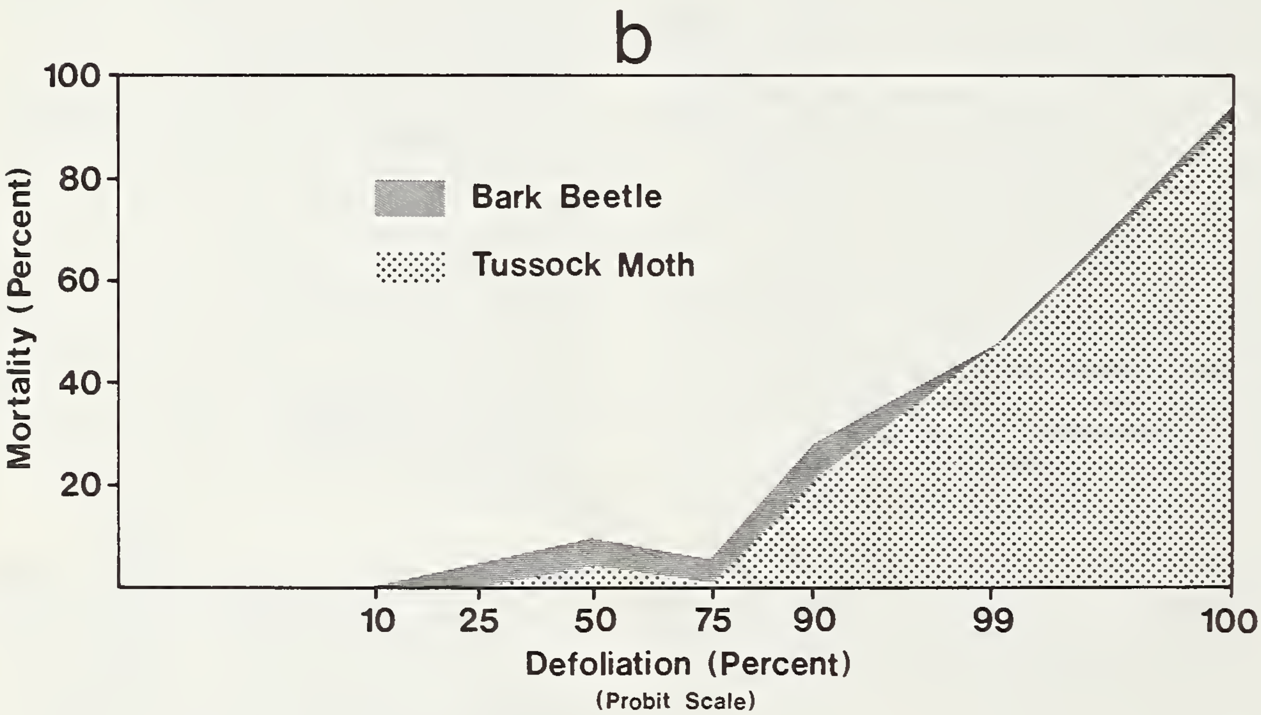


Figure 7.--a, Percent grand fir (number) killed by tussock moth and bark beetles by individual-tree classes, 1972-1976, Blue Mountains; b, percent Douglas-fir (number) killed by tussock moth and bark beetles by individual-tree classes, 1972-1976, Blue Mountains.

defoliation occurred only in the 50-percent or greater defoliation categories. And the 50-percent category suffered only 1-percent loss of grand fir and 4-percent loss of Douglas-fir. For both species, over 90 percent of the mortality from effects of defoliation alone occurred in trees defoliated 90 percent or greater. The discrete data for the 99-percent defoliation category was surprising. That category was improvised in the field because some defoliated trees fell between the 90 and 100 percent categories. Most of these trees had only one branch with green needles or sometimes just a few green needles, so were not truly 100-percent defoliated. In the 99-percent defoliated category, only 48 percent of the grand fir and 46 percent of the Douglas-fir succumbed, but in the 100-percent defoliation category, 93 and 92 percent, respectively, died. Combined mortality for both species as related to degree of defoliation is graphed in figure 7c and compared with mortality of white fir after an earlier California outbreak (Wickman 1963).

C

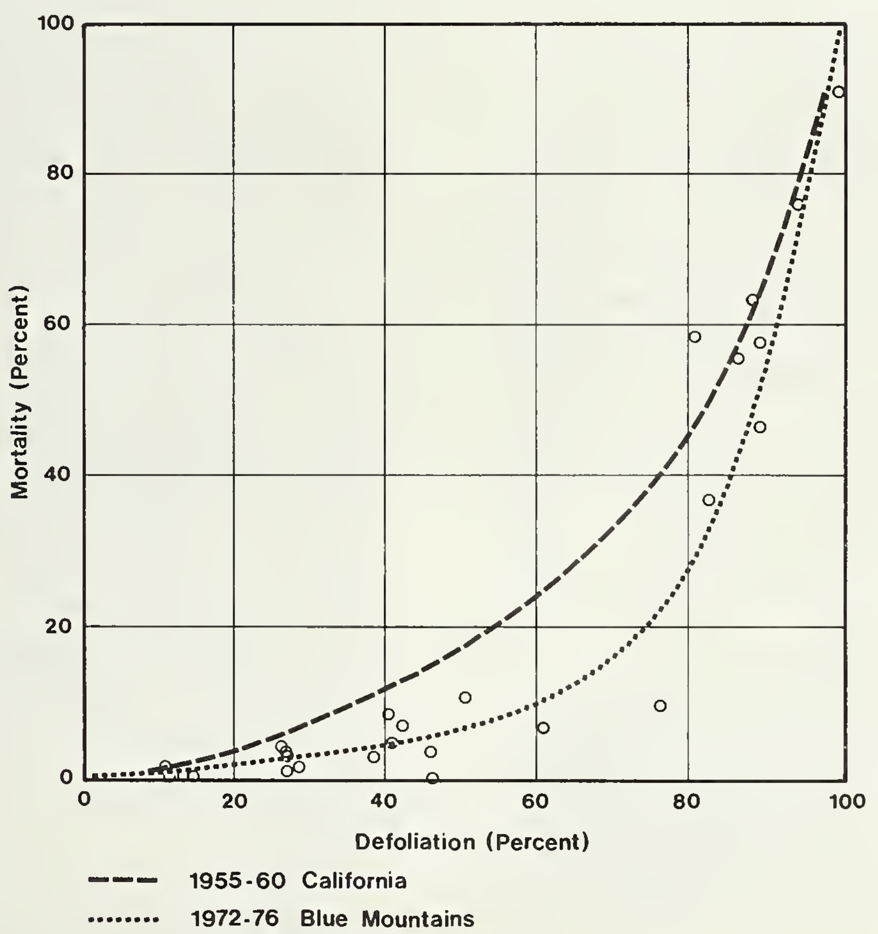


Figure 7.--c, Total tree mortality related to degree of defoliation of white fir in California, 1956-1960, and grand fir and Douglas-fir in the Blue Mountains, 1972-1976.

The two graphs are compared because many predictions of tree mortality since 1963 have been made based on the curve. If the 1963 data are used as a predictor of damage for this outbreak, then the deviation of 1972-1976 data from the expected may be explained by lower mortality from bark beetles in the Blue Mountains outbreak. These secondary mortality relations are discussed in some detail in the remainder of this section.

Mortality from secondary attacks by bark beetles was related to degree of defoliation, but not so strongly in Douglas-fir as in grand fir. Mortality caused by bark beetles in grand fir was distributed fairly evenly through the 75 to 100 percent categories, with the highest occurrence in the 90-percent category (7 percent). With Douglas-fir, the mortality was fairly evenly distributed through the 25- to 90-percent categories with the 90 percent again suffering slightly higher mortality (7 percent). This distribution of mortality caused by Douglas-fir beetle suggests that defoliation intensity alone was not responsible for susceptibility to secondary insect attack. No published data are available on mortality caused by Douglas-fir beetles of trees defoliated by tussock moth, but some unpublished data were located on this subject. In 1946, W. J. Buckhorn[3/] established a study of a series of 50 defoliated Douglas-fir in an area of heavy defoliation after the 1946-1947 tussock moth outbreak near Troy, Oregon. Percent defoliation was estimated for each tree to the nearest 5 percent after 1946 defoliation; then the tagged trees were reexamined annually until 1951 to determine cause of death. Defoliation intensity ranged from 5 to 95 percent with an average of 34.1 percent, similar to the average defoliation on all Douglas-fir in this study in 1972 (31.4 percent). Tree diameters averaged 21.1 inches, ranging from 10 to 36 inches. Buckhorn recorded no mortality from defoliation alone but mortality from Douglas-fir beetle started in 1947 with 14 percent killed; in 1948, 26 percent were killed and in 1949, 3 percent were killed. No additional mortality occurred the next 2 years. The mortality occurred in all defoliation classes, but over 50 percent of the total mortality occurred in trees defoliated from 5 to 35 percent. Most of the initial mortality in 1947 (5 of 7 trees), however, occurred in trees defoliated 80 to 95 percent, indicating that the Douglas-fir beetle populations may have initially developed in severely defoliated trees, and then attacked trees indiscriminately the next year before the population declined. Some evidence of similar patterns of damage by Douglas-fir beetles occurred in my study. For instance, the total mortality was distributed through most of the defoliation categories, not just the heaviest; however, mortality progressed through time as follows: 1973, 2.4 percent killed (mostly in heavy defoliation categories); 1974, 7.6 percent; 1975, 2.7 percent; and 1976, 0.4 percent. Studies of the relation of bark beetles to defoliated stands were terminated in 1976, because of the extremely widespread logging activities since 1973 around

[3/] Unpublished data on file at the Forestry Sciences Laboratory, Corvallis, Oregon.

most of the plots. Logging influences on Douglas-fir beetle populations--if the results of earlier studies on this relation are relevant here--are probably masking the effects of tussock moth defoliation (Lejeune et al. 1961; Rudinsky 1962; Johnson and Belluschi 1969).

Losses in grand fir from fir engraver beetle, *Scolytus ventralis* Lec., were apparently not as great as they were in white fir in two California outbreaks. There, after a 1956 infestation, three-quarters of the tree mortality in 1957 was because of fir engraver beetles and the roundheaded fir borer, *Tetropium abietis* Fall. (Wickman 1958). In an earlier outbreak in California (Mammoth Lakes 1938), 12 percent of the white fir were killed by defoliation alone and 17.1 percent by secondary attack by bark beetles (Wickman 1963). Apparently, therefore, in this outbreak fir engraver beetles did not reach a high level.

Many of the trees rated as killed by defoliation in 1972 and 1973 had attacks, but little or no brood production because of sour phloem with very high water content, a condition also found by Wright and Berryman.[4] Conversely, some trees that appeared to have good bark beetle brood production may have ultimately died from the effects of defoliation alone. Exact cause of death, immediately after defoliation, is difficult to determine because defoliation effects and secondary insect attacks may be so strongly related. The important fact is that trees over 90-percent defoliated have a high probability of dying, and mortality probably occurs whether bark beetles attack or not, thus explaining the similarity of total mortality in several past outbreaks.

From these data and Buckhorn's, only trees severely defoliated (80-percent or more) appear to have a high probability of being attacked by bark beetles the first 1 or 2 years after defoliation takes place, but then continued bark beetle activity is dependent on other environmental factors.

The aspect of importance with bark beetles is identifying the cause and timing of a population build-up capable of killing healthy as well as slightly weakened trees. Because several studies now have shown a great deal of variation in postoutbreak tussock moth and bark beetle populations, recent definitive studies may identify this threat more precisely.[5] An understanding of the population dynamics of the bark beetles, plus the influences of logging and subnormal precipitation will have to be considered, along with the presence of trees weakened by defoliation.

Undesignated mortality, such as wind and snow breakage, shading of suppressed trees, and unknown (presumed to be disease-caused), are summarized in table 1. Note that Douglas-fir suffered

[4] Wright, L. C., and A. A. Berryman. Host resistance to the fir engraver beetle: Effect of defoliation on moisture stress of *Abies grandis* (Unpublished report to USDA Expanded Douglas-fir Tussock Moth Research and Development Program).

[5] Personal communication, Alan A. Berryman, Washington State University, Pullman, Washington.

Table 1--*Percent mortality by other causes for each tree defoliation category*

Species	Percent defoliation						
	10	25	50	75	90	99	100
Grand fir	3	1	2	2	5	7	1
Douglas-fir	7	8	1	0	10	15	1

double the mortality of grand fir by these other causes. Most of this mortality was caused by wind and snow breakage and was distributed throughout the study period. Some or all of the mortality from unknown causes and suppression could have been related to defoliation, but we had no way of determining this relation.

TREE MORTALITY RELATED TO D.B.H.

Mortality of grand fir and Douglas-fir by diameter class was summarized by each tree on all plots and graphed to show the distribution of mortality caused by defoliation alone and bark beetles (fig. 8). For grand fir, the mortality is fairly evenly distributed in all d.b.h. classes except no mortality from bark beetles occurred in the 1- to 6-inch class.

