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RADIAL GROWTH RECOVERY OF DOUGLAS-FIR IN DIFFERENT SITE AND STAND CONDITIONS AFTER WESTERN SPRUCE BUDWORM DEFOLIATION

by

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Radial Growth Recovery of Douglas-fir in Different Site and Stand Conditions after Western Spruce Budworm Defoliation (87 pp.)

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Relationships between the radial growth recovery of individual Douglas-fir trees and tree, site and plot conditions during and after infestation were investigated four years after the end of a decade long western spruce budworm (WSBW) infestation. Differences between surviving Douglas-fir and Douglas-fir that died during infestation were assessed.

Nonhost trees were used to isolate WSBW influence from other environmental influences on Douglas-fir (host) radial growth. Both an equation comparing paired host and nonhost radial growth and a "cumulative growth function" (Carlson and McCaughey 1982) were used to classify surviving Douglas-fir into three 'Recovery Classes'(RC1 through RC3).

Douglas-fir which had no growth reduction from infestation (RC1 trees) tended to be found on plots with significantly lower mean percentage of host tree basal area at infestation onset, and had significantly lower frequencies of current biotic and abiotic damage than Douglas-fir with growth reduction during infestation (RC2 and RC3 trees). Douglas-fir with no growth rate increase after infestation (RC3 trees) tended to be on plots with highest proportion of "average maximum basal area" during and after infestation, although mean values were significantly different only from RC1 trees and only during the infestation. Crown ratios were significantly lower for RC3 trees after the infestation.

Four discriminant analysis models were developed to predict Recovery Class membership. The most parsimonious model contained host tree crown ratio, percent topkilling, and plot percentage of host tree basal area as predictive variables. Classification success rates ranged from 55% to 62%.

Douglas-fir which died during infestation were significantly smaller in height and diameter, were more heavily topkilled, defoliated, and had lower crown ratios prior to death than surviving Douglas-fir.

Results and silvicultural management implications are presented in a hypothetical context.

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Most of all, thanks to my wife Gretchen, for her continued love, encouragement, and good humor.

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INTRODUCTION

The western spruce budworm (Choristoneura occidentalis Freeman) is a serious and periodic defoliator of western forests. Depending on locale, epidemic infestations may last in excess of a decade, and often result in severe radial growth loss, topkilling, and sometimes death of host trees (Johnson and Denton 1975). Contemporary research has indicated that western spruce budworm epidemic population densities vary under different forest conditions. In addition, western spruce budworm damage differs between individual host trees and changes under different site and stand conditions.

Study History

In 1978, at the end of a ten-year western spruce budworm (Choristoneura occidentalis Freeman) (WSBW) outbreak on the Lolo National Forest, Cooperative Forestry and Pest Management (CFPM) personnel conducted a survey of WSBW damage throughout the U.S.D.A. Forest Service Northern Region (Bousfield 1979). A series of permanent forest inventory plots, established by Northern Region Timber Management personnel in 1974, were remeasured by CFPM to obtain a representative estimate of region wide WSBW impact.

These data provided a unique opportunity to relate post-infestation radial growth recovery to:

1. site and stand conditions during and after a WSBW infestation and
2. intensity of WSBW defoliation and topkilling at the end of the

infestation.

In 1982, a subsample of these forest inventory plots on the Lolo National Forest were remeasured in order to evaluate radial growth recovery of Douglas-fir. CFPM supplied data from the 1974 forest inventory and the 1978 WSBW survey. A data set was then constructed which included:

1. the radial growth of host trees before,during and after the infestation,
2. cumulative defoliation, topkilling, and inventory remeasurements taken in 1978, and
3. 1974 stand conditions midway through the infestation.

Using these data, the objectives of this study were to:

1. determine the relationship of site, stand and individual host tree characteristics to the degree of host tree radial growth recovery after WSBW infestations by using nonhost trees to differentiate WSBW from climatic influence on host tree radial growth;

2. determine characteristics of host tree which survived the WSBW infestation and those that died during the infestation;

3. develop a model which predicts the degree of radial growth recovery after infestations, and evaluate variables within the model in terms of their biological implication and silvicultural management potential.

An understanding of the relationship between host tree radial growth recovery (and host tree mortality) after WSBW infestations, and tree, site, and stand characteristics is valuable for several reasons.

First of all, although defoliation intensity is a measure of infestation severity, radial growth loss from defoliation is a more accurate measure of the effect of infestations on wood production. Extending this concept, an investigation of post-infestation radial growth recovery leads to greater understanding of the long term impact of infestations on forest growth. Little research has assessed growth recovery of different trees, sites or stands, yet this information should increase the understanding of different vulnerability of various forest types, especially when added to, or compared with, the existing body of knowledge examining relationships between site or stand conditions and defoliation intensity or radial growth loss. The additional understanding of radial growth recovery in different conditions should therefore broaden the scope of WSBW stand hazard-rating models.

For the silviculturist, an understanding of radial growth recovery has both economic and biological implications. Stands stagnated by WSBW infestations, or stands with predictably slow recovery rates could be prioritized for harvesting before stands which recover quickly to pre-infestation growth rates. Identification of those site and stand characteristics most related to rate or type of radial growth recovery could in turn guide silvicultural practices designed to enhance recovery potential of host stands.

REVIEW OF LITERATURE

WESTERN SPRUCE BUDWORM - FOREST DYNAMICS

Mott (1963) reasoned that forest condition influences spruce budworm (Choristoneura fumiferana [Clem.]) populations, and conversely, that budworm influences forest condition. He defined susceptibility as " the probability...of a forested area being attacked ", whereas forest vulnerability indicates " the probability that damage will result from the attack ". Susceptibility indicates relative suitability of a forest stand to support increasing budworm populations, while vulnerability first implies some degree of susceptibility, but also indicates the ability of a stand or host tree to withstand budworm infestation. Vulnerability therefore suggests host tree vigor and presumably is related to environmental conditions that influence tree vigor, such as severity of site or tree competition. Mott (1963) indicated that vulnerability varies under different forest conditions even when budworm intensity of attack, or susceptibility, is held constant. Vulnerability then, encompasses susceptibility, but does not imply a given degree of susceptibility. Williams et al. (1971), for example, found that open grown stands of Douglas-fir supported higher populations of WSBW, in contrast to higher mortality in dense, stressed, smaller stands of Douglas-fir where WSBW populations were lower.

The life cycle of the WSBW takes place in one year. After mating in late July to mid August, the gravid female moth lays eggs in clustered groups on the underside of conifer needles. Eggs hatch in about ten days and the tiny first instar larvae disperse to find shelter in bark crevices, or under lichens, where they spin hibernacula and overwinter. The following May or June, the larvae, now in the second instar, emerge and bore into vegetative or reproductive buds or mine older needles. New foliage is preferred by larvae; older foliage is only fed upon when supplies of new foliage are exhausted. WSBW larvae continue to feed on expanding new foliage until the larvae reach the end of the sixth instar when they pupate, generally in early July. Adult moths emerge about ten days later, fly, mate, and complete the life cycle (Fellin and Dewey 1982).

The WSBW preferentially defoliates several conifers including Douglas-fir, grand fir (Abies grandis [Dougl.] Forbes), subalpine fir (Abies lasiocarpa [Hook.] Nutt.), western larch (Larix occidentalis Nutt.), and Engelmann spruce (Picea engelmanii Parry). Other conifers are only occasionally but not extensively defoliated (Johnson and Denton 1975). Western larch is preferred early in the season because of its early bud burst, but WSBW larvae soon move to other host species. WSBW can sever terminal leaders of young western larch (Fellin and Schmidt 1973).

In stands of mixed host species, vulnerability of host species roughly followed their relative shade tolerance (Carlson et al. 1983; Johnson and Denton 1975; Williams 1966,1967). The true firs (Abies) generally were more heavily defoliated, topkilled, and suffered greater radial growth reduction than Douglas-fir (Bousfield, 1979,1980; Brubaker and Greene 1979; Mika and Twardus 1983; Scott and Nichols 1983; Stoszek et al. 1981; Williams 1966,1967). Mortality was highest in stands primarily composed of grand fir (Mika and Twardus 1983) and subalpine fir (Bousfield and Williams 1977; Bousfield 1979,1980). Engelmann spruce received about the same level of damage as Douglas-fir (Williams 1966) while grand fir was slightly more defoliated than subalpine fir (Stozek et al. 1981). However Douglas-fir was most heavily defoliated on sites where it was the climax species (Sutherland 1983). Douglas-fir was most often reported defoliated and killed during WSBW infestations (Johnson and Denton 1975).

Severity of WSBW infestations may be greatest in habitat types where climax host species are under the greatest physiological or competitive stress. Carlson et al. (1982) noted greater infestation severity in dry Douglas-fir habitat types than in moderately mesic subalpine fir habitat types. Severity of past WSBW infestations did not influence probability of regeneration stocking in moist Douglas-fir habitat types, warm and moist grand fir, subalpine fir, or western red cedar habitat types, or moist subalpine fir habitat types (Carlson et al. 1982). Stoszek et al. (1981) noted heavier defoliation in grand fir and subalpine fir unions than stands in the mountain hemlock or western red cedar unions. The grand fir union was the warmest and droughtiest, and the subalpine fir union was the coolest and least productive of these unions. Host species of WSBW were the climax species within these unions (Stoszek et al. 1981). A union is a group of habitat types having the same climax tree species (Daubenmire and Daubenmire 1968).

The common practice of excluding fire from western forests in the twentieth century has greatly altered forest composition and favored ingrowth of the more climax, shade tolerant species. Ingrowth of these species probably greatly increased susceptibility and vulnerability of western forests to the WSBW (Gruell et al. 1982).

Stand susceptibility and vulnerability increases as proportion of host trees within stands increases. Fauss and Pierce (1969) noted an increase in defoliation intensity with increased percent Douglas-fir in stands. Host tree radial growth loss increased as percent of stand host basal area increased (Bennett 1978; Carlson and Theroux 1982; Harvey 1982; Mika and Twardus 1983). Anderson (1981), when developing a probability model for defoliation, noted that increased percent crown coverage of true fir (Abies) and Douglas-fir was in part related to increased probabilty of defoliation.

Higher stand densities increase vulnerability to WSBW by increasing competitive stress and lowering vigor of host trees. Higher stand densities may also be related to ingrowth of shade tolerant species preferred by WSBW. Williams et al. (1971) noted greater mortality of defoliated Douglas-fir in dense stressed stands. Defoliation intensity increased in more densely stocked stands of mixed Douglas-fir and ponderosa pine, although increased stocking was also associated with increased percent Douglas-fir (Fauss and Pierce 1969). Scott and Nichols (1983) found stand density significantly correlated with duration of WSBW infestations. Stoszek et al. (1981) noted increased defoliation with increased crown competition factor in subalpine fir series habitat types. In western hemlock series habitat types, however, defoliation intensity decreased with increasing crown competition factor and greater variability in stand age.

Stand structure, primarily in terms of tree height variability, influences susceptibility and vulnerabilty of stands or of individual host trees within stands. In multistoried stands, understory Douglas-fir were more heavily defoliated (Fauss and Pierce 1969). Scott and Nichols (1983) found heavier defoliation in lower crown classes of some stands, whereas in other stands this relationship was reversed. In all cases, defoliation trends between crown classes were weak. Alfaro et al. (1982) found no correlation between defoliation intensity and host tree crown class or diameter. However supressed and intermediate host trees suffered greater mortality. Mika and Twardus (1983) indicated that smaller diameter trees were most often topkilled, although growth loss and mortality were highest in single-storied pure host stands.

Carlson et al. (1982) stated that mature, multistoried stands were probably more susceptible and vulnerable to WSBW because host trees of intermediate strata catch and sustain larvae which would otherwise drop to the forest floor. The taller trees in a multistoried stand probably presented more favorable oviposition, overwintering, and larval development sites for WSBW.

More spruce budworm egg masses were found in stands with older taller trees, or in the tallest trees within stands (Greenbank 1963; Mott 1963). Older balsam fir stands with irregular tree heights have greater crown exposure to sunlight and provide warmer, drier conditions more favorable for budworm survival (Mott 1963). Blais (1952) indicated that older, flowering balsam fir had greater numbers of egg masses and larvae and were more frequently killed than younger, nonflowering balsam fir.

Very small seedlings in the lowest strata may not be severly damaged by WSBW. Unpublished research by Fellin (1981) indicated that trees less than twenty centimeters in height received the least defoliation in a multistoried Douglas-fir stand. Carlson et al. (1982) studied five to fifteen-year old regeneration in clearcuts and concluded that these trees were not heavily defoliated because they provide small targets for dispersing WSBW larvae. However there was a weak trend towards heavier defoliation of regeneration as residual tree basal area increased. Because of the small stature of regeneration, most dispersing larvae probably fell to the ground and starved or were eaten by predators (Carlson et al. 1984). Batzer (1968) found a similar trend with understory balsam fir in the east; the balsam fir was more heavily defoliated when near taller residual black spruce (Picea mariana [Mill.] B.S.P.) or white spruce (Picea glauca [Muench.] Voss.).

Host trees on severe sites are more susceptible and vulnerable to WSBW. Fauss and Pierce (1969) found heavier WSBW defoliation on more severe sites where Douglas-fir had lower site indices than on better sites. Defoliation was higher in stands on dry side slopes than moister bottoms. WSBW populations and defoliation intensities were higher on upper slopes and ridgetops (Terrell 1959; Stoszek et al. 1981). Stands on harsh southwest aspects tended to suffer heavier defoliation (Stoszek et al. 1981). Carlson and Theroux (1982) found past WSBW infestations more severe in dry Douglas-fir habitat types on steeper slopes and at low elevations. Fellin (1980) noted that the heaviest WSBW damage to Douglas-fir east of the Continental Divide occurs on sites with dry and shallow soils.

Stand susceptibility and vulnerability to WSBW varies with elevation. WSBW emergence and development is delayed with increasing elevation (Silver 1960; Wagg 1958). Stoszek et al. (1981) found that most heavily defoliated elevational zones coincided with stands that contained the greatest proportions of host species. Elevation where heaviest defoliation occurs varies by locale. An eastern Washington study showed defoliation intensity to increase to 3400 feet and then decline at higher elevations (Anderson 1981). In northern Idaho, a probability model indicated maximum likelihood of defoliation at 6000 feet (Anderson 1981); whereas Stoszek et al. (1981) noted stands at 4000 to 5600 feet were most heavily defoliated. In western Montana, stands at 3500 feet had most severe infestations, with severity declining at higher elevations (Carlson et al. 1982). Regardless of locale, temperature decreases, moisture generally increases, and tree growing season shortens with increasing elevation. These combined factors likely control availability and vigor of host species as well as controlling environmental suitability for WSBW survival. These conditions probably are indirectly reflected by varied defoliation intensities and infestation severity at different elevations.

Defoliation Influence on Radial Growth and Mortality

Site and stand conditions moderate the influence of defoliation on radial growth and mortality of host trees. Alfaro et al. (1982) noted that host tree mortality rates were higher in the lower crown classes, although defoliation intensity was not different between crown or diameter classes. Scott and Nichols (1983) likewise found no consistent relationships between defoliation intensity and crown class, but found that larger diameter trees suffered less radial growth loss at all levels of defoliation. Diameter was not constant between study sites however, so that the diameter relationship may have reflected site differences. Variables describing tree size relative to surrounding trees were nonsignificant in a model describing tree growth, however slope and aspect significantly influenced host tree growth over all levels of defoliation (Scott and Nichols 1983).

Alfaro et al. (1982) found that the relationship between current year defoliation and current year radial growth was highly variable early in WSBW infestations but variability decreased in later years of infestation. They suggested that defoliation and radial growth were not highly correlated early in WSBW outbreaks because other factors "such as competition, crown class, and size of food stores" were more important in determining growth at this time.

Duration of attack, or defoliation history, was related to degree of radial growth reduction (Alfaro et al. 1982; Scott and Nichols 1983). Proportional diameter increment (i.e. ratio of actual to potential growth) for a given year of infestation could be predicted with a function combining current years defoliation with the summation of average stand defoliation for all previous years of infestation (Alfaro et al. 1982). A variable indexing duration of WSBW outbreak minus number of recovery years was significant in a model predicting ratio of actual to potential host tree growth (Scott and Nichols 1983).

Host tree mortality is related to cumulative yearly defoliation percent. Alfaro et al. (1982) found that Douglas-fir mortality did not occur until summation of annual percent defoliation reached 175%. At a cumulative defoliation of 350%, frequency of mortality reached 80%.

Radial growth reduction did not occur until one year after onset of defoliation (Brubaker and Greene 1979) and radial growth recovery did not begin until one year after defoliation cessation (Alfaro et al. 1982). Diameter increment between successive years of infestation was not reduced significantly when defoliation did not exceed 50% (Alfaro et al. 1982). After defoliation cessation, recovery to pre-outbreak diameter increment levels took about as long (Alfaro et al. 1982) or a little less than (Scott and Nichols 1983) the length of infestation.

Host tree mortality may not occur until several years after onset of defoliation. Alfaro et al. (1982) noted that defoliation-caused mortality did not begin until the third year of infestation and reached the highest levels two years after defoliation had ceased. Mortality rate recovered to pre-outbreak frequencies by five years after epidemic cessation.

Results differ in studies that have compared infestation period radial growth loss between host trees growing at different rates prior to infestation. Williams (1967) noted that the most rapidly growing grand fir prior to infestation suffered less percent growth reduction during infestation. However, of four externally distinguishable damage classes, only the class of least damaged trees grew significantly faster before the infestation. Pre-infestation growth rates of trees in the other damage classes were about the same, but growth loss during infestation was successively greater for more severely damaged trees (Williams 1967).

Mclintock (1955) compared balsam fir growth during spruce budworm infestation with five year pre-infestation growth rates. The fastest growing balsam fir prior to infestation suffered the greatest percent growth loss; a 75% growth decrease for fast growing trees as opposed to a 60% growth reduction in trees that grew more slowly prior to infestation. Miller (1973) noted that balsam fir growing most slowly prior to infestation suffered a 27% growth reduction, as opposed to a 53% growth loss for trees with intermediate pre-infestation growth rates and 39% growth loss for trees that grew most rapidly prior to infestation.

Radial growth loss due to WSBW defoliation is not distributed evenly over the host tree stem. Williams (1967) noted that radial growth increment was reduced least at the stump level and most at midcrown levels in grand fir, Douglas-fir and Engelmann spruce. Thomson and Van Sickle (1980) and Scott and Nichols (1983) also noted the greatest radial growth loss occurred in upper bole portions of WSBW defoliated Douglas-fir. Mott (1957) indicated that growth loss of balsam fir defoliated by spruce budworm was greatest in the upper bole.

WSBW defoliation or drought conditions in some instances caused formation of false rings, missing rings, or partial rings (Brubaker and Greene 1979; Thomson and Van Sickle 1980; Swetnam 1983). Scott and Nichols (1983) found that of 196 sampled Douglas-fir, ten trees formed partial rings for one or more years and four trees had missing rings. All abnormal ring formation occurred during infestation years and during years where even non-defoliated trees had decreased growth. The above were suppressed trees in dense stands.

ESTIMATING WSBW INFLUENCE ON RADIAL GROWTH

At least three methods have been used to evaluate the influence of defoliating insects on radial growth of host trees. All methods depend on estimates of potential host tree growth (in the absence of defoliation) in order to determine the degree to which defoliation has influenced growth.

Using Non-defoliated Host Trees on Different Sites

Growth of defoliated host trees has been compared to nondefoliated host trees at different locations to estimate defoliation influence. In order to estimate Douglas-fir tussock moth (Orgyia pseudotsugata [McDunnough]) defoliation impact on diameter and basal area growth, Wickman et al. (1980) compared defoliated grand fir and Douglas-fir to the same undefoliated species on different sites. An assumption was made that the ratio of pre-infestation to post-infestation growth was similar between defoliated and nondefoliated trees. Potential growth of defoliated host trees was calculated as the post-infestation value necessary to equilibrate growth ratios of defoliated and nondefoliated host trees. Growth loss was estimated as one minus the ratio of actual growth to potential growth of defoliated host trees (Wickman et al. 1980).