In an earlier study in California white fir (Wickman 1963), I found that the mortality from defoliation alone was not evenly distributed; most of it occurred in trees 2 to 10 inches d.b.h. In that study, mortality from defoliation and bark beetles of

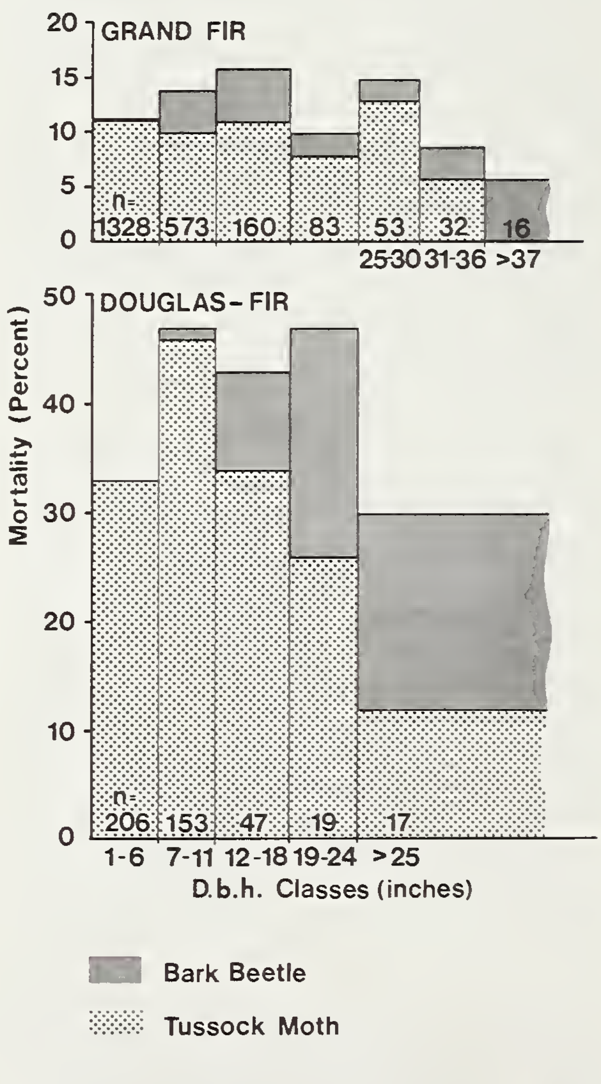


Figure 8.--Percent mortality by species, diameter class, and cause. 1972-1976, Blue Mountains.

saplings and small poles averaged 27.4 percent, and sawtimber mortality averaged 13.8 percent. Grand fir in the Blue Mountains outbreak did not suffer such a pattern of mortality, but this may have been in part, because of lower fir engraver populations. In the Blue Mountains outbreak, all 16 of the plot trees larger than 36 inches d.b.h. that died were killed by bark beetles.

Douglas-fir mortality from defoliation alone was concentrated in the smaller trees, and mortality from bark beetles in the larger trees--and at a higher level than secondary mortality of grand fir. Most mortality caused by Douglas-fir beetle was in trees 12-inch d.b.h. or larger, and trees over 20-inch d.b.h. were the most susceptible.

TREE MORTALITY RELATED TO CROWN CLASS

Mortality of grand fir and Douglas-fir by crown class was summarized using individual trees on all plots. A distribution of percent mortality for both species by crown class is given in table 2. This summary shows an apparent trend of mortality in Douglas-fir killed by defoliation. Dominant and codominant trees have almost 50 percent more mortality than intermediate and suppressed trees. All four crown classes for grand fir suffered nearly equal amounts of mortality from defoliation alone. But mortality from bark beetles occurred mainly in dominant and codominant trees for both species.

Crown classes are normally related to d.b.h. class. Most trees over 12-inch d.b.h. are dominant or codominant, and most trees smaller than 12 inches are intermediate or suppressed. This distribution is related to the distribution of mortality for both species shown in figure 8.

TREE MORTALITY IN THE FOUR DEFOLIATION CLASSES

The next two summaries and analyses are stratified two different ways.

Table 2--*Percent grand fir and Douglas-fir mortality by crown class and cause*

Crown class	Species	Mortality	
		Defoliation	Bark beetles
Dominant	GF	11.8	5.4
	DF	46.7	7.8
Codominant	GF	11.0	4.8
	DF	44.2	6.7
Intermediate	GF	11.6	1.6
	DF	25.8	0
Suppressed	GF	9.7	0.1
	DF	30.5	0

1972 mapped defoliation classes.--The percent stand (volume and number) mortality for each year, defoliation class, and tree species is shown in table 11, appendix. This includes mortality from both defoliation and bark beetles. This summary excludes most back country plots because they did not fall in the replicated population plot design. Two clusters of heavily defoliated plots from the back country were used, however, to provide enough data for analysis of the heavy class.

Plot data are stratified by the broad aerially mapped classes. In other words, any mapped class could be expected to contain a mosaic or mixture of several defoliation classes. The total mortality for each defoliation class in this arrangement is shown in figure 9. It indicates highest mortality occurred in the heavy defoliation class areas with 38.6 percent of the stand (number) and 45.3 percent of the volume killed by the outbreak.

Individual-plot defoliation classes.--These data are from the same plots used in the previous section. For this analysis, however, each plot was stratified strictly by the average plot defoliation into one of the four classes (table 12, appendix).

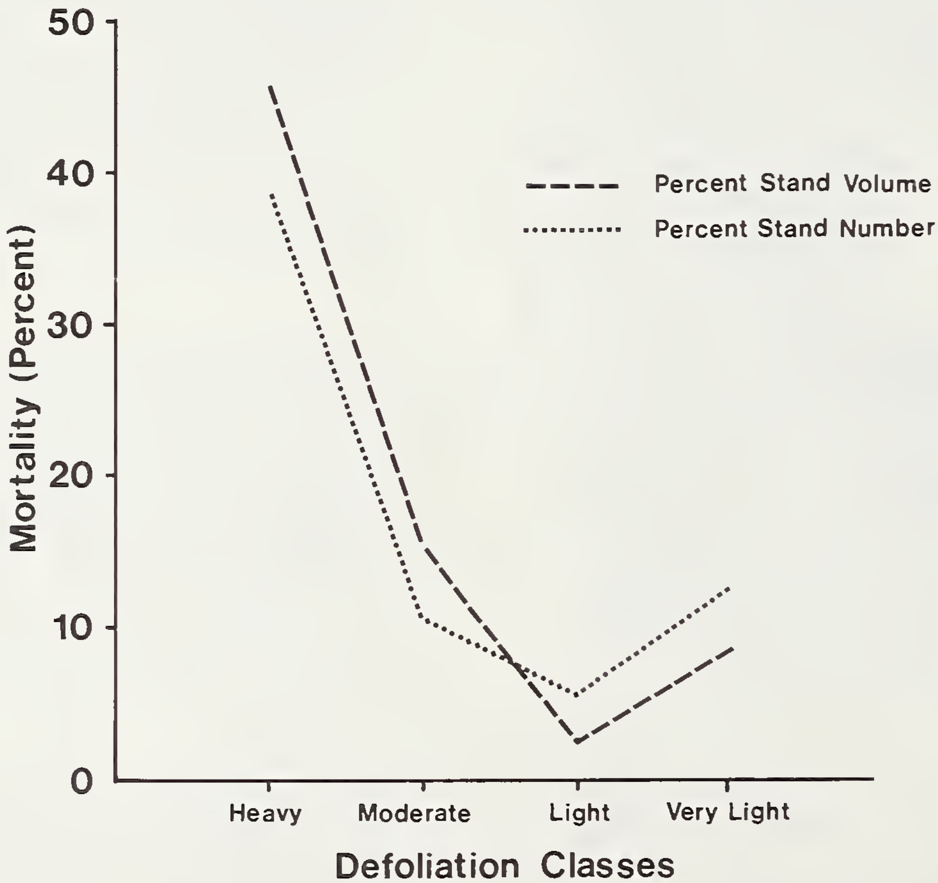


Figure 9.--Percent mortality of grand fir and Douglas-fir killed by tussock moth and bark beetles, by mapped defoliation classes.

That is, each plot within a cluster is classed according to its individual defoliation level in 1972. Therefore, the heavy class is composed of only heavy class plots, moderate class is composed only of moderate class plots, and so on. More plots were included in this analysis because all back country plots were used. A comparison of tables 11 and 12, appendix, shows a shift in the number of heavy class plots to the moderate and light classes and some additional redistribution of plots from the mapped stratification of plot clusters to the individual plot stratification. This occurs because of the more precise classification of individual plots in this summary. The change of plot totals for each defoliation class from the mapped to the individual-plot classification is shown in table 3. For instance, of 76 heavy defoliation class plots in the mapped stratification, 54 percent remained in the heavy class using the individual-plot stratification, 36 percent were actually in the moderate class, and 10 percent in the light class. Another large discrepancy occurred in the change of 42 percent of the mapped light class plots to moderate class plots using the individual-plot stratification.

Total mortality graphed by defoliation class in this analysis (fig. 10) now shows more precise breakdown by defoliation class with 72-percent mortality (number) in the heavy class, 5.2-percent in the moderate class, 6.3-percent in the light class, and 11.1-percent in the very light class. Only the light and very light classes are similar for both analyses.

Cumulative annual mortality compared on mapped versus individual-plot defoliatin classes.--The mortality trends are similar for data analysis by both methods of plot stratification (illustrated by figs. 11a-11d), but the totals for most classes are different. Graphs 11a and 11b show the cumulative mortality for plots in the mapped area and 11c and 11d for the ground-classed plots. Again, as in figure 10, graphs 11c and 11d reflect a better correlation of mortality with defoliation class within plot clusters. Data for graphs 11a and 11b may be more easily estimated and extrapolated using aerial mapping, but they are not an accurate accounting

Table 3--*Breakdown of plot numbers and changes according to method of analysis*

Mapped defoliation class[1]	No. plots	Breakdown by individual-plot defoliation class[2]			
		Heavy	Moderate	Light	Very light
Heavy	76	41(54%)	27(36%)	8(10%)	0(0%)
Moderate	86	6(7%)	76(88%)	4(5%)	0(0%)
Light	60	0(0%)	25(42%)	35(58%)	0(0%)
Very light	63	0(0%)	0(0%)	4(6%)	59(94%)

1/ Total number of plots by mapped defoliation class = 285.

2/ Total number of plots by individual-plot defoliation class = 342.

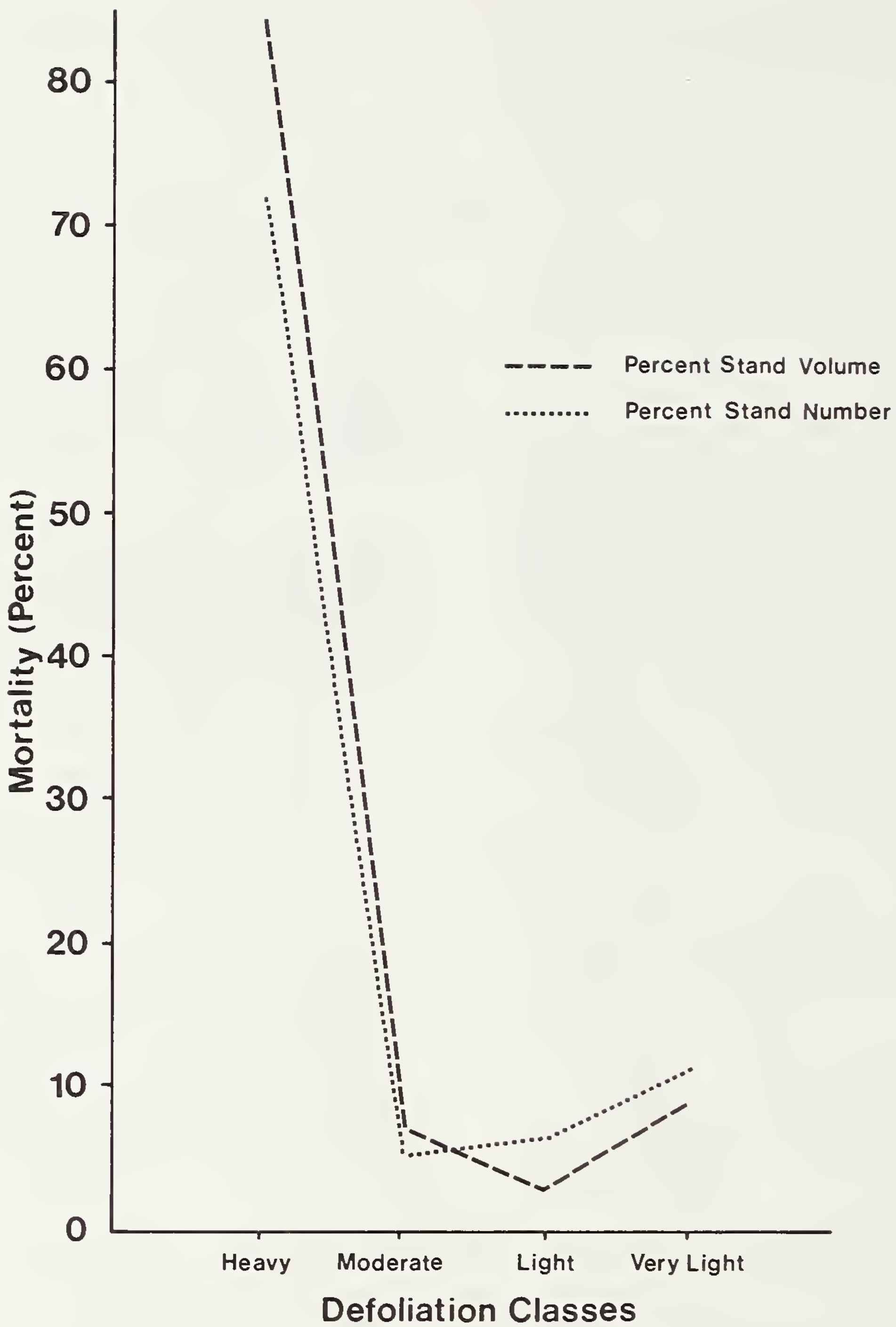


Figure 10.--Percent mortality of grand fir and Douglas-fir killed by tussock moth and bark beetles, by individual-plot defoliation classes.

of the tree mortality for the manager who wants information acre by acre. The differences in the heavy and moderate classes in the two analyses must be considered in making predictions for management purposes.