Batzer (1973) compared host trees in insecticide sprayed stands to trees in unsprayed stands on similar sites. The growth of the nondefoliated (sprayed) stands was then used as an estimate of potential growth in defoliated (unsprayed) stands. Because sprayed and unsprayed stands were on similar sites, growth differences due to different climate or site quality were controlled.

Using Pre-Infestation Growth of Host Trees

Williams (1967) compared ten to twelve year pre-infestation growth of WSBW defoliated grand fir, Douglas-fir and Engelmann spruce to infestation period growth of the same trees. Pre-infestation growth was adjusted to base values using covariance techniques. Radial increments of disks taken at stump height, base of live crown, and at two positions within the crown were averaged together to compare pre-infestation to infestation period growth.

Thomson and Van Sickle (1980) used pre and post-infestation growth patterns to interpolate or extrapolate Douglas-fir potential growth during WSBW infestation and recovery periods. Two methods were used. To develop the first method, Thomson and Van Sickle (1980) cited an observation by Duff and Nolan (1953) that ring width generally increases to a maximum in the first few rings from the pith, then declines gradually to the bark. Two least squares lines were fit: one line from the pith to just before maximum increment; and a second line from maximum increment to most current growth. Infestation and recovery years were excluded from least squares line development. Growth loss during infestation and recovery years were calculated as the difference between actual growth and the value of the least squares line(s) for that year.

The second method required the calculation of average increment for five-year periods including: initial five years of radial growth; five year period centered on maximum increment year; and five-year periods before and after infestation and recovery episodes. Line segments were then extended, connecting average growth points for the five-year periods. Potential growth was represented by the line segment interpolated across the infestation period (Thomson and Van Sickle 1980). Alfaro et al. (1982) applied the second method when studying WSBW effect on radial growth of Douglas-fir.

Scott and Nichols (1983) used an adaptation of an individual tree based growth model "Prognosis" (Wykoff et al. 1982), to project potential diameter growth estimates of Douglas-fir into a WSBW infestation and recovery period. "Prognosis" estimates future growth as a function of prior growth as well as moderating tree, site and stand factors . Actual growth during infestation was compared to the Prognosis estimate of potential growth (Scott and Nichols 1983).

Mika and Twardus (1983) evaluated diameter growth loss of WSBW infested Douglas-fir, grand fir and subalpine fir in eastern Oregon. They modelled a ten-year pre-infestation growth period as a function of time and the reciprocal of time (Diameter = $b_0 + b_1(\text{time}) + b_2(1/\text{time})$)

and extrapolated the model into the infestation period in order to estimate potential growth in the absence of defoliation. Growth loss was estimated by comparing actual infestation growth to potential growth.

Using Nonhost Trees to Determine WSBW Influence on Host Growth

Brubaker and Greene (1979) compared radial growth of ponderosa pine and lodgepole pine to grand fir and Douglas-fir in known WSBW defoliated areas and known Douglas-fir tussock moth defoliated areas. Nonhost trees were not used, however, to estimate potential host tree growth during defoliation periods. Instead, a negative exponential or linear curve was fit to the radial increment series after a method developed by Fritts (1976). After curve fitting, each increment value was divided by the value of the fitted curve at that point. This technique resulted in growth indices which are homogeneous in size and variance across the increment series. Potential growth for any given year is assumed to be the mean value of the growth index line, growth loss is the percent difference between actual and potential growth (Brubaker and Greene 1979).

Swetnam (1983) used nonhost ponderosa pine and pinon pine (Pinus edulis Engelm.) to differentiate between environmental influences and WSBW effects on Douglas-fir. After transforming radial increment series into growth indices, as described by Fritts (1976) and Graybill et al. (1982), all Douglas-fir index series for each site were averaged. Next the averaged index series for each site were subjected to a "low pass filter". The filtering process minimizes short term growth fluctuation by "multiplying each index value and surrounding values by a set of symmetrically weighted values" (Mitchell et al. 1965). Swetnam (1983) mathematically compared filtered host and nonhost growth indices in order to remove common environmental influences while preserving the WSBW influence. The technique, developed by Nash, Fritts and Stokes (1975), as used by Swetnam (1983) makes use of the formula:

$$\mathrm{CI} = \mathrm{INDEX(H)} - \mathrm{PRI}$$

where: CI=corrected host growth index (after removal of environment influences excepting WSBW).

INDEX(H)=uncorrected host index, PRI=growth fluctuations cau environmental influences common to host and nonhost given year.

more specifically:

$$\mathrm{PRI} = (\mathrm{SDEV(H)}/\mathrm{SDEV(NH)})(\mathrm{INDEX(NH)} - \mathrm{MEAN(NH)})$$

where: SDEV(H)=standard deviation of host index series

SDEV(NH)=standard deviation of nonhost index series

INDEX(NH)=index value of nonhost for a given year

MEAN(NH)=mean index value of nonhost (usually approx.=1)

(after Swetnam 1983).

Carlson and McCaughey (1982) tested the concept that nonhost ponderosa pine could be used to differentiate WSBW influence on Douglas-fir from environmental effects common to host and nonhost trees. Growth patterns of ponderosa pine and Douglas-fir were similar in areas with no WSBW infestation history, but dissimilar in areas with past known WSBW infestations (during the infestation periods).In addition, Douglas-fir and ponderosa pine responded similarly to seasonal precipitation fluctuations in nondefoliated areas.

In order to assess severity of past WSBW infestations, Carlson and McCaughey (1982) developed a graphical technique which depicted the cumulation of squared annual increment from the oldest to most recent year. These squared and cumulated increments tended to accentuate changes in growth rate and long term growth reduction. For each stand, host and nonhost mean cumulative squared annual radial increment was graphed and compared to verify the presence of WSBW-caused growth reduction in Douglas-fir. Potential growth in the absence of defoliation was estimated by extrapolating a line into the infestation period based on the shape of the curve during pre-infestation growth. Finally, a "Severity Index" was developed by comparing actual versus potential cumulative squared increment during infestation such that:

$$SI = 1- (T-G)/(P-G)$$

where: SI = Severity Index
G = cumulative squared annual radial growth at infestation ons
T = cumulative squared annual radial growth at end of infestat

P = projected cumulative squared annual radial growth at end o infestation

(After Carlson and McCaughey 1982).

METHODS

History and Design of Study Areas

Douglas-fir radial growth recovery was measured in 1982 in 25 stands using a combined total of 102 plots. These plots comprised a subset of a larger group of permanent inventory plots originally established by U.S. Forest Service personnel during a forest-wide inventory in 1974. The plots consisted of a series of permanently established 40 basal area factor (40 BAF) variable radius-plots with a 1/300 acre circular plot located at the same center point and were systematically located on a five-by-ten chain grid. Each tree on the 40 BAF plot was marked with a numbered metal tag allowing relocation of trees at future measurements. The sample grid was confined to a Forest Service subcompartment, which is an administrative land division generally delineated by topographical boundaries, property boundaries, or other administrative boundaries. Sampled subcompartments were randomly selected, probability proportional to size, on the Lolo National Forest (Dick Deden, pers. comm. 1985).

A 1978 WSBW survey, conducted by CFPM, utilized this permanent plot system to estimate the impact of WSBW infestations on the Lolo National Forest. Survey crews again took forest inventory measurements, and additionally recorded cumulative defoliation and topkilling of WSBW host trees. To make the sampling process more efficient, CFPM personnel measures only plots or subcompartments containing WSBW host trees.

In 1982 a subset of three forest inventory subcompartments, encompassing the 25 stands on the Lolo National Forest, were selected using the following criteria:

1. Subcompartments had to fall within WSBW infested areas for at le years, but could not be defoliated for at least three consecutive years to the 1982 measurement so that radial growth recovery could begin. Maps taken from yearly aerial surveys of WSBW infestations were supplied CFPM, and were used to determine candidate subcompartments (Table 1).

2. At least two-thirds of plots in the candidate subcompartments ha stocked and contain WSBW host trees, in order to make efficient use of f time.

3. Subcompartments had to be within several hours of Missoula, Mont within several hours of each other to minimize travel time.

Forest inventory data were again recorded in 1982, and two increment cores were taken at breast height from each tree greater than 2.4 inches d.b.h. (Table 2). Numbered metal tags fixed to trees on variable plots allowed positive re-identification of these trees, so that a data chronology from the three plot measurements could be constructed for each tree. Although trees on the 1/300 acre plots were not marked with numbered tags, many surviving trees could be re-identified using other characteristics indicated in the data of the previous measurement, as for example diameter. Therefore untagged trees above 2.4 inches d.b.h. on 1/300 acre plots were also increment bored if they could be identified using data from prior measurements. All plots within selected subcompartments were revisited, with the exception of nonstocked plots.

Table 3 describes the location and characteristics of the three subcompartments measured in 1982. The Mountain Creek subcompartment is located approximately 4 miles northwest of Alberton, Montana. Russian Bill and Quartz Creek subcompartments lay approximately 11 miles south and 13 miles southeast of Superior, Montana, respectively (straight line distance). Mountain Creek and Quartz Creek plots fall predominantly within *Pseudotsuga menziesii*/ *Physocarpus malvaceus* habitat types (Pfister et al. 1977). Russian Bill Creek has the most diverse habitat types, ranging from *Pseudotsuga menziesii*/ *Agropyron spicatum* habitat types to *Thuja plicata*/ *Clintonia uniflora* and *Abies lasiocarpa*/ *Xerophyllum tenax* habitat types. *Pseudotsuga menziesii*/ *Physocarpus malvaceus* habitat type is again the most prevalent habitat type within this subcompartment however.

TABLE 1. Defoliation History of Subcompartments as indicated by Aerial Surveys.

	Subcompartment		
Year	409-4	422-22	758-23
1962			
1963			
1964			
1965			
1966			
1967	/	/	/
1968	/	/	/
1969	/	/	/
1970	/	/	/
1971	X	X	X
1972	X	X	X
1973	X	X	X
1974	MH	MH	M
1975	MH	M	M
1976	/	M	M
1977	LM	L	/
1978	/		
1979	L		
1980			
1981			
1982			

Legend: / = Defoliation indicated on region wide maps only.
X = Defoliation indicated on forest maps and region wide maps (no forest maps could be located for 1968 - 1970).
L = Low defoliation intensity observed.
LM = Low to medium defoliation intensity observed.
M = Medium defoliation intensity observed.
MH = Medium to high defoliation intensity observed.