Table 4 which summarizes averages and standard errors for mortality in each defoliation class stratified by mapped and individual defoliation classes, indicates greater variation when heavy and moderate defoliation

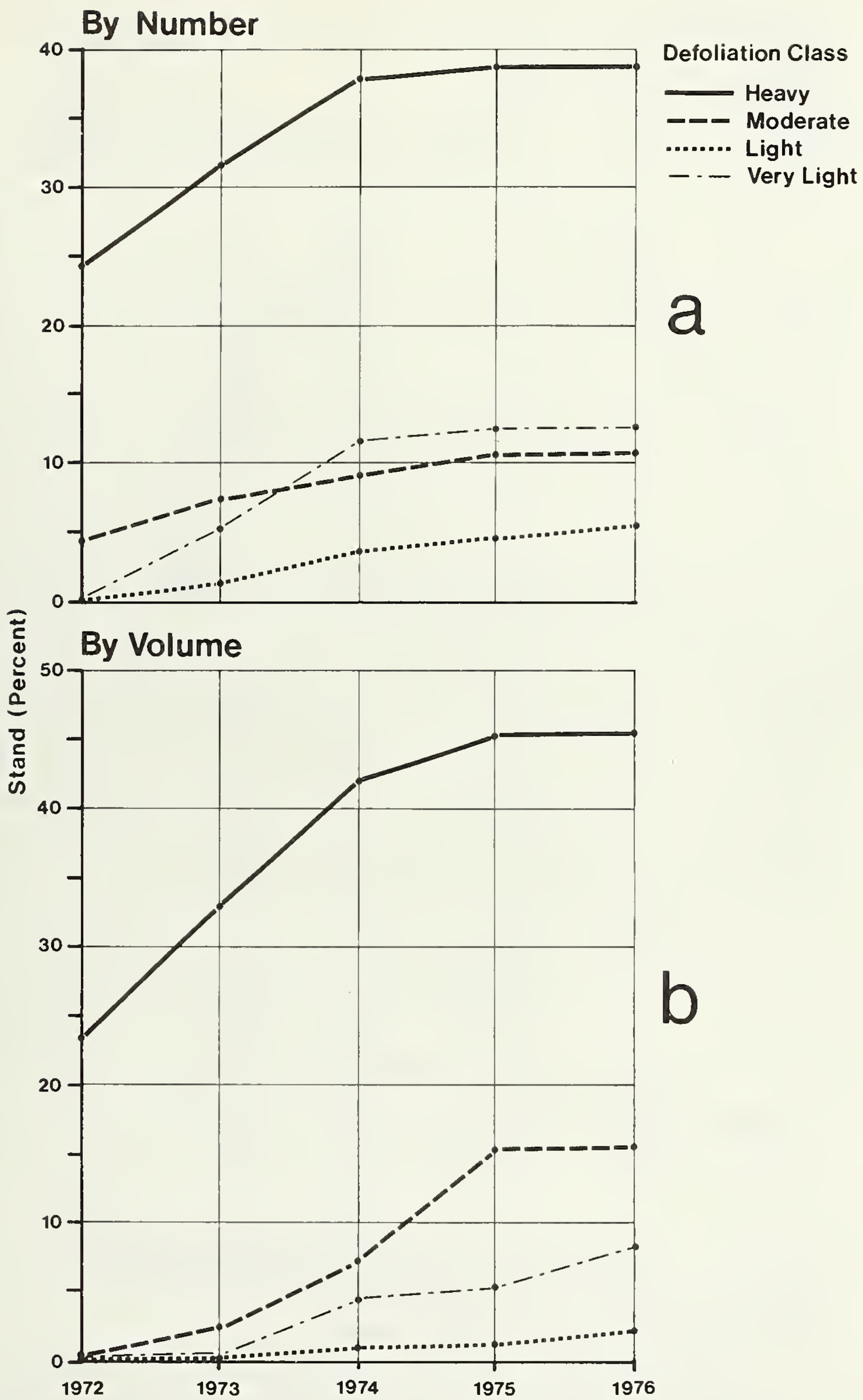


Figure 11.--a, Cumulative percent stand (number) killed by tussock moth and bark beetles for each mapped plot defoliation class; b, cumulative percent stand (volume) killed by tussock moth and bark beetles for each mapped plot defoliation class.

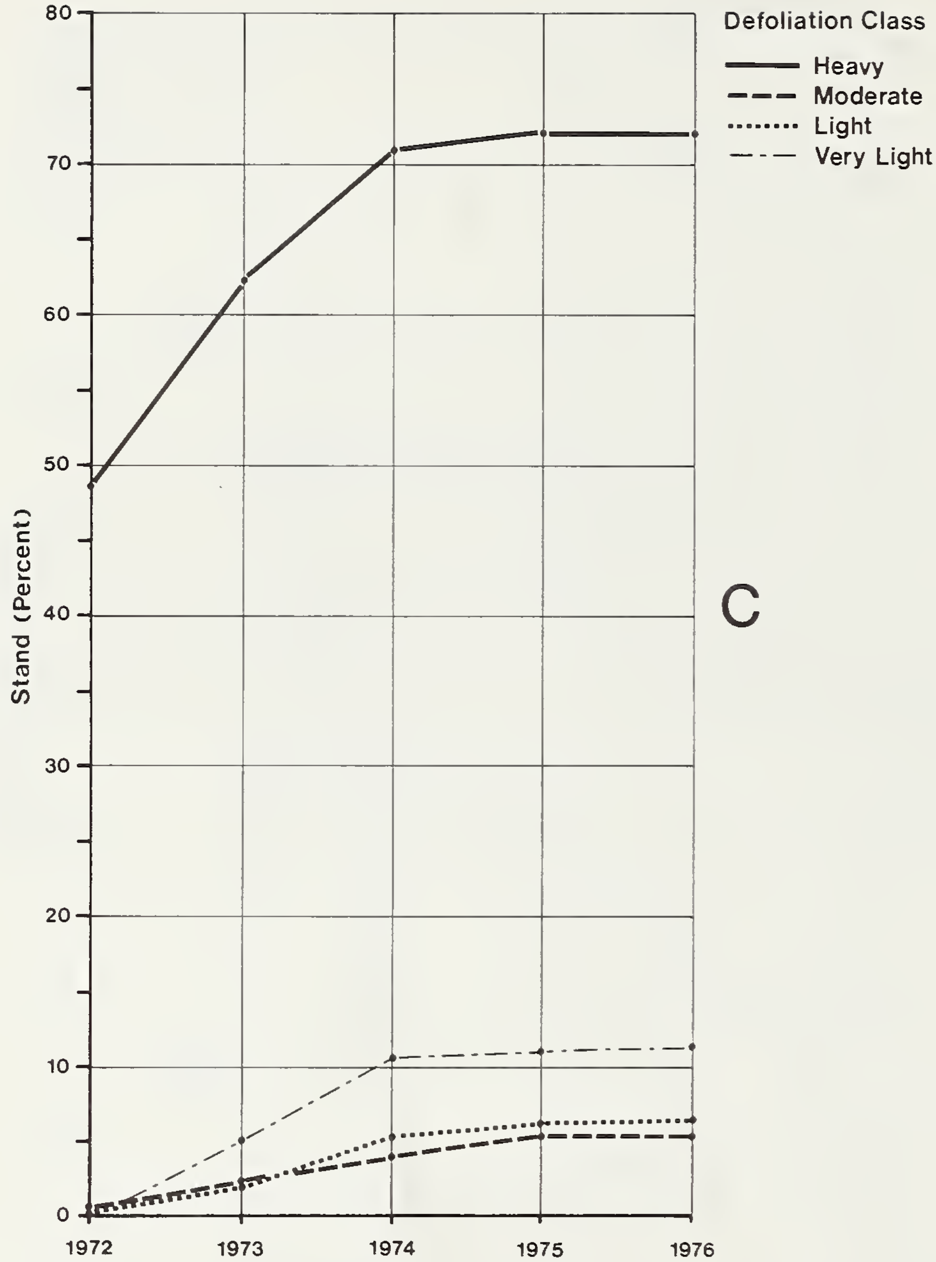


Figure 11.--c, Cumulative percent stand (number) killed by tussock moth and bark beetles for each individual defoliation class.

plots are stratified by mapped classes. The standard error of the means reach almost 50 percent by this analysis, compared to about 10 percent of the mean for heavy and moderate classes in the individual-plot stratification. Little change occurs for plots in the light and very light classes. The higher variation for these two classes, for both forms of analysis, was the result of the range of none to very heavy mortality on some plots after 1973 defoliation.

From these data, we can see problems and sources of error in making damage predictions based solely on mapped classes. Within

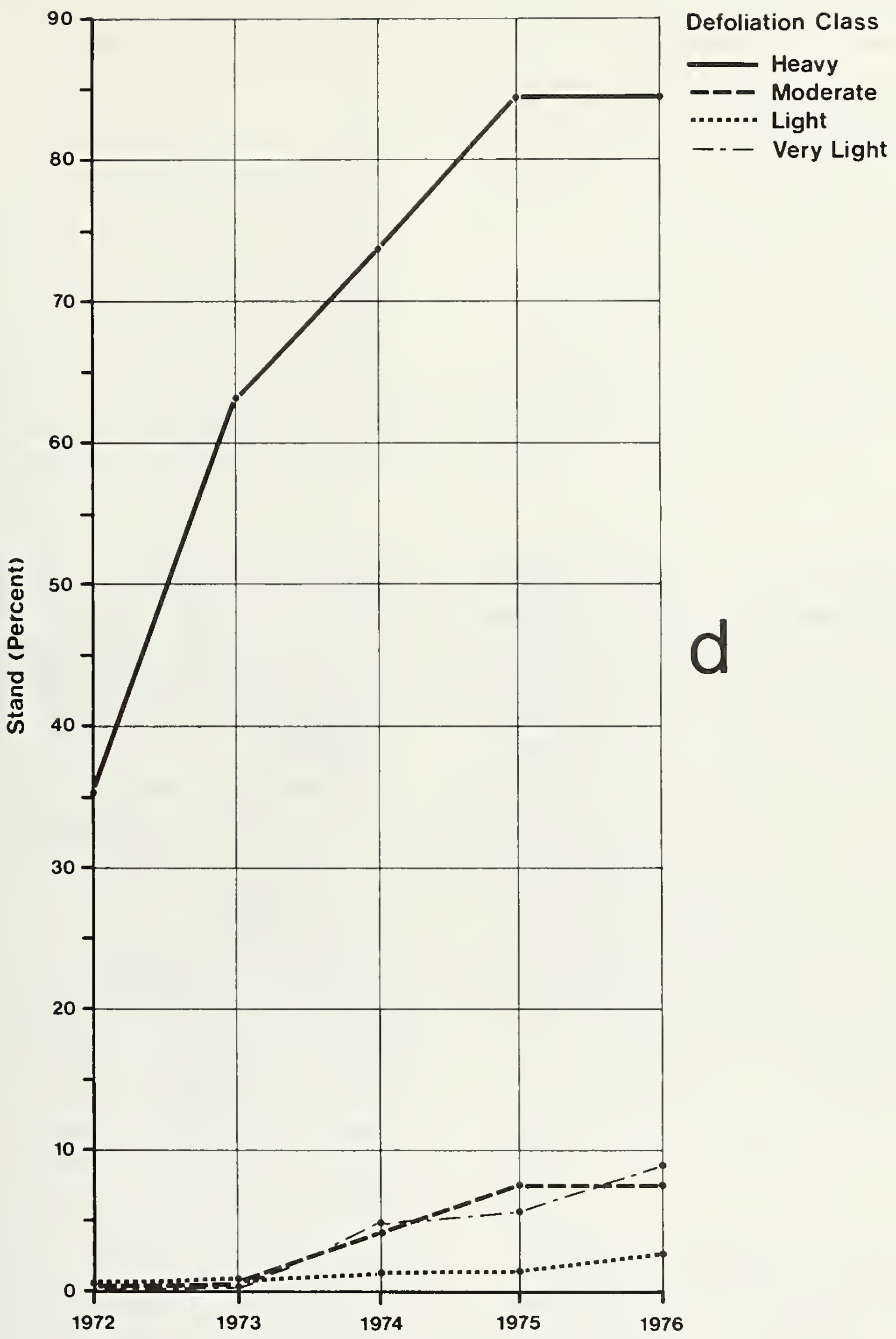


Figure 11.--d, Cumulative percent stand (volume) killed by tussock moth and bark beetles for each individual defoliation class.

each mapped class is a mixture of several levels of defoliation, because tussock moth populations are not evenly distributed. They tend to be aggregated at higher levels in scattered clumps, and defoliation patterns reflect this population distribution. Therefore, the analysis by each individual-plot defoliation class is more accurate, in terms of what is happening acre by acre;

Table 4--*Average mortality and standard error of plots stratified by mapped and individual-plot defoliation classes*

Defoliation class	Mapped defoliation classes		Individual-plot defoliation class	
	$\overline{X}$	S.E.	$\overline{X}$	S.E.
Heavy	38.6	16.8	72.0	6.1
Moderate	10.6	4.8	5.2	0.9
Light	5.3	2.8	6.3	3.5
Very light	12.6	9.0	11.1	9.0

but the technique is less practical for a pest manager to use if he relies mostly on aerial mapping. Ideally, if predictions of damage are to be made based on defoliation early in an outbreak, they should combine aerial mapping with some ground sampling to determine the true loss per acre for defoliation classes as well as the total number of acres. Aerial mapping tended to overestimate expected damage on heavy defoliation class areas because the mapped classes, although actually a mixture of several classes, are treated as a single homogeneous class and mortality predicted as such.