TABLE 2. Data collected at the three plot measurements, (1974, 1978, 1982).

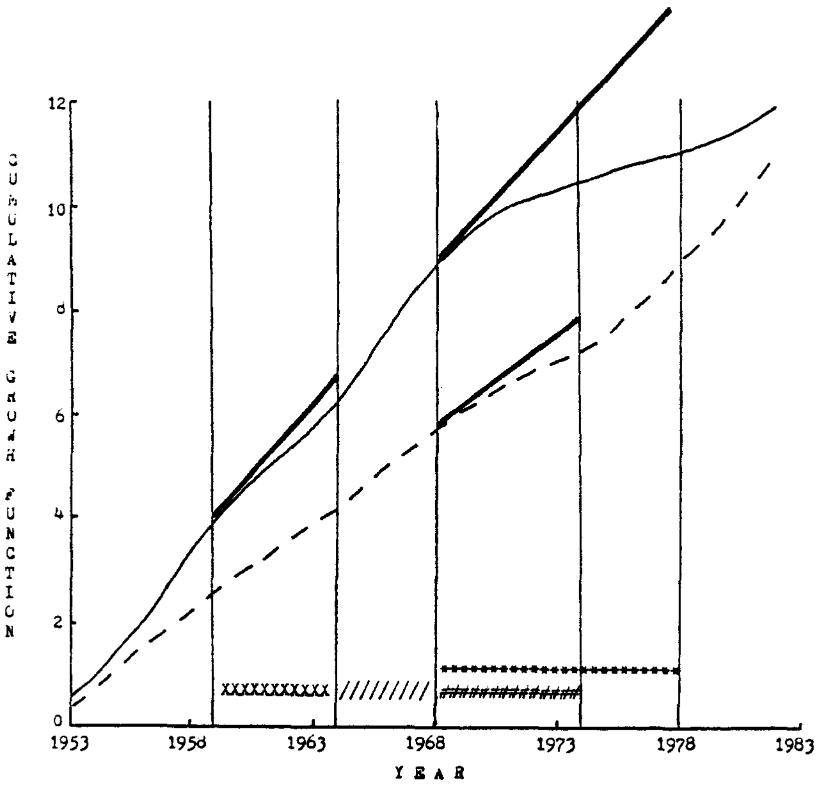
Tree Measurements	Plot Measurements
Species	Basal Area
Diameter breast height	Habitat type (Pfister et al. 1977)
Height	Aspect
Age	Slope
Crown Class	Elevation
Crown Ratio	Physiographic Site
Cumulative % Defoliation (1978)	
Percent Topkilling (1978)	
Other biotic and abiotic damage (1978,1982)	
Radial Growth Series (two increment cores from each tree)	

TABLE 3. Description of study areas.

	Subcompartment			
	409-34	422-22	758-23	Total
Name and Location	Mountain Creek T15N R23W	Quartz Creek T15N R26W	Russian Bill Crk. T15N R26W	
Number of Stands	10	6	9	25
Number of Plots	30	32	40	102
Elevation range	3900-5200'	3700-5300'	4500-6100'	3700-6100
Slope range	20-70%	20-70%	10-80%	10-80%
Predominant Habitat types	PSME/PHMA PSME/CARU	PSME/PHMA PSME/CARU	PSME/PHMA PSME/CARU ABGR/XETE PSME/VAGL	
Number of Host trees sampled:				
Live, Recovery Class	48 DF	51 DF	80 DF 2 GF	177 DF 2 GF
Live, non-Recovery Class		2 DF	23 DF 3 GF	27 DF 3 GF
Dead	36 DF	19 DF	63 DF	118 DF
Number of non-host trees paired with Recovery Classes	15 PP 2 WL	21 PP	6 PP 18 LP	

DF = Douglas-fir
GF = grand fir
PP = ponderosa pine
LP = lodgepole pine
WL = western larch

Figure 1. Average Cumulative Growth Functions of Dominant and Codominant Douglas-fir and ponderosa pine in subcompartment 409-34.



——— Douglas-fir

\- - - ponderosa pine

XXXXXX interpreted WSBW infestation

////// no WSBW influence on host radial growth, interpreted

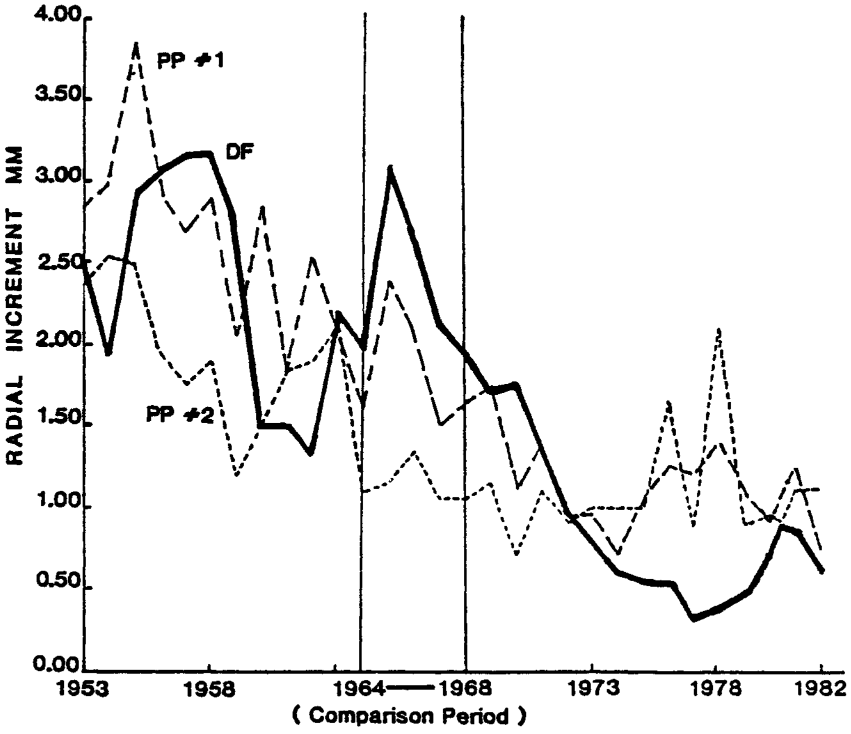
interpreted climatic influence on host and nonhost radial growth decline

****** WSBW infestation documented, effect on host radial growth interpreted

▬▬▬ Extrapolated potential growth (in the absense of WSBW infestation or climatic fluctuation)

Figure 2. Annual radial increments of candidate host and nonhost pairs. Because, during the comparison period, ponderosa pine # 1 (PP # 1) had the greatest number of peaks and troughs coinciding with the Douglas-fir (DF), these two trees were paired for further analysis.

PAIRING HOST with NONHOST



"Best" Pair : DF with PP#1

RADIAL GROWTH ANALYSIS

To prevent drying of increment cores, each core was sealed in a plastic straw immediately after collection, according to a method described by Carlson and McCaughey (1982). Age to pith and width of annual rings were determined using an Addo-X measuring device set to a precision level of 0.1 mm. Annual ring width for each tree was averaged using the two increment cores taken from each tree.

Graphical Depiction of Radial Growth and Derivation of Recovery Classes

Radial growth of individual host trees was graphically depicted, using a "cumulative growth function" (Carlson and McCaughey 1982), in order to classify each tree into one of three growth recovery classes:

RECOVERY CLASS 1; host trees showing no growth reduction due to WSB defoliation (RC1).

RECOVERY CLASS 2; host trees with radial growth reduction from defoliation, but showing growth rate increase (re after defoliation (RC2).

RECOVERY CLASS 3; host trees with radial growth reduction from defoliation, but with no growth rate increase (no recovery) after epidemic cessation (RC3).

The cumulative growth function (CGF) was calculated by squaring and cumulating yearly annual radial increment with the previous year(s) cumulative squared increment(s) such that:

radial increment growth for year i = g_i and:

$$\text{cumulative growth for year } n = g_i^2 + g_{i+1}^2 + g_{i+2}^2 + \ldots + g_{n-1}^2 + g_n^2$$

(after Carlson and McCaughey 1982)

In this study CGF was calculated for a thirty year period from 1953 to 1982.

Determining Recovery Class 1 Membership

Originally, Recovery Class 1 (RC1) membership was to be determined by using nonhost trees to isolate WSBW influence on host tree radial growth, according to methods described by Carlson and McCaughey (1982). Where the CGF of host, but not nonhost trees was depressed, this growth depression would be interpreted as caused by WSBW infestation. However examination of CGF curves indicated that growth of nonhost trees was depressed at the beginning of the WSBW infestation. This growth depression was interpreted as caused by climatic influence. Because growth of host trees might also be depressed in part because of climatic influence (in addition to WSBW influence), simple comparison of CGF of host and nonhost trees could not adequately differentiate the effect of WSBW defoliation from climatic influence on Douglas-fir radial growth

(Figure 1). Instead, an alternate method was used to differentiate climatic from WSBW influence on host radial growth. First, a procedure to pair individual host and nonhost trees was developed. Second, an equation was developed, using the paired host and nonhost trees, to determine whether WSBW growth reduction of host trees had occurred.

Pairing Host and Nonhost Trees

Annual radial increment of host and nonhost trees, during a time period free of WSBW influence on host radial growth, was used to select the best host/nonhost pairs. Examination of average CGF of host trees indicated two periods of growth depression, from approximately 1959 to 1963 and from 1969 to 1978, which were interpreted as caused by WSBW infestation. The time period from 1964 to 1968 was selected as apparently free from WSBW influence on host radial growth and this period was used to pair host and nonhost according to the following method.

Those host and nonhost trees with radial increment graphs having the greatest number of coincident peaks and troughs from 1964 to 1968 were considered to form the best host/nonhost pair (Figure 2). A preferential sequence was followed for selecting candidate host/nonhost pairs. First, host trees were compared only to the set of nonhost trees on the same plot, and each host tree was paired with the best corresponding nonhost tree from that set. Second, if no nonhost trees were on a given plot, then the candidate nonhost tree set was selected from adjacent plots within the same stand as host trees on that given plot. Finally, if no nonhost trees were present on plots within a sampled stand, nonhost trees from adjacent stands most similar in aspect and elevation were paired with host trees in the first stand. Stand, aspect, and elevation similarities were determined from original plot location maps that delineated stand boundaries and topographic contours. Host/nonhost trees within the same crown class were paired, except where no pair within the same crown class could be found. In the latter situation, host/nonhost pairs were determined solely on similarity of annual radial increment graphs irrespective of crown class. Due to these pairing criteria, in several instances a single nonhost trees became the most suitable candidate for pairing with more than one host tree. Number of host trees paired with a single nonhost tree ranged from one to ten host trees.

Equation for Determining Recovery Class 1 Membership

A ratio of average pre-defoliation radial growth to radial growth during defoliation was calculated for each host and nonhost tree. The ratio of host and nonhost tree growth for each host/nonhost pair was then compared. If the host tree ratio was greater than or equal to the nonhost tree ratio, then the host tree was considered to not be influenced by WSBW defoliation and assigned to Recovery Class 1. Host trees not meeting this criteria were considered to have suffered radial growth decline from WSBW defoliation, and were assigned to Recovery Class 2 or 3 using other criteria.

In order to calculate the ratio, average annual increment for the defoliation period (1969-1978) was divided by average annual increment for the pre-defoliation period (1964-1968):

if: $Hd/Hb >= NHd/NHb$, then the host tree was classified into
Recovery Class 1.

where: Hb = Average host tree radial increment, 1964-1968
Hd = Average host tree radial increment, 1969-1978
NHb = Average nonhost tree radial increment, 1964-1968
NHd = Average nonhost tree radial increment, 1969-1978

Wickman et al. (1980) used similar comparisons of growth ratios when comparing DFTM defoliated and nondefoliated host trees.

Determining Recovery Class 2 and 3 Membership

CGF graphs of host trees not assigned to Recovery Class 1 were further examined, and assigned to Recovery Class 2 or 3 using the following definitions:

1. If the CGF curve of the host tree showed an upward deflection at any time after 1978, the tree was assigned to Recovery Class 2 (RC2).

2. If the CGF curve of the host tree showed no upward deflection after 1978, the tree was assigned to Recovery Class 3 (RC3).

Recovery was therefore defined as an increase in radial growth rate at any time after defoliation had ceased and non-recovery was defined as no increase in growth rate from defoliation period growth rate (1979 to 1982 was considered to be the post-defoliation growth period).

Descriptive Variables

Variables derived from the data chronology were used in discriminant analysis and Duncan Multiple Range tests to assess individual tree, plot and site differences between Recovery Classes. All host trees which survived the infestation, including those trees less than 2.4 inches d.b.h. and therefore not assigned to a Recovery Class as well as Recovery Class trees, were compared to host trees that died during the infestation. Students-t tests were used to assess descriptive variable differences between live and dead host trees.

Descriptive variables fall into three general categories: 1. Variables describing severity of WSBW damage to host trees, for example defoliation and topkilling, 2. Variables describing host tree stature and condition, for example diameter, height, crown ratio, and non-WSBW biotic and abiotic damage, and 3. Variables describing plot conditions surrounding the host tree, for example plot slope, elevation and basal area. Table 4a,b,c describes these variables in greater detail.

The variable 'BAR', or 'ratio of actual plot basal area to potential maximum average basal area for that site' is similar to a variable "Vigor", which was suggested for use in WSBW-stand hazard models (Wulf and Carlson 1985)(Table 4c). A computerized hazard model using this and other variables is currently being developed (Bousfield, Carlson and Wulf 1985). Vigor is an index of stand basal area divided by maximum average basal area for that site. The adaptation of this variable was used to compare relative stocking levels associated with dead and live host trees and in Recovery Class analysis where:

"BAR" = Plot basal area / Average maximum plot basal area

Average maximum basal area has been determined by Region One Timber Management for specific habitat type groups in western Montana. Average maximum basal area is a function of stand age, varies by habitat type group, and is determined by equations (Annon. 1984). Average maximum basal area is an estimate of potential site productivity in terms of potential stand basal area at different stand ages.

TABLE 4a DESCRIPTIVE VARIABLES: WSBW Damage

* Live and dead host trees compared using Students'-t tests.
\+ Used in discriminant analysis and Duncan Multiple Range tests.

Variable Description	Code	Measurement
Cumulative Defoliation in 1978*+	DEFOL	Each host tree rated in one of three categories for amount of total foliage removed. Category 1: < 10% Defoliated Category 2: 11 - 70% Defol. Category 3: > 70% Defoliated Midpoint values, that is 5, 40 and 75% respectively, were assigned to each category for the statistical analysis.
Topkill in 1978*+	TOPK	Each host tree rated in one of four categories for proportion of live crown topkilled. Category 1: No Topkill Category 2: < 10% Topkill Category 3: 10 - 33% Topkill Category 4: > 33% Topkill Midpoint values, that is 0, 5, 22 and 66% respectively, were assigned to each category for the statistical analysis.
Topkill in 1982+	TOP82	Topkill rated same as in 1978. However 1982 measurement allowed for potential host tree recovery.

TABLE 4b DESCRIPTIVE VARIABLES: Host Tree Stature and Condition

* Live and dead host trees compared using Students'-t tests.
\+ Used in discriminant analysis and Duncan Multiple Range tests.

Variable Description	Code	Measurement
Diameter, 1974*, 1982+	DBH	Diameter breast height in 1974,1982
Height, 1974*, 1982+	HGT	Total tree height in 1974,1982
Crown Class, 1974*, 1982+	CC	Crown class in 1974, 1982. Dominant or Open Grown = 1 Codominant = 2, Intermediate = 3, Suppressed = 4
Crown Ratio, 1978*, 1982+	CR	Crown ratio in 1978,1982. Proportion of total stem covered by live crown 1 = 10% live crown,.... 9 = 90% live crown
Age, 1974*, 1982+	AGE	Host tree age at d.b.h. in 1974,1982
Non-WSBW caused biotic or abiotic damage in 1982*	OD82	Coded as a dummy variable for analysis: No damage = 0 Damage = 1
Individual host tree height divided by ave. stand height, 1982*	HGTSR	Individual host tree height/ Average stand tree height
"Maturity" (suggested by Wulf and Carlson, 1985)*	MATUR	Calculated in this study as: Individual host tree age multiplied by individual host tree basal area

TABLE 4c DESCRIPTIVE VARIABLES: Plot Variables

* Live and dead host trees compared using Students'-t tests.
+ Used in discriminant analysis and Duncan Multiple Range tests.

Variable Description	Code	Measurement
'Ratio of actual plot basal area to potential maximum basal area for that site'. This value was attached to each individual host tree for the analysis, and was estimated for the beginning of the infestation (approx. 1969)*+, and calculated for the years 1974*+, 1978*+, 1982*+	BAR,i.e. (BAR69), (BAR74), (BAR78), (BAR82)	Plot basal area in year (est.1969, 1974,1978,1982) divided by average maximum basal area of plot for same year. (i.e. beginning of infestation = BAR69, 1974 = BAR74, 1978 = BAR78, 1982 = BAR82)
Host tree percent of total plot basal area estimated at time of infestation onset*+.	PHPBA69	(Total live and dead host tree plot basal area in 1974 divided by total live and dead tree plot basal area in 1974), multiplied by 100.
Host tree percentage of total plot basal area in 1982*+	PHPBA82	(Live host tree plot basal area in 1982 divided by total live tree plot basal area in 1982), multiplied by 100.
Ratio of plot basal area at beginning of infestation to plot basal area in 1982*+	B69CHA	Plot basal area at beginning of infestation (estimated using live and dead tree basal area in 1974) divided by live tree plot basal area in 1982.
Ratio of plot basal area in 1974 to plot basal area in 1982*+	BACHA	Plot basal area in 1974 divided by plot basal area in 1982.

TABLE 4c : Continued

* Live and dead host trees compared using Students'-t tests.
\+ Used in discriminant analysis and Duncan Multiple Range tests.

Variable Description	Code	Measurement
Coefficient of variation of tree heights by plot in 1982+ (after similar variable "size class structure" suggested by Wulf and Carlson, 1985)	CVPHGT	Plot standard deviation of tree heights divided by plot mean tree height.
Coefficient of variation of tree crown class by plot in 1982+	CVPCC	Plot standard deviation of tree crown class divided by plot mean tree crown class.
Coefficient of variation of tree d.b.h. by plot in 1982+	CVPDBH	Plot standard deviation of tree d.b.h. divided by plot mean tree d.b.h.
Coefficient of variation of tree crown ratio by plot in 1982+	CVPCR	Plot standard deviation of tree crown ratio divided by plot mean tree crown ratio.
Sine multiplied by aspect multiplied by slope (Stage 1976)+	SSA	Aspect in degrees, slope in percen
Cosine multiplied by aspect multiplied by slope (Stage 1976)+	CSA	Aspect in degrees, slope in percen
Tangent of slope*+ (Stage 1976)	TANSLOP	Slope percent divided by 100
Plot elevation*+	EL	Elevation of plot (feet) divided b 100
Habitat type+(Pfister et al 1977)	HABT	An attempt was made to stratify data by habitat types

Bousfield (pers. comm. 1984) supplied equations to calculate average maximum basal area. Average maximum basal area was calculated based on 1982 tree ages. BAR was estimated for onset of infestation by combining basal area of trees now dead but living in 1974 with live tree basal area in 1974. BAR for the remaining time periods (1974,1978,1982) was calculated using only live tree basal area.

DATA ANALYSIS

Discriminant analysis was used as an exploratory technique to select a set of descriptive variables which optimally distinguish the Recovery Classes and to determine the relative predictive value of the descriptive variables. A stepwise discriminant analysis computer program was used to develop and evaluate the predictive model. Options used in this program allowed combined forwards and backwards stepwise entry of discriminant variables. Minimization of Wilks' lambda was used as the criterion for stepwise entry. Variables which no longer contributed significantly to the discriminant model after entry of subsequent variables were removed from the analysis (SPSSx 1983). Stepwise entry and removal of variables were limited by a probability of F to enter of .05 and a probability of F to remove of .10. Although Recovery Class sample sizes were unequal, prior probability of group membership was assumed to be equal for all groups.