This problem is also evident when data from the Blue Mountains outbreak are compared with tree mortality in past outbreaks. Damage classes used from year to year and area to area must be similar before data can be meaningfully compared. Mortality recorded for the heavy defoliation area in the Stowe Reservoir infestation in California were comparable to those of the heavy defoliated plots in this study (83.9 percent in California compared with 72 percent here), but the mortality reported for heavily defoliated areas in two other California outbreaks are not comparable because the classification of "heavy" defoliation was dissimilar.

MORTALITY RELATED TO YEARS OF DEFOLIATION

The graphed mortality data have shown a trend of mortality for each of the four defoliation classes regardless of the method of analysis. The heavy defoliation class areas suffered the most severe mortality, and most of it occurred in 1972 and 1973. When mortality rates by years (fig. 11) are compared with the average defoliation levels in each class for 1972-1973 (fig. 3), no increased defoliation occurred in the heavy class areas in 1973, and most of the mortality occurred in 1972. The data imply that the most severe outbreak mortality in terms of percent loss in the heavy defoliation class was directly related to 1972 defoliation. Some light and very light class areas suffered enough defoliation in 1973 to cause tree mortality, but the average total mortality for the light and very light class areas was not nearly as high as it was on the heavy class areas in 1972. The moderate class areas fall somewhat between these two, but they also had a relatively low total mortality.

Several analyses were made to illustrate the differential effect of 1972 and 1973 defoliation and the additive effects of two consecutive years of defoliation. To do this, we used trees from some very light class plots and a few light class plots, which had little or no 1972 defoliation but very heavy 1973 defoliation, to show mortality caused by the 1973 defoliation. These data were then compared with 1972 mortality for trees defoliated 50, 75, 90, 99, and 100 percent from heavy class areas (table 5). Table 5 includes mortality occurring the same year of defoliation (1972 mortality for 1972 defoliation and 1973 for 1973 defoliation) and total mortality in 1976 for both years of defoliation, because mortality from severe defoliation actually continues for several years after the year of defoliation. Much of the new foliage on heavy class areas was defoliated to various degrees in 1973, so some cumulative effects were present which defoliated areas in 1973 did not have. The table indicates more mortality occurring after 1972 defoliation than after 1973 defoliation in all five defoliation categories (with two exceptions).

The effects of cumulative defoliation in 1972 and 1973 are summarized in table 6. The upper right quadrant of the table (percent mortality both Douglas-fir and grand fir) reading from left to right on the top row shows 0.68 percent

Table 5--*Grand fir and Douglas-fir mortality resulting from 1972 defoliation (heavy class areas) and 1973 defoliation (very light areas)*

Defoliation category	Sample trees				Mortality (defoliation and bark beetles)							
					1972 defoliation				1973 defoliation			
	1972 defoliation		1973 defoliation		Died 1972		Total 1976		Died 1973		Total 1976	
	GF	DF	GF	DF	GF	DF	GF	DF	GF	DF	GF	DF
Percent	Number				Percent							
50	255	23	135	47	0	0	3.9	13.0	0	0	3.7	4.3
75	90	11	35	27	0	0	15.6	18.2	2.9	0	5.7	3.7
90	115	21	47	22	3.5	4.8	49.6	61.9	0	0	12.8	27.3
99	6	1	24	14	16.7	0	50.0	100	8.3	14.3	62.5	35.7
100	126	113	29	28	84.9	75.2	97.6	99.1	62.1	50.0	89.7	92.9

Summary of 90, 99, and 100 percent categories combined.

Species	Sample trees		Mortality in year of defoliation		Total mortality	
	1972	1973	1972	1973	1972	1973
	Number		Percent			
Grand fir	247	100	45.3	20.0	74.1	47.0
Douglas-fir	135	64	63.7	25.0	85.9	57.8

Table 6--*Mortality based on trees defoliated in both 1972 and 1973 (effect of cumulative defoliation)*

Percent defoliation 1972	Total trees Percent defoliation 1973					Percent mortality (both Douglas-fir and grand fir) Percent defoliation 1973				
	50	75	90	99	100	50	75	90	99	100
50	147	43	26	7	3	0.68	6.98	19.23	14.29	66.7
75	25	30	22	7	2	4.0	16.7	27.27	28.57	50
90	8	12	58	24	20	12.5	2.5	44.83	66.7	100
99	--	--	--	2	2	--	--	--	100	100
100	--	--	3	7	9	--	--	100	85.71	100

Percent defoliation 1972	Percent mortality (Douglas-fir) Percent defoliation 1973					Percent mortality (grand fir) Percent defoliation 1973				
	50	75	90	99	100	50	75	90	99	100
50	8.3	0.0	20.0	50.0	--	0.0	7.3	19.0	0.0	66.7
75	0.0	0.0	0.0	50	100	4.2	18.5	33.3	20.0	0.0
90	0.0	0.0	60	66.7	100	14.3	27.3	43.4	66.7	100
99	--	--	--	--	100	--	--	--	100	100
100	--	--	--	100	100	--	--	100	83.3	100

mortality of trees defoliated 50 percent in 1972 and 50 percent or no change in 1973; 6.98-percent mortality for trees defoliated 50 percent in 1972 and 75 percent (or an additional 25 percent) in 1973; 66.7-percent mortality for trees defoliated 50 percent and 100 percent; and so on.

These data illustrate some additive effect of defoliation, with mortality increasing with increasing amounts of defoliation the second year.

DIFFERENTIAL MORTALITY BETWEEN GRAND FIR AND DOUGLAS-FIR

When mortality data are summarized by tree species, Douglas-fir suffers proportionally higher amounts. This relation can be traced back to figure 3 which shows Douglas-fir consistently suffered higher levels of defoliation in 1973 than did grand fir. And table 5 indicated that Douglas-fir had an apparently higher level of mortality after 1973 defoliation and in 1976. This was most likely because of higher secondary mortality caused by bark beetles; direct mortality (caused by defoliation alone) was similar for both species.

This differential mortality is also shown in figure 12. In these graphs, mortality of Douglas-fir almost equals that of grand fir even though Douglas-fir averaged only 20 percent of the stand.[6] Looked at another

[6] Bolsinger and Berger (1975), in a report on the timber resources of the entire Blue Mountains area, state Douglas-fir accounts for 20 percent of the volume and true firs 19 percent. Most of our plots were concentrated in true fir stands where Douglas-fir occurred mainly as a minor component.

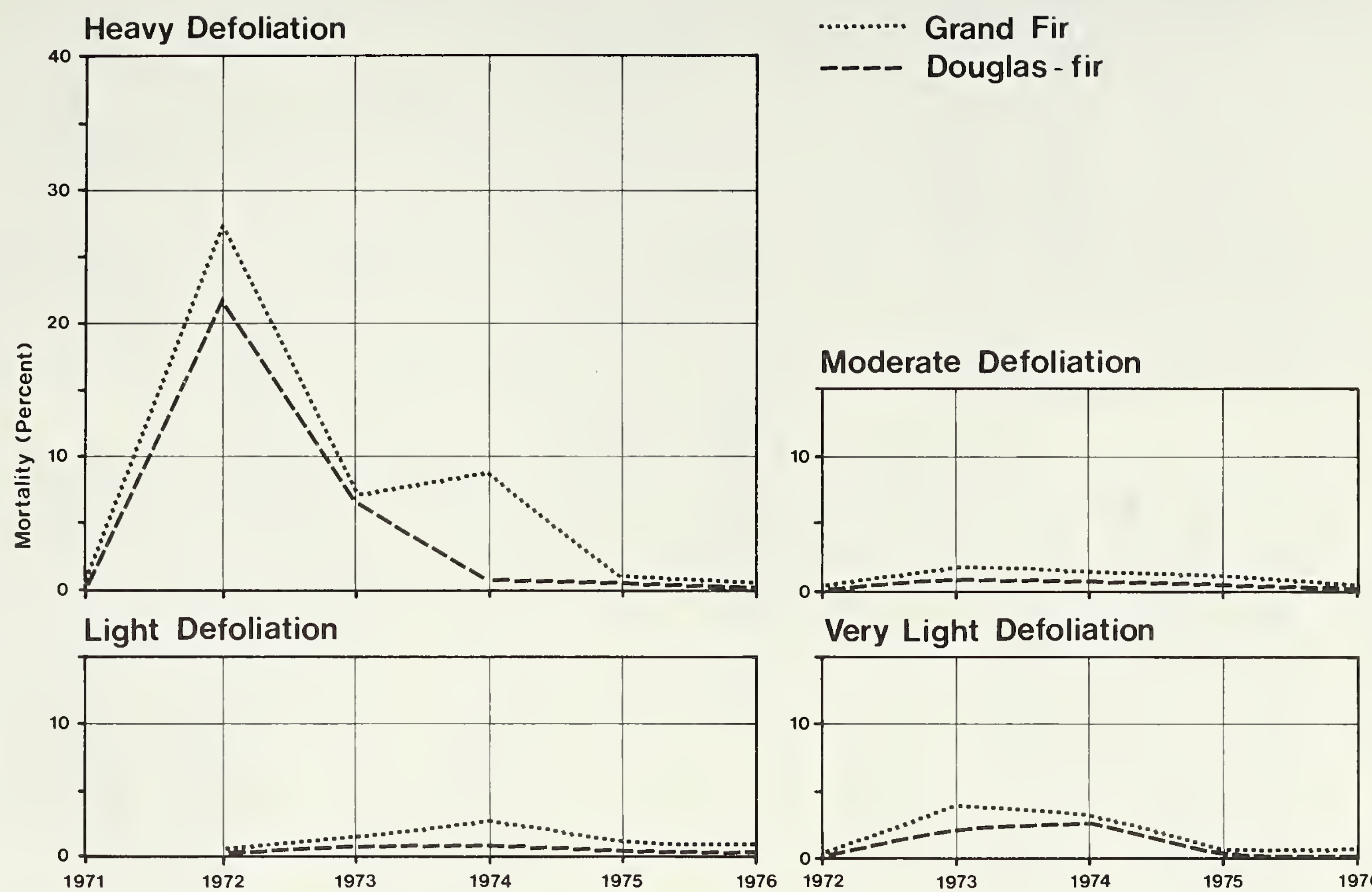


Figure 12.--Percent stand (number) killed by tussock moth and bark beetles, 1972-1976.

way (table 7), when total mortality is compared by species, Douglas-fir mortality surpasses that of grand fir in all four defoliation classes and by all causes.

We also compared mortality of Douglas-fir and grand fir in relation to defoliation. If mortality rates differed, then perhaps Douglas-fir was more susceptible to death after the same level of defoliation. The data were analyzed with χ^2 test (shown in table 13, appendix) for four tree-defoliation categories.

The probability that $\chi^2 \geq 2.25 \simeq .66$; therefore, the hypothesis of independence was not rejected; examination of the data in table 13, appendix, discloses that mortality vectors for the two species are not detectably different. This implies that Douglas-fir is not more susceptible to mortality from the same level of defoliation, but rather the species is more susceptible to defoliation. Some feeding behavior implications may influence this defoliation relation. Mason (1976) has mentioned that forest composition may have influenced the intraseason rate of larval population survival. The percent of Douglas-fir in a stand

Table 7--*Summary of tree mortality and survivors by individual-plot defoliation class and cause, 1972-1976*
(Percent mortality-number)

Cause of mortality	Defoliation class			
	Heavy	Moderate	Light	Very light
GRAND FIR				
Killed by tussock moth	63	3	3	6
Killed by beetles[1/]	4	1	2	2
Survivors	33	96	95	92
Other mortality	6	5	5	5
Current percent green stand (1976)	27	91	90	87
DOUGLAS-FIR				
Killed by tussock moth	84	9	11	24
Killed by beetles[2/]	1	9	1	3
Survivors	15	82	88	73
Other mortality	9	13	15	6
Current percent green stand (1976)	6	69	73	67

[1/] *Scolytus ventralis* and *Tetropium abietis*.

[2/] *Dendroctonus pseudotsugae*.

may slow population decline. Laboratory studies using larvae and foliage from our study areas in 1973 also suggested differential larval feeding behavior on Douglas-fir and grand fir (Beckwith 1976). This relation is being pursued by Beckwith[7] with increasing evidence of differences in feeding behavior and needle consumption rates on the two species.