Duncan Multiple Range tests were used to interpret discriminant analysis results. Means and significant differences of descriptive variables were determined for the Recovery Classes, allowing a more quantitative characterization of the Recovery Classes in terms of these variables.

Students-t tests were used to determine descriptive variable differences between host trees that survived the infestation and host trees that were killed during or just after WSBW infestation. A significance probability $<=$ .05 constituted a significant difference.

RESULTS and DISCUSSION

Comparison of Live and Dead Host Trees

Students-t tests indicate that, on the average, host trees which died during infestation were significantly smaller in diameter, shorter in height, and had smaller crown ratios prior to death than surviving host trees. Defoliation and topkilling also averaged highest for dead trees (prior to death). Although statistically nonsignificant, mean age followed diameter and height trends, that is, dead trees tended to be slightly younger than surviving host trees (Table 5).

'Ratio of actual plot basal area to potential average maximum basal area' (BAR) was calculated for each measurement and compared between live and dead host trees. At the onset of defoliation, trees that di during infestation tended to be on plots with highest BAR (BAR69), although this value was barely nonsignificant (prob. = .053). However by the post-infestation measurement (BAR82) mean BAR of dead trees was significantly lower than live trees.

The variable BACHA or 'ratio of plot basal area in 1974 to plot basal area in 1982', suggests similar information suggested by BAR trends. Significantly lower mean BAR in 1982 and significantly higher mean BACHA associated with dead trees indicates that these trees had a tendency towards spatial concentration as opposed to being more evenly distributed among live host trees. This trend towards concentration of mortality may explain similarity of mean crown class values for live and dead host trees. That is, mortality was not relegated to lower crown classes where it was not intermixed with taller, more dominant live trees.

The tendency of mortality to occur on plots with high BAR values at defoliation onset probably indicates that these trees were under greater competitive stress than trees which survived the infestation. Smaller crown ratios of dead trees (prior to death) tends to support this hypothesis. Williams (1967) similarly found that greater mortality occurred in smaller, densely stocked, stressed Douglas-fir stands than in more open grown stands during WSBW infestations.

Mean percentage of plot host tree basal area (PHPBA69) was not significantly different for live and dead host trees, indicating that more mortality did not tend to occur on plots with higher PHPBA69. The smaller stature of dead trees probably had a tendency to minimize PHPBA69 associated with this group. On the other hand, BAR is related to tree age, because maximum average basal area (a component of BAR) is reached at lower basal areas on plots with younger trees. Thus the tendency of dead trees to be slightly younger than live trees may have had a tendency to increase BAR for dead trees (although age of dead trees was not significantly different from live host trees).

Results are in general agreement with other research (Alfaro et al. 1982; Johnson and Denton 1975; Mika and Twardus 1983). Although cumulative defoliation was measured only once in this study, mean cumulative defoliation appears to be significantly greater for mortality

TABLE 5. Descriptive Variables Comparing Live and Dead Host Trees. Separate variance estimates were used for live and dead tree groups.

Variable	Host tree group	N	Mean	Std. Dev.	Std. Error	T	D.F.	2-tail Prob.
Diameter breast height (DBH)	Live	208	10.7	6.7	0.47	6.39	270.0	.000
	Dead	118	6.2	5.9	0.54			
Height (HGT)	Live	136	54.9	27.4	2.34	6.02	210.4	.000
	Dead	89	34.6	22.8	2.42			
Crown Class (CC)	Live	179	3.0	0.79	0.06	0.46	66.5	.646
	Dead	52	2.9	1.11	0.16			
Crown Ratio (CR)	Live	179	4.5	1.88	0.14	6.33	81.0	.000
	Dead	48	2.7	1.69	0.24			
Age (AGE)	Live	165	104.6	55.82	4.35	1.09	23.9	.289
	Dead	19	83.6	48.39	11.10			
Cumulative Defol.% (DEFOL)	Live	209	22.7	20.99	1.45	-4.55	33.0	.000
	Dead	31	53.1	36.30	6.52			
Topkilling Percent (TOPK)	Live	209	0.7	2.93	0.20	-3.08	30.2	.004
	Dead	31	11.8	19.87	3.57			
Elevation (EL)	Live	209	48.71	5.43	0.38	-0.42	266.9	.675
	Dead	118	49.96	4.84	0.45			
Tangent of Slope (TANSLOP)	Live	209	0.50	0.11	0.01	0.24	235.4	.810
	Dead	118	0.49	0.11	0.01			

TABLE 5. Continued.

Variable	Host tree group	N	Mean	Std. Dev.	Std. Error	T	D.F.	2-tail prob.
Proportion of Max. Ave. Basal Area at Defol. Onset (BAR69)	Live	209	0.84	0.37	0.03	-1.95	172.4	.053
	Dead	105	0.94	0.47	0.05			
Proportion of Max. Ave. Basal Area in 1974 (BAR74)	Live	209	0.77	0.33	0.02	0.33	183.0	.741
	Dead	109	0.76	0.40	0.04			
Proportion of Max. Ave. Basal Area in 1978 (BAR78)	Live	209	0.76	0.34	0.02	1.66	193.5	.099
	Dead	111	0.69	0.40	0.04			
Proportion of Max. Ave. Basal Area in 1982 (BAR82)	Live	209	0.77	0.33	0.02	4.60	205.5	.000
	Dead	118	0.57	0.40	0.04			
Ratio of Plot Basal Area in 1974 to B. A. in 1982 (BACHA)	Live	209	1.05	0.28	0.02	-3.17	117.0	.002
	Dead	118	6.06	17.16	1.58			
Ratio of Plot Basal Area at Defol. onset to B. A. in 1982 (B69CHA)	Live	209	1.15	0.34	0.02	-3.92	117.0	.000
	Dead	118	10.92	27.10	2.50			
Host % of Plot Basal Area (PHPBA69)	Live	209	78.3	25.82	1.79	0.47	225.4	.640
	Dead	118	76.9	28.22	2.60			

than for live trees. This result is in general agreement with Alfaro et al. (1982).

Discriminant Analysis of Live Tree Recovery Classes

Four discriminant models are presented because several descriptive variable combinations resulted in significant models with similar predictive power. Although all models are statistically significant, predictive power of the models are low. Classification success rates ranged from 55% overall correct classification of Recovery Class (for Model 3) to 62% correctly classified (for Model 2). Because classification accuracy was tested against the same data used to develop models, classification success rates are likely upward biased (Klecka 1980). Tau, which estimates model improvement over success rate of purely random classification (Klecka 1980), ranged from 32% improvement (for Model 3), to 43% improvement (for Model 2) (Table 6). Low predictive power and plurality of models suggests that a number of tree, site and plot variables significantly but weakly predict growth recovery. Lack of consistently significant differences of the descriptive variables across the Recovery Classes, as indicated by Duncan Multiple Range tests, may in part account for the low predictive power of models. Klecka (1980) indicated that variables whose means are not significantly different tend to perform poorly as discriminating variables.

Model 1 contains the variables most competitive in stepwise entry (Table 7). 'Ratio of plot basal area in 1974 to plot basal area in 1982' (BACHA) was entered instead of 'host tree percentage of total plot basal area' (PHPBA69) in Model 2. BACHA may not account for as much variability in models as PHPBA69, perhaps allowing entry of additional variables before the probability of F to enter is exceeded. Predictive power of Model 2 is slightly higher than Model 1. Models 3 and 4 indicate variable entry when OD82 is removed from the data set, with BACHA substituted for PHPBA69 in Model 4. These models are presented for comparison, as use of dummy variables in discriminant analysis violates theoretical assumptions of normality of independent variables although the technique is robust.

Interpretation of Models

Crown ratio (CR) is the most powerful discriminating variable in all models, as indicated by stepwise order of entry (Table 7). In stepwise entry, the variable with the greatest univariate discriminating power is the first to be selected. Subsequently, those variables are selected which most contribute to the discriminating power of the variable combination (Klecka 1980).

CR also has the highest structure matrix correlation and standardized coefficient in function 1 of all models, with the exception of Model 4 (Table 8). The first discriminant function to be derived tends to account for the largest percentage of variability explained by the discriminant model. The within groups structure matrix indicates bivariate correlation between independent variables and the discriminant functions. These correlations are not lessened when two variables account for similar variability in the model. Standardized discriminant function coefficients indicate relative magnitude of variable contribution to discriminant functions, but when two or more independent variables are correlated, contribution of each variable to the discriminating power of the function is minimized. Comparison of structure matrix correlations and standardized coefficients may indicate where independent variable correlation occurs (Klecka 1980).

Mean CR was significantly higher for trees in RC2 than either RC1 or RC3. Mean CR for RC1, although higher, was not significantly different from mean CR for RC3 (Table 9). Comparison of mean values of discriminating variables across the Recovery Classes allows characterization of the Recovery Classes with respect to these variable means.

PHPBA69 enters second in stepwise order when included in the variable pool (models 1 and 3). PHPBA69 has the highest structure matrix correlation and standardized coefficient in function 2 of models 1 and 3. PHPBA69 precludes entry of BACHA when both are present in the stepwise entry pool. When PHPBA69 is not present (in Models 2 and 4), BACHA is second in stepwise entry order and has high structure matrix correlations and standardized coefficients in function 2 suggesting that PHPBA69 and BACHA perform similarly in discriminant models. Mean

PHPBA69 for RC1 trees is significantly lower than either RC2 or RC3. RC2 and RC3 means are not significantly different. Mean BACHA is significantly lower for RC1 than for RC2 and RC3, but RC2 and RC3 are not significantly different. Similar performance of these variables probably occurs because both variables are basal area descriptors and may be correlated. Furthermore, higher PHPBA69 values appear to coincide with greater basal area reductions over time (BACHA). The implication is that Recovery Class 2 and 3 trees tend to be found on plots where slightly more mortality occurs.