THE ASSOCIATION OF DOUGLAS-FIR AND STAND MORTALITY

To determine if the amount of Douglas-fir in the stand affected combined mortality of grand fir and Douglas-fir, we stratified all the plots by percent Douglas-fir in each plot stand and found the following relation:

Percent Douglas-fir	0-10	11-25	26-50	>50
Percent mortality of Douglas-fir & grand fir	13.9	16.3	14.5	39

This analysis showed no significant relation until stands contained over 50 percent Douglas-fir; then, the percent stand mortality more than doubled. When the plot data stratified by mapped classes of percent Douglas-fir in the stand and percent mortality were graphed, a relation of differential mortality related to stand composition became apparent (fig. 18, appendix). A regression analysis showed a positive relation with an r^2 value of .35, significant at the .05 level, for light and very light class plots (1973 defoliation only) and an r^2 of .37, significant at the .01 level, for all four classes and both years of defoliation. The only plots suffering tree mortality from 1973 defoliation alone were light and very light class plots with a high proportion of Douglas-fir. The relations, though not strong, are intriguing. One interpretation could be that the percent Douglas-fir in the stand is an indicator of an environmental gradient; e.g. more Douglas-fir indicates a drier site, a drier site suffers higher tree mortality.

In the Blue Mountains of Oregon and Washington, the stand composition in terms of proportion of Douglas-fir may have an important influence on the behavior of populations and levels of tree damage. Other studies and analysis in progress may help clarify this relation.

[7] Personal communication, R. C. Beckwith, Forestry Sciences Laboratory, Corvallis, Oregon.

TOP-KILL

Heavy defoliation by the Douglas-fir tussock moth is known to cause top-kill in white fir in California (Wickman 1963). No studies have been published of top-kill in other host species and in other areas. The top-kill damage was examined carefully and continuously through the course of this outbreak and the results are summarized similarly to the tree-mortality data. The top-kill summaries that follow are based on percent of total trees alive in 1976 except for the analysis of the relation of susceptibility of top-killed trees to mortality caused by bark beetle.

Related to individual-tree defoliation categories.--Five top-kill classes were compared for each of six defoliation categories (table 14, appendix). The most severe top-kill occurred in the trees suffering highest amounts of defoliation, and leader damage was the most common class of top-kill (figs. 13a and 13b). Trees with 1 to

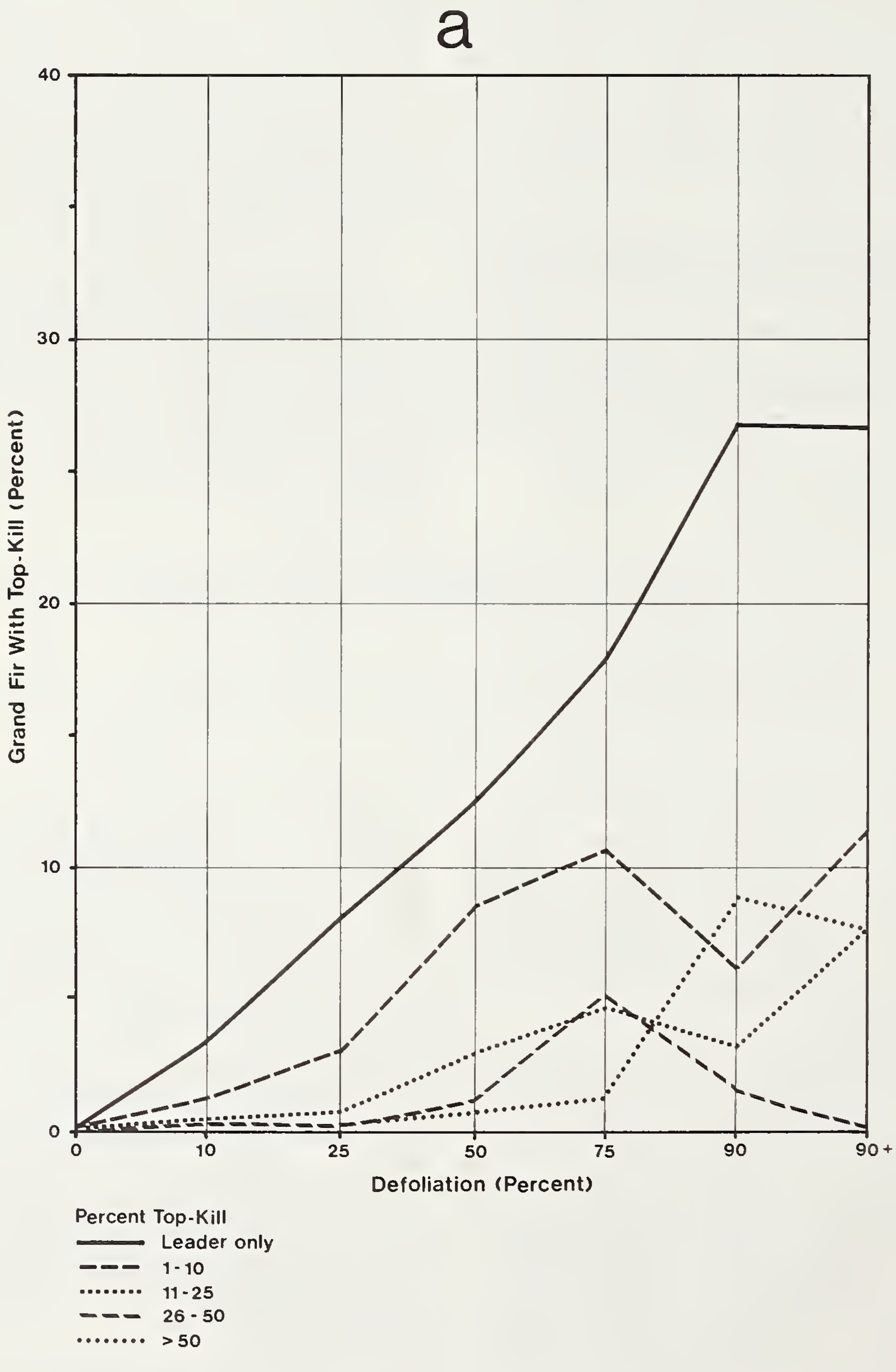


Figure 13.--a, Percent of grand fir in various top-kill classes by percent defoliation.

Figure 13.--b, Percent of Douglas-fir in various top-kill classes by percent defoliation.

10 percent of the crown top-killed were the next highest class, and most of this damage occurred in trees defoliated 25 to 75 percent. In grand fir, 4.8 percent of the top-kill occurred in this class and, in Douglas-fir, it was 12.7 percent. A consistent trend of top-kill incidence was found,

severity increased with severity of defoliation of grand fir, with a total of 8.4 percent of the trees suffering top-kill exclusive of leader-only damage. Leader mortality temporarily affects growth, but it rarely causes deformity in the tree crown. Within a year or two of the leader damage, a lateral is established as a new terminal; and detecting the damage later is almost impossible. Some deformity can occur when two laterals continue to maintain dominance in terminal growth, resulting in a fork-top tree.

In Douglas-fir, the trend was not as consistent except for the leader-only class. Top-kill peaked in the 75-percent defoliation category, and then dropped off in the 90- and 90+-percent categories with a total of 16.4 percent of the Douglas-fir suffering top-kill exclusive of leader-only damage.

Severe top-kill (greater than 25 percent of the crown) amounted to only 2 percent of the total for both tree species, and most of this damage occurred in trees defoliated 75 percent or more. Top-kill of this magnitude would usually be included in salvage logging programs.

Related to d.b.h. class.--Top-kill was also summarized in d.b.h. classes and the five top-kill classes (table 15, appendix). For grand fir, 17 percent of the trees larger than 12 inches d.b.h. suffered some top-kill exclusive of leader-only damage (fig. 14a). In Douglas-fir, 8.8 percent of trees 12- to 24-inch d.b.h. suffered 1 to 10 percent of their crown length top-killed, and 25 percent of the trees larger than 24-inch d.b.h. suffered some form of top-damage exclusive of leader-only (fig. 14b).

These figures are comparable to the 12 percent of merchantable white fir (larger than 12-inch d.b.h.) top-killed in heavily defoliated areas in California (Wickman 1963). In that study, no further breakdown was made of top-damage by defoliation categories or d.b.h. classes. After the Stowe Reservoir outbreak, however, we found 19-percent top-kill with a similar distribution by diameter class (Wickman 1978).[8/]

The long-term effects of top-kill damage are related to d.b.h. class. Trees 25-inch d.b.h. and larger with less than 25 percent of the crown killed are probably not a significant economic loss because the trees are growing slowly at that age and harvest is imminent. Trees 25-inch d.b.h. and larger with more than 25 percent of the crown killed amounted to 4.5 percent of the top-killed grand fir and 8.3 percent of the top-killed Douglas-fir in this d.b.h. class, and most of these trees will probably be salvage logged where accessible. The next smaller merchantable size class (12- to 24-inch d.b.h.) are intermediate in harvest priority, but crowns top-killed more than 25 percent should be salvaged with the larger trees.

Decay volumes increased with age and basal diameter of dead tops in a recent study of top-kill caused by tussock moth in the Blue Mountains.[9/] In

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[8/] Unpublished data on file at Forestry Sciences Laboratory, Corvallis, Oregon.

[9/] Aho, Paul E., Boyd E. Wickman, and Lee Roe. Incidence and rate of decay in host trees top-killed by Douglas-fir tussock moth in the Blue Mountains. In preparation for publication, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

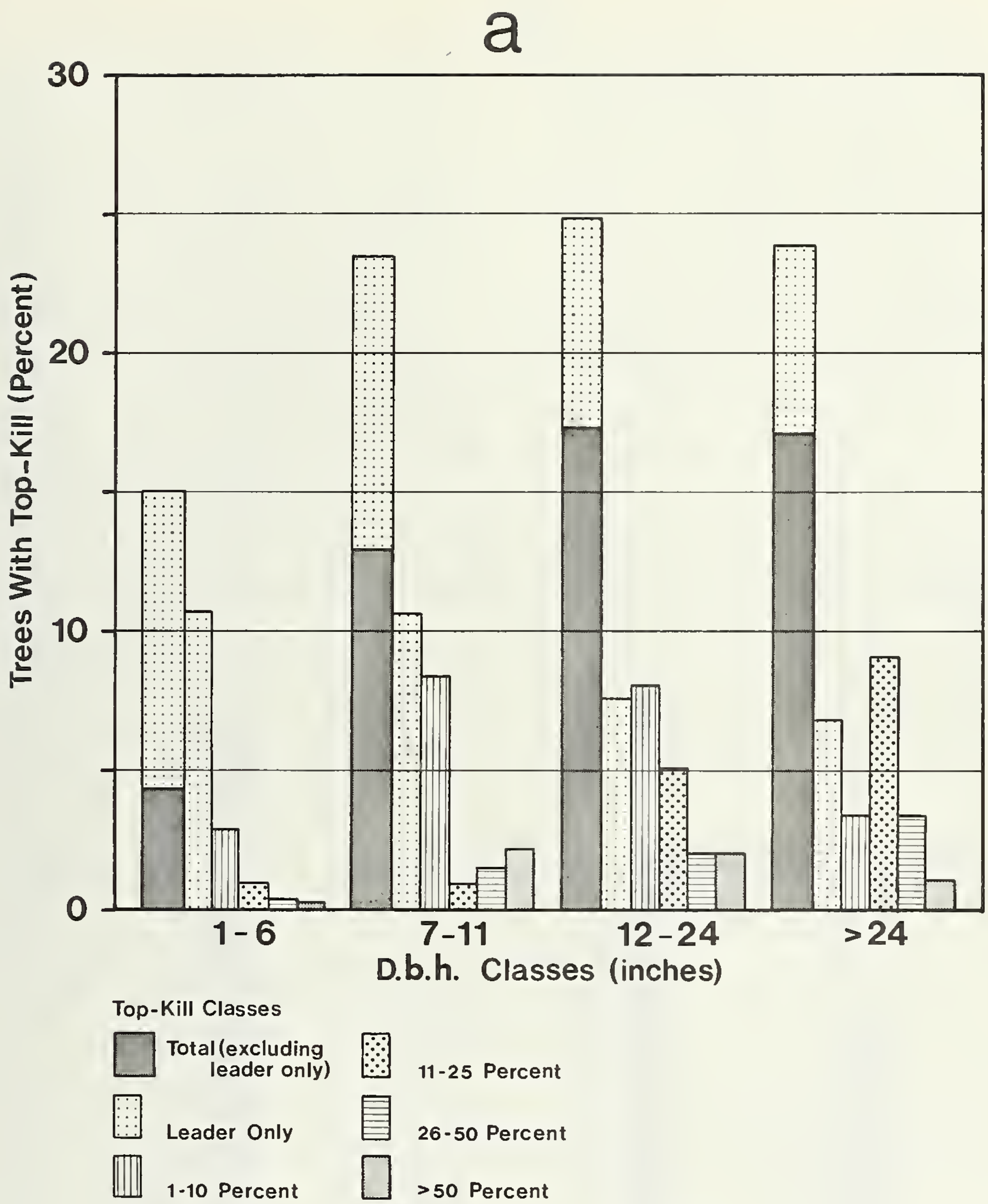

Figure 14.--a, Percent of grand fir trees in various top-kill classes (percent of crown killed) by d.b.h. classes (based on living trees, 1976).

stands of white fir on the east side of the Sierra Nevada fir stands, however, the threat of decay was not economically serious in merchantable trees 35 to 40 years after top-kill (Wickman and Scharpf 1972).

Top-kill in trees smaller than 12-inch d.b.h. is much more serious in terms of future growth and merchantability. In grand fir, 4.3 percent of the trees in the 1- to 6-inch d.b.h. class and 12.9 percent of the trees in the 7- to 11-inch d.b.h. class suffered top-kill, exclusive of leader-only damage. In Douglas-fir, the concentration of top-damage in these d.b.h. classes was much higher at 14.6 and 21.1 percent, respectively.