Host tree percentage of total plot basal area was also calculated using the 1982 measurement of basal area (PHPBA82). No means are significantly different across Recovery Classes for this measurement, although there is still a tendency for mean PHPBA82 to increase from RC1 to RC3. Possibly a combination of slightly higher mortality associated with RC2 and RC3 and more basal area growth on RC1 tended to minimize differences between Recovery Classes. PHPBA69 is apparently a better predictor of Recovery Class as PHPBA82 did not enter stepwise discriminant models and was not significantly different across the Recovery Classes.

Significance of PHPBA69 (as opposed to PHPBA82) suggests that PHPBA69 indexes initial plot susceptibility and vulnerability to WSBW and that initial plot vulnerability is an important predictor of the occurance of growth reduction. However, PHPBA69 does not appear to differentiate very well between type of growth recovery (i.e. RC2 vs

RC3) after initial growth has occurred. Post infestation host percent o plot basal area (PHPBA82) may not differentiate between the Recovery Classes because a combination of host tree mortality on vulnerable plots, and host tree growth on less vulnerable plots minimizes differences in average host percentage of plot basal between the Recovery Classes by the post-infestation period. This may indicate that relative vulnerability of plots (stands) changes over time.

Higher proportions of host tree basal area were related to greater amounts of host tree radial growth loss (Bennett 1978; Carlson and Theroux 1982; Harvey 1982; Mika and Twardus 1983) and greater defoliation intensities (Anderson 1981; Fauss and Pierce 1969) in other studies.

Because the 'non-WSBW caused biotic or abiotic damage' variable (OD82) was coded as a dummy variable, frequencies of this variable by Recovery Class were compared using Chi-squared contingency tables (Table 10). RC3 tended to have a significantly higher frequency of OD82 than RC1 or RC2. RC1 and RC2 OD82 frequencies were not significantly different at the .05 level. When present in the variable pool, OD82 entered all stepwise discriminant models; suggesting that this variable may be very important in predicting Recovery Class, despite limitations as a dummy variable. Use of ranked damage codes may have been a better solution to presentation of this variable in the discriminant models.

All external damage symptoms with the exception of topkilling in 1982 were combined in the variable OD82. Types and percentages of damage include current beetle attack (14.3%), mechanical top damage or breakage (7.1%), thinning foliage (usually indicative of root disease)(10.7%), rotten center (heartrot) (42.9%), and branch dieback (25.0%), which may be the result of defoliation (Williams 1967) or be symptomatic of Phaeolus schwienitzii root disease .

Williams (1967) noted that the greatest radial growth reduction of WSBW defoliated grand fir and Engelmann spruce occurred in those trees with most severe post-infestation branch dieback and least crown recovery. In contrast, Douglas-fir were little damaged by WSBW, creating fewer post infestation damage categories, and radial growth reduction was not significanly different between damage categories (Williams 1967). However Douglas-fir was not the climax species in areas studied by Williams (1967).

Mean percent topkill (TOPK) was significantly greater for RC3 trees than for RC2 trees. Mean TOPK for RC1 was not significantly different from RC3, probably because standard deviation was not minimized by sample size for RC1 as it was for RC2. TOPK entered stepwise in three of the four discriminant models. Topkilling occured at fairly low frequencies across all Recovery Classes. RC3 trees received the highest frequency of topkilling at 15.9%.

The 1982 measurement of topkill (TOP82), did not enter stepwise in any discriminant model, and means were not significantly different across Recovery Classes. However 1982 values followed the same general trends as the 1978 measurement of topkill, with RC3 having the highest mean topkill. Poor performance of TOP82 is surprising because this post-infestation topkill rating should best indicate final effect of WSBW infestation, indicating recovery from topkill in some trees and progression of topkill in others. Expression of TOP82 as a separate variable from OD82 may have been an artificial distinction. A better approach would have been to include all 1982 tree damage information in a single variable, in effect assuming that topkill has a similar relationship to growth recovery as other types of biotic and abiotic tree damage.

'Individual host tree height divided by average stand height' (HGTSR) was a significant component of two of the four models. Mean HGTSR was lowest for RC1 trees and highest for RC2 trees, only mean values for RC1 and RC2 were significantly different. Mean height measured in 1982 was also lowest for RC1 trees, and RC1 and RC2 means were significantly different.

High mean HGTSR values for RC2 and RC3 trees reflects several relationships. Relatively taller host trees is related to greater host tree basal area, increasing both total basal area and PHPBA. Proportionately fewer nonhost trees should also raise HGTSR of host trees. As nonhost trees tend to be seral species, one expects them to be the tallest trees in stands, at least at earlier stages of stand development. During latter stages of stand development, climax host species should dominate basal area and also height of stands. The highest mean value of HGTSR associated with RC2 may reflect greater height dominance and vigor of this Recovery Class, predisposing this class to better growth recovery. This conclusion is speculative however, as mean HGTSR for RC2 and RC3 are not significantly different.

Mean values of 'coefficient of variation of tree crown class by plot' (CVPCC) and 'coefficient of variation of tree diameter by plot' (CVPDBH) were not significantly different across the Recovery Classes. This suggests that entrance of these variables in the models may be due to data idiosyncracies. Alternatively, this may reflect real differences between Recovery Classes and be related to descriptive variable interactions. Standardized coefficients of CVPDBH and CVPCC are relatively large in Models 2 and 4, however structure matrix correlations are low for both variables. While CVPDBH and CVPCC are weakly correlated with discriminant functions, large standardized coefficients suggest that these variables account for unique variability in the models.

Mean CVPDBH is lowest for RC2 and highest for RC3. Although nonsignificant in discriminant models and in multiple range tests, mean 'coefficient of variation of tree height by plot' (CVPHGT) showed the same trends. High mean values associated with RC3 do not refute Wulf and Carlsons' (1985) contention that stand hazard increases with increasing stand height variability. Because tree diameter and height are related, one would expect CVPDBH and CVPHGT to show similar trends. Intermediate values of mean CVPDBH and CVPHGT for RC1 may be related to greater percentages of nonhost trees associated with RC1. These relationships were probably confounded by using nonhost trees in the calculation of CVPDBH and CVPHGT. Calculation of CVPDBH and CVPHGT using only host trees, as suggested by Wulf and Carlson (1985), would have been a better approach to this problem. Estimating CVPHGT and CVPDBH at the onset of infestation could also have reflected more clearcut differences between Recovery Classes because plot variability at this time may have been more directly related to vulnerability to WSBW; just as host percentage of total plot basal area estimated at the beginning of the infestation (PHPBA69) was a better predictor of Recovery Class than host percent of total plot basal after the infestation (PHPBA82).

Mean values of CVPCC across the Recovery Classes seem to contradict, in part, trends of CVPDBH and CVPHGT. However CVPCC and HGTSR trends across Recovery Classes are similar. Mean values of CVPCC are lowest for RC1 and highest for RC2. One interpretation is that RC1 trees tended to be on plots with the least variability in competitive status even though nonhost trees increased height variability on these plots. Scattered large nonhost trees probably did not increase variability in rating of competitive status. Differences between mean CVPCC for RC2 and RC3 are harder to explain. Lower CVPCC for RC3 may be related to a tendency of RC3 trees to be on plots where slightly more mortality ocurred, eliminating trees in lower crown classes. Of course, the nonsignificant differences between mean values could represent nothing more than random sampling error. The subjective nature of estimation of crown class further confounds interpretation of this variable.

RC3 trees tended to be on plots at the lowest elevations (EL), whereas RC2 trees tended to be at higher elevations. Mean EL for RC2 was significantly different from RC3. No other means were significantly different. Maximum difference between Recovery Class mean elevation was only slightly over 300 feet, suggesting that in practical terms elevational differences did not greatly distinguish Recovery Classes. A tendency of Recovery Classes to be associated with certain site or plot conditions may also suggest a trend towards spatial concentration which might be distinguished by elevation in this study. Nevertheless, elevation was significant in three of the four discriminant models. Comparison of structure matrix correlations and standardized coefficients of Models 2 and 4 suggests that elevation, in part, explains similar variability as other independent variables in the model.

Other studies have shown that past severity of WSBW infestation (Carlson and Theroux 1982) and defoliation intensity (Anderson 1981; Stoszek et al. 1981) varied with elevation.

TABLE 6. Classification success rates and Tau values for the Discriminant Models.

MODEL 1

Actual		Predicted Recovery Class		
Recovery Class	N	RC1	RC2	RC3
RC1	31	61.3%	29.0%	9.7%
RC2	103	29.1%	54.4%	16.5%
RC3	42	28.6%	16.7%	54.8%
TOTAL	176			

Tau = .34

Average correct classification percent = 55.7%

MODEL 2

Actual		Predicted Recovery Class		
Recovery Class	N	RC1	RC2	RC3
RC1	30	66.7%	23.3%	10.0%
RC2	103	20.4%	62.1%	17.5%
RC3	41	19.5%	24.4%	56.1%
TOTAL	174			

Tau = .43

Average correct classification percent = 61.5%

TABLE 6. Continued.

MODEL 3

Actual Recovery Class	N	Predicted Recovery Class		
		RC1	RC2	RC3
RC1	31	58.1%	22.6%	19.4%
RC2	103	26.2%	59.2%	14.6%
RC3	42	26.2%	33.3%	40.5%
TOTAL	176			

Tau = .32

Average correct classification percent = 54.6%

MODEL 4

Actual Recovery Class	N	Predicted Recovery Class		
		RC1	RC2	RC3
RC1	30	63.3%	20.0%	16.7%
RC2	103	17.5%	59.2%	23.3%
RC3	41	24.4%	26.8%	48.8%
TOTAL	174			

Tau = .37

Average correct classification percent = 57.5%

TABLE 7. Discriminant Function Statistics and Variables in Models. Number preceeding variable indicates order of stepwise entry.