Distribution in four defoliation classes.--Top-kill was also summarized by the four de-

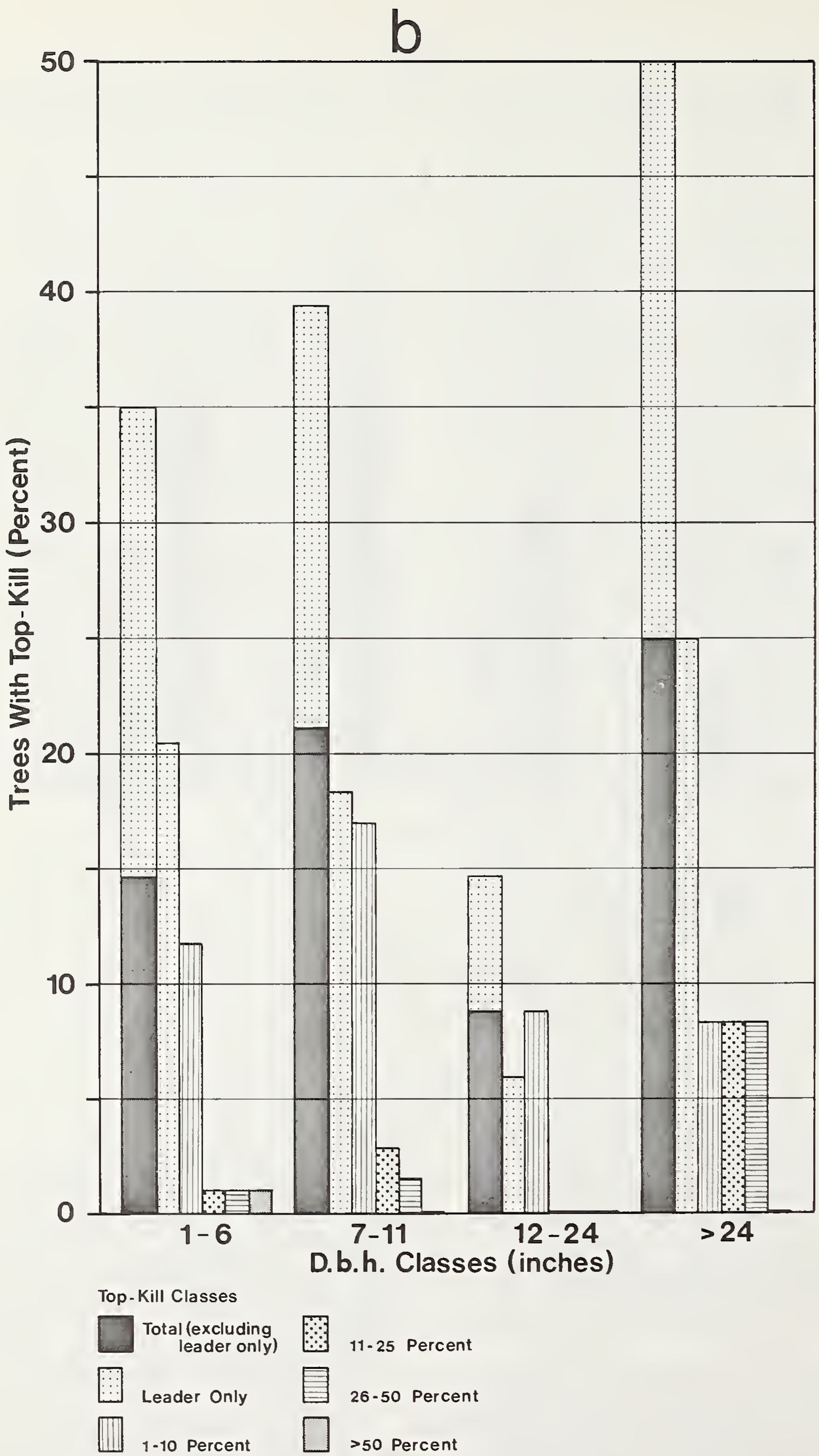

Figure 14.--b, Percent of Douglas-fir trees in various top-kill classes (percent of crown killed) by d.b.h. classes (based on living trees, 1976).

foliation classes of 1972. It was further stratified by the four mapped classes (table 16, appendix) and the four individual-plot defoliation classes (table 17, appendix) just as the tree mortality was organized earlier. These tables break down the percent top-kill in each of the top-kill classes by each of the broad defoliation classes. When top-kill is stratified by mapped defoliation class areas, most of the top-kill occurred in Douglas-fir, and the top damage was fairly evenly distributed through all four classes for both species. When stratified by the individual-plot defoliation class areas, Douglas-fir again suffers more than double the amount of top-kill of grand fir--but, most important, the top-kill is more realistically concentrated in the heavy class for grand fir and the heavy and moderate classes for Douglas-fir. Total top-kill, exclusive of leader-only damage for each of the tree species and the four mapped defoliation classes and four individual-plot classes is illustrated in figure 15.

The differences between the two methods of stratifying damage is not as pronounced in the relation of top-kill as they are for tree mortality. For both forms of damage, however, more tree damage occurs in the heavy class when stratified by individual-plot classes than by the mapped classes. The overall trend of top-kill in the four classes, by both methods of stratification, is similar to the trends of tree mortality presented earlier. The most striking relation in figure 15 is that Douglas-fir suffered more than double the amount of top-kill as grand fir.

One other interesting fact regarding top-kill emerged during this analysis of top-kill in the four defoliation classes. That was the level of top-kill before the outbreak, shown in table 8. Because this is not based on living trees in 1976, but rather on top-kill at the time of plot establishment, it gives some insight into "normal" or nonoutbreak-related top-kill in this section of the Blue Mountains. Top-kill before the outbreak for both grand fir and Douglas-fir was 8 and 6 percent, respectively.

When graphed (fig. 19, appendix) the low level of preoutbreak top-kill on heavy defoliation areas is evident. The reasons for this are not known. Perhaps it relates to population behavior of the tussock moth. The most dense populations may need full-crowned trees with a low level of chronic top-kill.

The Blue Mountains, or at least the outbreak areas, seem to suffer a chronic top-kill problem, related to a variety of biological and environmental causes. A windstorm in the winter of 1974, for instance, caused some severe top breakage on many of our plots. Other causes are bark beetles, mistletoe in Douglas-fir, porcupines, and snow damage.

Grand fir and Douglas-fir top-kill compared.--Figure 15 compares top-kill between grand fir and Douglas-fir for the four defoliation classes. Douglas-fir, suffering more than double the top-kill of grand fir--similar to the tree mortality relation--demonstrated more damage. This relation was investigated further by totaling the top-kill by species for each of the individual tree defoliation categories from table 14, appendix, and then graphing them separately (fig. 16). This graph shows that the trend for each species was similar, with the percent of Douglas-

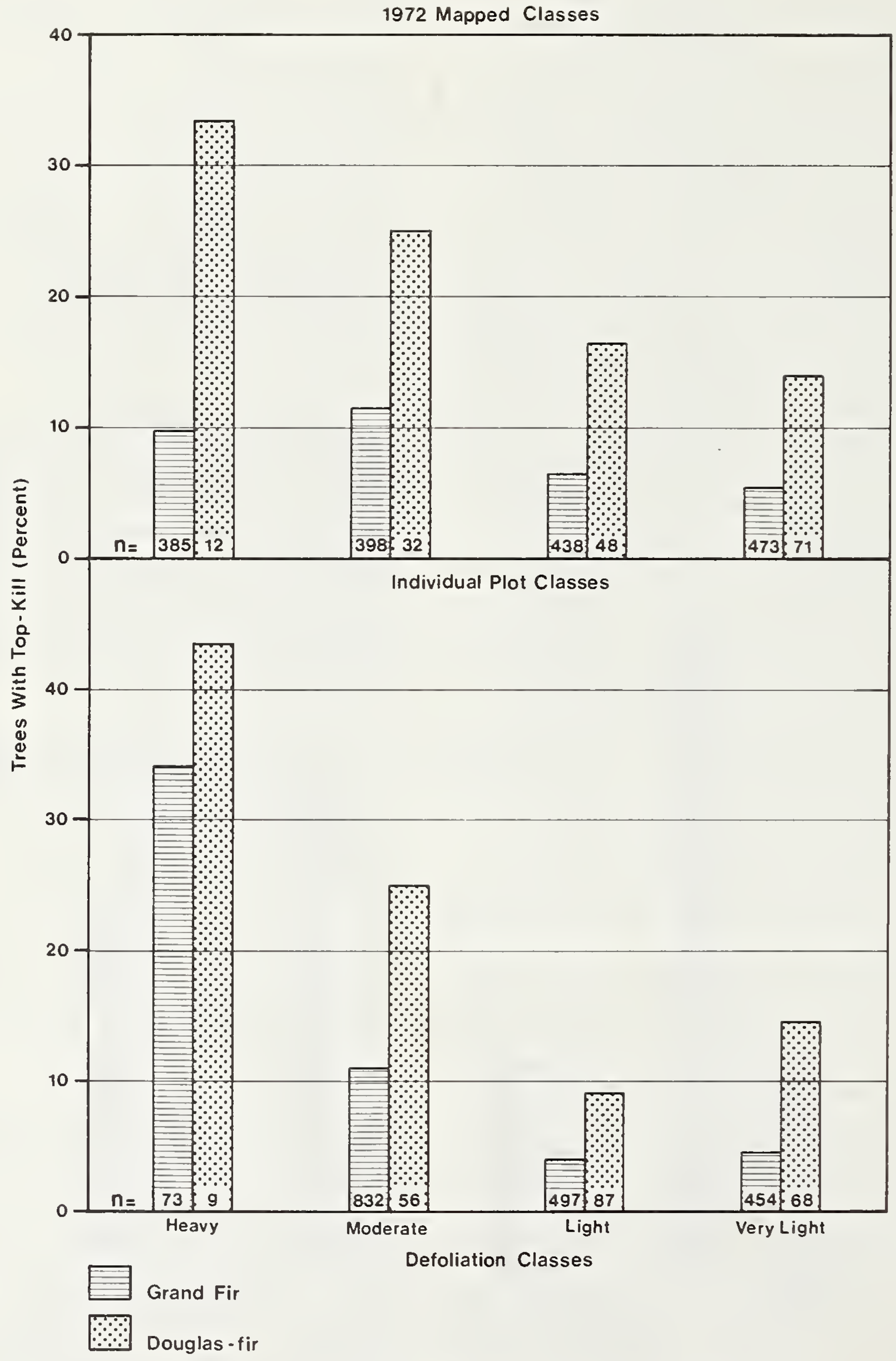

Figure 15.--Percent of trees with top-kill each 1972 defoliation class, exclusive of leader-only damage (based on living trees, 1976).

Table 8 --*Percent of trees with top-kill before Douglas-fir tussock moth defoliation, by defoliation classes*

Defoliation class	Mapped defoliation classes		Individual-plot defoliation classes	
	Grand fir	Douglas-fir	Grand fir	Douglas-fir
Heavy	3.7	2.2	1.1	1.4
Moderate	12.1	13.0	9.9	13.6
Light	8.7	11.9	6.6	5.0
Very light	8.7	6.5	9.3	6.9
Total	8.0	6.7	7.9	5.9

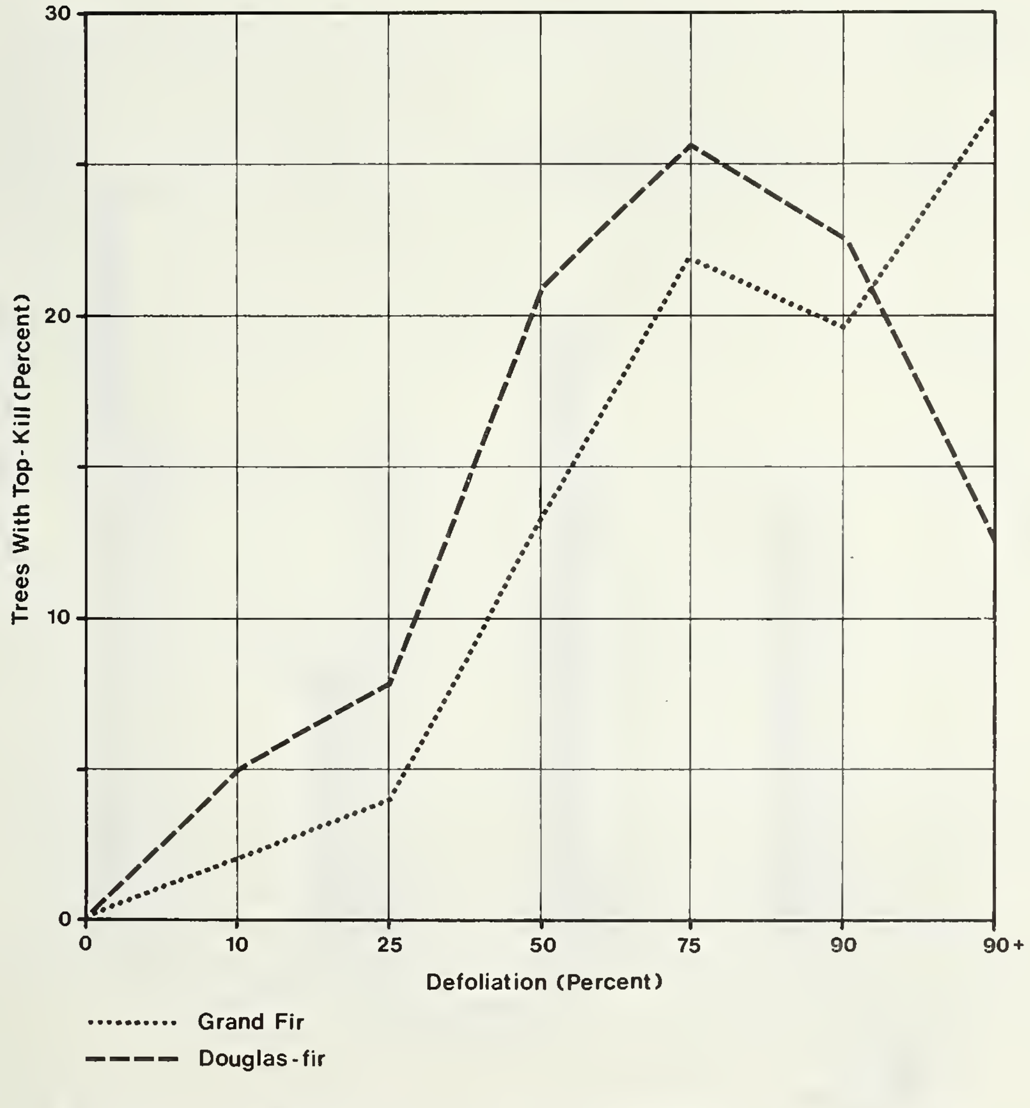

Figure 16.--Percent top-kill by defoliation categories (excluding leader-only damage).

fir top-kill higher than for grand fir up to the 90+-percent defoliation category when the trends drastically reversed. Almost 27 percent of the grand fir in this category suffered some top-kill (exclusive of leader-only), but Douglas-fir declined sharply to 12.5 percent of the survivors of this class with top-kill. This anomaly may not be significant because the data point consists of an eight-tree sample.

Next, the percent top-kill in each of the d.b.h. classes was summarized by species from table 15, appendix, and graphed in figure 17. And again, Douglas-fir suffered more top-kill in all except the 12- to 24-inch d.b.h. class. The trend here was drastically reversed with Douglas-fir suffering half as much top-kill as grand fir in this class (8.8 to 17.3 percent). The reason for this was unknown.

The pattern of Douglas-fir suffering more tree damage than grand fir in this outbreak remained consistent through the top-kill analysis as well as defoliation levels and tree mortality.

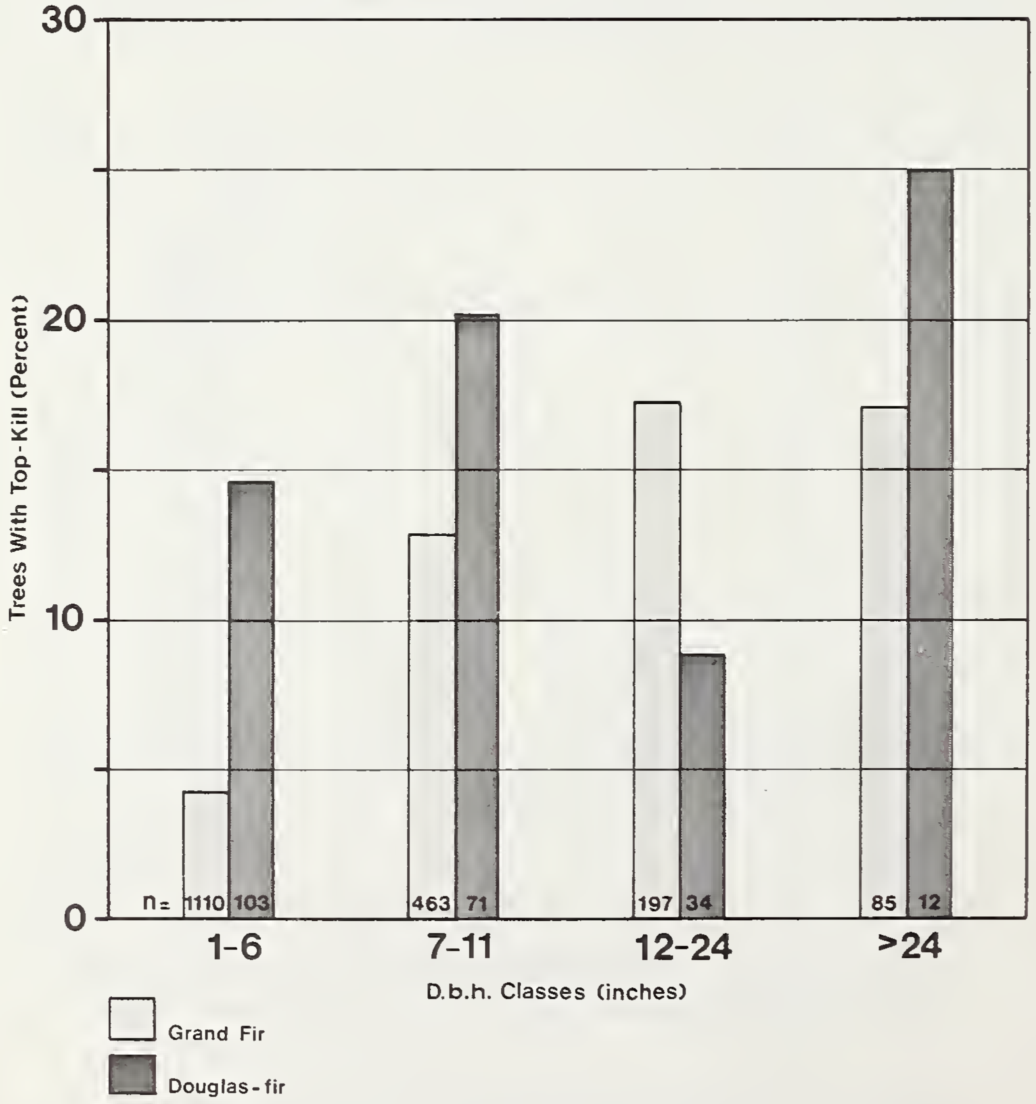

Figure 17.--Percent top-killed trees by d.b.h. classes (excluding leader-only damage).

Related to tree mortality from bark beetles.--In past outbreaks, for several years some top-killed white fir seemed to absorb repeated attacks by bark beetles near the top-killed portion of the crown, sometimes resulting in progressive crown die-back and tree mortality (Wickman 1963). An analysis was made to see if some top-kill classes were more susceptible to mortality from bark beetles than others. Mortality was tallied by year and cause for each species from 1974, when outbreak-caused top-kill could first be determined, to 1976 for each top-kill class (table 9).

A trend of increasing mortality from bark beetles with increased percent of crown top-killed is evident for Douglas-fir killed by Douglas-fir beetle. The trend is less evident for grand fir killed by fir engraver beetles, except in the 50-percent or greater top-killed class, where 47.2 percent of the trees were subsequently killed. The data base for the Douglas-fir is not large, but obviously both species with more than 50 percent of the crown top-killed have a high probability of being killed by bark beetles for at least several years after the outbreak subsides. This relation has also been used as a predictor for mortality from bark beetles in the Douglas-fir tussock moth outbreak model (see footnote 1). It should also be useful to the forest manager, when used in combination with percent of crown totally defoliated, for predicting tree mortality. Trees with 90 percent of the crown defoliated or 50 percent or more of the crown subsequently top-killed have a high probability of dying after a Douglas-fir tussock moth outbreak.

Table 9--*Percent of each top-kill class that was killed by bark beetles for Douglas-fir and grand fir (trees killed by tussock moth or other causes were excluded)*

Species	Percent of crown top-killed				
	Leader only	0-10	11-25	26-50	>50
Grand fir	0.5	2.2	3.0	5.3	47.2
Douglas-fir	0.0	3.4	33.3	25.0	66.7

Species	Total trees by top-kill classes (living trees and trees killed by bark beetle)				
	Leader only	0-10	11-25	26-50	>50
Grand fir	190	91	33	19	36
Douglas-fir	39	29	6	4	3

Acknowledgments

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Appendix

Table 10--*Comparison and t-test for significance between percent defoliation means of Douglas-fir (DF) and grand fir (GF) for each defoliation class in 1972 and 1973*

Defoliation class	Year	Species	Mean	S.E.	T value	
Heavy	1972	DF	92.38	2.40	1.17	N.S.
		GF	88.73	1.93		
	1973	DF	86.35	4.96	0.80	N.S.
		GF	82.26	2.54		
Moderate	1972	DF	39.02	3.64	0.31	N.S.
		GF	38.03	1.31		
	1973	DF	54.09	3.68	3.65	* *
		GF	42.47	1.32		
Light	1972	DF	10.82	0.52	1.58	N.S.
		GF	12.52	0.71		
	1973	DF	46.34	4.97	2.93	* *
		GF	30.87	2.78		
Very light	1972	DF	0.30	0.30	0.42	N.S.
		GF	0.18	0.13		
	1973	DF	57.25	5.62	3.09	* *
		GF	36.67	3.86		

N.S. = Not significant.

* * = Significant at .01 level.

Table 11--*Percent mortality and total number of Douglas-fir (DF) and grand fir (GF) by year of death and mapped defoliation class*

Year	Defoliation class							
	Heavy		Moderate		Light		Very light	
	DF	GF	DF	GF	DF	GF	DF	GF
	Percent stand (volume)							
1972	3.0	20.4	0.0	0.3	0.0	0.0	0.0	0.0
1973	3.7	5.9	1.1	1.1	0.6	0.0	0.3	0.0
1974	2.6	6.4	4.6	0.1	0.4	0.0	3.1	1.1
1975	0.8	2.5	2.7	5.5	0.1	0.0	0.3	0.4
1976	0.0	0.0	0.0	0.0	0.4	0.7	0.0	3.1
Totals	10.1	35.2	8.4	7.0	1.5	0.7	3.7	4.6
	45.3		15.4		2.2		8.3	
	Percent stand (number)							
1972	11.7	12.7	0.4	3.8	0.0	0.2	0.0	0.0
1973	3.0	4.1	1.4	1.8	0.2	0.8	2.1	3.2
1974	0.7	5.6	0.6	1.0	0.8	1.7	2.3	4.0
1975	0.3	0.5	0.8	0.8	0.2	0.8	0.3	0.5
1976	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.2
Totals	15.7	22.9	3.2	7.4	1.4	3.9	4.7	7.9
	38.6		10.6		5.3		12.6	

Total number of trees by defoliation class

Species	Heavy	Moderate	Light	Very light	Total
Grand fir	596	446	478	548	2,068
Douglas-fir	138	54	53	108	353
Total	734	500	531	656	2,421

Table 12--*Percent mortality and total number of Douglas-fir (DF) and grand fir (GF) by year of death and individual-plot defoliation class*

Year	Heavy DF	Heavy GF	Moderate DF	Moderate GF	Light DF	Light GF	Very light DF	Very light GF
	Percent stand (volume)							
1972	4.6	30.7	0.0	0.2	0.0	0.0	0.0	0.0
1973	16.6	11.1	0.1	0.1	0.7	0.0	0.3	0.0
1974	0.2	9.6	3.5	0.1	0.5	0.0	3.3	1.2
1975	1.2	10.5	1.6	1.6	0.2	0.0	0.3	0.4
1976	0.0	0.0	0.0	0.0	0.5	0.8	0.0	3.2
Totals	22.6	61.9	5.2	2.0	1.9	0.8	3.9	4.8
	84.5		7.2		2.7		8.7	
	Percent stand (number)							
1972	21.3	27.2	0.1	0.4	0.0	0.1	0.0	0.0
1973	6.8	6.9	0.4	1.3	0.9	0.9	1.8	3.2
1974	0.4	8.4	0.6	1.2	0.9	2.5	2.3	3.1
1975	0.5	0.5	0.4	0.8	0.1	0.5	0.3	0.2
1976	0.0	0.0	0.0	0.0	0.1	0.3	0.0	0.2
Totals	29.0	43.0	1.5	3.7	2.0	4.3	4.4	6.7
	72.0		5.2		6.3		11.1	

Total number of trees by defoliation class

Species	Heavy	Moderate	Light	Very light	Total
Grand fir	268	911	548	518	2,245
Douglas-fir	140	81	120	101	442
Total	408	992	668	619	2,687

Table 13--*Chi-square test for difference in probability of mortality between Douglas-fir and grand fir and in different individual tree defoliation categories*

Defoliation categories	Number of trees				
	Con-dition	Douglas-fir	Grand fir	x^2 (1)	Signif-icance
0-75	alive	206	1,801	0.52	N.S.
	dead	2	10		
90	alive	46	160	0.62	N.S.
	dead	12	31		
99	alive	14	31	0.04	N.S.
	dead	12	29		
100	alive	14	11	1.27	N.S.
	dead	133	167		

Table 14 --*Percent of trees in various top-kill classes by percent defoliation categories (based on living trees, 1976)*

Percent defoliation category	No.	Percent of crown top-killed						Total minus leader
		Leader only	1-10	11-25	26-50	>50	Total	
				GRAND FIR				
10	537	3.4	1.3	0.4	0.4	0.0	5.4	2.0
25	571	8.2	3.0	0.7	0.2	0.0	12.1	3.9
50	448	12.5	8.5	2.9	1.1	0.7	25.7	13.2
75	150	18.0	10.7	4.7	5.3	1.3	40.0	22.0
90	126	27.0	6.3	3.2	1.6	8.7	46.8	19.8
90+	26	26.9	11.5	7.7	0.0	7.7	53.8	26.9
Total	1,858	10.2	4.8	1.7	1.0	1.0	18.6	8.4
				DOUGLAS-FIR				
10	40	7.5	5.0	0.0	0.0	0.0	12.5	5.0
25	39	15.4	7.7	0.0	0.0	0.0	23.1	7.7
50	67	16.4	19.4	0.0	1.5	0.0	37.3	20.9
75	35	25.7	17.1	5.7	2.9	0.0	51.4	25.7
90	31	22.6	9.7	6.5	3.2	3.2	45.2	22.6
90+	8	37.5	12.5	0.0	0.0	0.0	50.0	12.5
Total	220	17.7	12.7	1.8	1.4	0.5	34.1	16.4

Table 15--*Percent of trees in various top-kill classes by d.b.h. class (based on living trees, 1976)*

D.b.h. class (inches)	No.	Percent of crown top-killed						Total minus leader
		Leader only	1-10	11-25	26-50	>50	Total	
				GRAND FIR				
1 - 6	1,110	10.7	2.8	0.9	0.4	0.3	15.0	4.3
7 - 11	463	10.6	8.4	0.9	1.5	2.2	23.5	12.9
12 - 24	197	7.6	8.1	5.1	2.0	2.0	24.9	17.3
>24	88	6.8	3.4	9.1	3.4	1.1	23.9	17.1
Total	1,858	10.2	4.8	1.7	1.0	1.0	18.6	8.4
				DOUGLAS-FIR				
1 - 6	103	20.4	11.7	1.0	1.0	1.0	35.0	14.6
7 - 11	71	18.3	16.9	2.8	1.4	0.0	39.4	21.1
12 - 24	34	5.9	8.8	0.0	0.0	0.0	14.7	8.8
>24	12	25.0	8.3	8.3	8.3	0.0	50.0	25.0
Total	220	17.7	12.7	1.8	1.4	0.5	34.1	16.4

Table 16--*Percent of trees in various top-kill classes stratified by 1972 mapped defoliation classes (based on living trees, 1976)*

Defoliation class	No.	Percent of crown top-killed						Number of trees with top-kill
		Leader only	1-10	11-25	26-50	>50	Total	
				GRAND FIR				
Heavy	385	15.1	5.2	1.6	1.6	1.6	24.9	96
Moderate	398	9.5	5.0	3.3	1.3	2.0	21.1	84
Light	438	3.9	4.6	1.1	0.7	0.2	10.5	46
Very.light	473	9.9	3.6	1.5	0.4	0.2	15.6	74
Total	1,694	9.4	4.5	1.8	0.9	0.9	17.7	300
				DOUGLAS-FIR				
Heavy	12	25.0	8.3	16.7	8.3	0.0	58.3	7
Moderate	32	18.8	15.6	3.1	6.3	0.0	43.8	14
Light	48	8.3	14.6	0.0	0.0	2.1	25.0	12
Very light	71	21.1	12.7	1.4	0.0	0.0	35.2	25
Total	163	17.2	13.5	2.5	1.8	0.6	35.6	58

Table 17--*Percent of trees in various top-kill classes stratified by 1972 individual-plot defoliation classes (based on living trees, 1976)*

Defoliation class	No.	Percent of crown top-killed						Number of trees with top-kill
		Leader only	1-10	11-25	26-50	>50	Total	
				GRAND FIR				
Heavy	73	34.2	13.7	4.1	6.8	9.6	68.5	50
Moderate	832	10.1	6.1	2.5	1.2	1.2	21.2	176
Light	497	7.4	3.0	0.4	0.2	0.2	11.3	56
Very light	454	9.5	2.9	1.2	0.4	0.0	14.1	64
Total	1,856	10.2	4.8	1.7	1.0	1.0	18.6	346
				DOUGLAS-FIR				
Heavy	9	44.4	22.2	22.2	0.0	0.0	88.9	8
Moderate	56	16.1	17.9	1.8	5.4	0.0	41.1	23
Light	87	14.9	8.0	0.0	1.1	1.1	24.1	21
Very light	68	19.1	13.2	1.5	0.0	0.0	33.8	23
Total	220	17.7	12.7	1.8	1.4	0.5	34.1	75

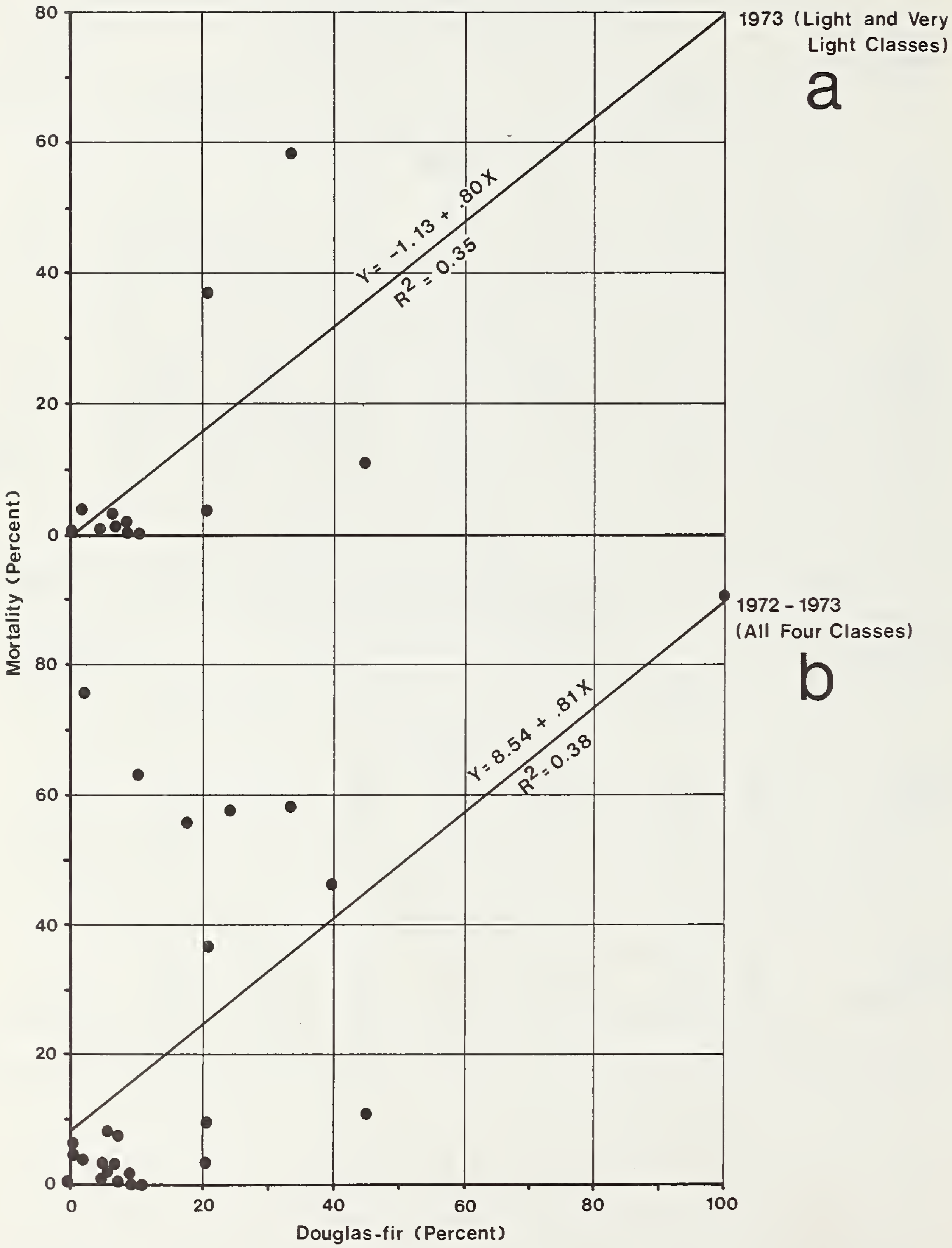

Figure 18.--The effect of percent Douglas-fir on total mortality of grand fir and Douglas-fir in light and very light classes from 1973 defoliation (a) and from 1972-1973 defoliation of all classes (b).

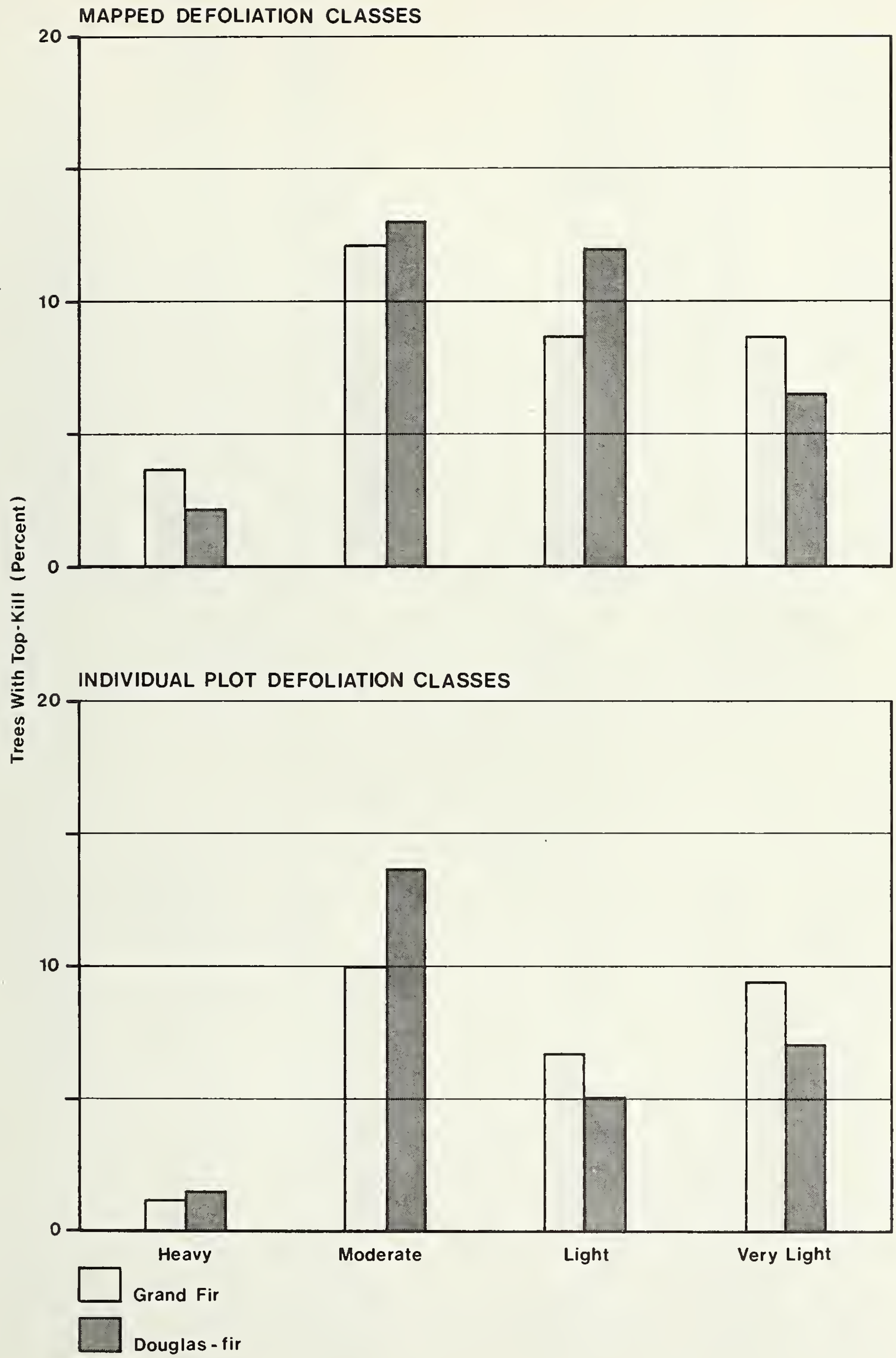

Figure 19.--Percent of trees with top-kill before tussock moth defoliation.

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Wickman, Boyd E.
1978. Tree mortality and top-kill related to defoliation by the Douglas-fir tussock moth in the Blue Mountains outbreak. USDA For. Serv. Res. Pap. PNW-233, 47 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Tree damage was studied from 1972 to 1976 following a severe DFTM outbreak. Tree mortality was strongly related to percent defoliation with most occurring in trees defoliated 90 percent or more. Top-kill was also more severe in heavily defoliated trees.

KEYWORDS: Insect damage (-forest, defoliation damage, Douglas-fir tussock moth, *Orgyia pseudotsugata*, Douglas-fir, *Pseudotsuga menziesii*, grand fir, *Abies grandis*, Oregon (Blue Mountains), Washington (Blue Mountains).

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Within this overall mission, the Station conducts and stimulates research to facilitate and to accelerate progress toward the following goals:

1. Providing safe and efficient technology for inventory, protection, and use of resources.
2. Developing and evaluating alternative methods and levels of resource management.
3. Achieving optimum sustained resource productivity consistent with maintaining a high quality forest environment.

The area of research encompasses Oregon, Washington, Alaska, and, in some cases, California, Hawaii, the Western States, and the Nation. Results of the research are made available promptly. Project headquarters are at:

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