MODEL 1

1. Crown Ratio (CR)
2. Host Percentage of Plot Basal Area (PHPBA69)
3. Topkill Percent (TOPK)
4. Other Biotic or Abiotic Damage (OD82)
5. Plot Elevation (EL)

Function	Canonical Correlation	Percent of Variance	After Function	Wilks Lambda	Chi-Squared	D.F.	Sign.
1	.440	76.54%	0	.751	48.4	10	.000
2	.262	23.46%	1	.931	12.0	4	.017

MODEL 2

1. Crown Ratio (CR)
2. Ratio of Plot Basal Area in 1974 to Basal Area in 1982 (BACHA)
3. Other Biotic and Abiotic Damage (OD82)
4. Topkill Percent (TOPK)
5. Plot Elevation (EL)
6. Tangent of Slope (TANSLOP)
7. Ratio of Individual Host Height to Average Stand Height (HGTSR)
8. Coefficient of Variation of Plot Crown Class (CVPCC)
9. Coefficient of Variation of Plot D. B. H. (CVPDBH)

Function	Canonical Correlation	Percent of Variance	After Function	Wilks Lambda	Chi-Squared	D. F.	Sign.
1	.489	59.79%	0	.63	77.6	18	.000
2	.418	40.21%	1	.83	32.0	8	.000

TABLE 7. Continued.

MODEL 3

1. Crown Ratio (CR)
2. Host Percentage of Plot Basal Area (PHPBA69)
3. Topkill Percent (TOPK)

```
                                               After    Wilks   Chi-
         Canonical   Percent of  Function Lambda  Squared   D. F.  Sign.
Function Correlation Variance    -------------------------------------
---------------------------------   0      I .81  I  35.8  I  6  I .000 I
I  1  I   .381    I   75.36%  I--------------------------------------
---------------------------------   1      I .95  I   9.2  I  2  I .010 I
I  2  I   .229    I   24.64%  I--------------------------------------
---------------------------------
```

MODEL 4

1. Crown Ratio (CR)
2. Ratio of Plot Basal Area in 1974 to B. A. in 1982 (BACHA)
3. Ratio of Individual Host Tree Height to Average Stand Ht. (HGTSR)
4. Coefficient of Variation of Plot Crown Class (CVPCC)
5. Coefficient of Variation of Plot D. B. H. (CVPDBH)
6. Elevation (EL)
7. Tangent of Slope (TANSLOP)

```
                                                 After    Wilks   Chi-
           Canonical   Percent of  Function Lambda  Squared   D. F.  Sign.
  Function Correlation Variance    -------------------------------------
----------------------------------   0      I .68  I  64.9  I  14 I .000 I
I    1    I   .469    I  65.68%  I--------------------------------------
----------------------------------   1      I .87  I  23.1  I   6 I .001 I
I    2    I   .359    I  34.32%  I--------------------------------------
----------------------------------
```

TABLE 8. Pooled Within Groups Structure Matrices and Standardized Canonical Discriminant Function Coefficients for the Discriminant Models.

MODEL 1

Structure Matrix

	Function 1	Function 2
CR	.700	.385
EL	.529	.088
TOPK	-.458	.120
PHPBA69	-.106	.815
OD82	-.399	.522

Standardized Coefficients

	Function 1	Function 2
CR	.543	.445
EL	.449	-.044
OD82	-.430	.444
TOPK	-.468	.076
PHPBA69	.039	.726

MODEL 2

Structure Matrix

	Function 1	Function 2
CR	.640	-.033
EL	.451	-.138
TOPK	-.359	.228
HGTSR	.317	.316
TANSLOP	-.288	-.268
CVPDBH	-.169	.038
BACHA	-.034	.488
OD82	-.246	.432
CVPCC	.207	.236

Standardized Coefficients

	Function 1	Function 2
CR	.571	.089
BACHA	.152	.582
CVPCC	.559	.458
TANSLOP	.040	-.562
EL	.436	-.541
CVPDBH	-.570	-.088
HGTSR	.225	.418
OD82	-.203	.475
TOPK	-.341	.224

TABLE 8. Continued.

MODEL 3

Structure Matrix

	Function 1	Function 2
CR	.867	.140
TOPK	-.518	.328
PHPBA69	-.015	.964

Standardized Coefficients

	Function 1	Function 2
CR	.855	.151
TOPK	-.501	.226
PHPBA69	.046	.939

MODEL 4

Structure Matrix

	Function 1	Function 2
CR	.635	-.319
EL	.417	-.356
HGTSR	.401	.221
TANSLOP	-.359	.179
CVPCC	.270	.179
CVPDBH	-.160	.118
BACHA	.093	.571

Standardized Coefficients

	Function 1	Function 2
CR	.601	-.238
BACHA	.257	.669
CVPCC	.670	.217
TANSLOP	-.125	-.609
EL	.293	-.740
CVPDBH	.625	.312
HGTSR	.367	.425

TABLE 9. Mean values and significant differences of discriminant variables across Recovery Classes. Differences determined for significance probability <= .05 using Duncan Multiple Range Tests.

Variable		Recovery Class (RC)			
		1	2	3	Total
CR	Mean	5.5	6.4	4.6	5.8
	Sign. Diff. from RC	2	3		
	Std. Dev.	2.19	2.21	2.07	2.30
PHPBA69	Mean	67.6	81.4	82.1	79.2
	Sign. Diff. from RC	2		1	
	Std. Dev.	23.8	24.7	26.1	25.3
BACHA	Mean	.91	1.05	1.11	1.04
	Sign. Diff. from RC	2		1	
	Std. Dev.	.23	.31	.30	.30
TOPK	Mean	.32	.34	1.57	.64
	Sign. Diff. from RC		3		
	Std. Dev.	1.25	1.26	4.79	2.65
EL	Mean	4870	4960	4630	4860
	Sign. Diff. from RC		3		
	Std. Dev.	511	560	5400	561
TANSLOP	Mean	.53	.48	.51	.50
	Sign. Diff. from RC	2			
	Std. Dev.	.12	.11	.10	.11
HGTSR	Mean	.83	.99	.92	.95
	Sign. Diff. from RC	2			
	Std. Dev.	.23	.27	.36	.29
CVPCC	Mean	.22	.32	.28	.29
	Sign. Diff. from RC				
	Std. Dev.	.25	.23	.18	.23
CVPDBH	Mean	.33	.30	.37	.32
	Sign. Diff. from RC				
	Std. Dev.	.22	.20	.24	.21

TABLE 10. Chi-squared test of significance for OD82, sign. prob. <= .05.

Variable		Recovery Class		
		1	2	3
OD82	Frequency of Occurrence	3.2%	13.5%	29.5%
	Freq. Sign. Diff. from RC	3	3	

Tangent of slope (TANSLOP) entered Models 2 and 4. TANSLOP tends to be steepest for RC1 and shallowest for RC2. Although these mean values are significantly different statistically, in practical terms slope differences are nonsignificant. Acccuracy of field measurement of slope percent is probably no less than +- 5%, suggesting that apparent slope differences may be related to data idiosyncracies in this study. Carlson and Theroux (1982) found that past WSBW infestations, indexed by host tree radial growth losses, were more severe on steeper slopes.

Variables not entering Discriminant Models

Cumulative defoliation in 1978 (DEFOL) did not enter discriminant models, although defoliation was expected to have a primary influence on host tree radial growth. RC3 trees had the highest mean defoliation and this value is significantly different from mean defoliation for RC2. RC1 trees had the lowest mean defoliation, however defoliation in this group was highly variable and was not significantly different from any other group (Table 11).

Lack of measurement sensitivity of the broad defoliation categories probably increases data variability, and potentially masked real between group differences in defoliation intensity. Alternatively, the relatively low defoliation intensities across all Recovery Classes may not have exceeded threshold levels necessary to adequately differentiate Recovery Classes.

Other research has shown defoliation to be a significant predictor of host tree radial growth. During infestations, Alfaro et al (1982), indicated that average stand cumulative defoliation (measured as the summation of average yearly defoliation) plus current years defoliation was a significant predictor of proportion of yearly potential radial increment during infestation. Scott and Nichols (1983) similarly found that duration of WSBW infestation minus years of recovery predicted ratio of actual to potential radial growth.

An alternate hypothesis explaining the absence of DEFOL in discriminant models is that post infestation growth recovery becomes less related over time to differences in defoliation intensity, and more related to current plot, site or tree condition. The presence of the damage variable OD82 in discriminant models supports this hypothesis because this variable accounts for a variety of current damage conditions that would lower vigor and preclude growth recovery. Recording branch dieback as one type of current damage may in part reflect ultimate response of some trees to defoliation. However removal of OD82 as a stepwise candidate in discriminant models did not allow DEFOL to enter discriminant models, suggesting low correlation between these two variables and indicating that DEFOL had little predictive power relative to other variables tested.

Alfaro et al. (1982) found that correlation between radial growth and WSBW defoliation intensity was low at the beginning of WSBW infestations, but increased as the infestation progressed. Logically the correlation between radial growth and defoliation probably also decreases with time after the end of WSBW infestations.

Measurements of BAR did not enter discriminant models, probably because other variables describing basal area or change in basal area (PHPBA69 and BACHA) were correlated with BAR and explained more variability in discriminant models. However comparison of mean BAR values across Recovery Classes, for each of the measurement periods, suggests some trends.

At the onset of infestation, RC1 trees tended to be on plots with lowest mean BAR, although this value was not significantly different from RC3 until the 1974 measurement (table 11). This relationship remained roughly the same throughout the infestation, however by the post-infestation measurement (1982), mean BAR of RC1 exceeded mean BAR of RC2 trees. Differences were not significant for the 1982 measurement however. RC3 trees tended to be on plots with the highest mean BAR throughout the infestation.

TABLE 11. Mean values and significant differences of variables not entering Discriminant Models. Differences determined for prob. <= .05 using Duncan Multiple Range Tests.

Variable		Recovery Class (RC)			
		1	2	3	Total
DEFOL	Mean	20.0	21.7	28.9	23.2
	Sign. Diff. from RC		3		
	Std. Dev.	23.73	18.06	19.10	19.56
BAR69	Mean	.72	.72	.88	.80
	Sign. Diff. from RC				
	Std. Dev.	.203	.356	.325	.330
BAR74	Mean	.69	.75	.85	.77
	Sign. Diff. from RC	3			
	Std. Dev.	.204	.339	.333	.321
BAR78	Mean	.69	.74	.85	.76
	Sign. Diff. from RC	3			
	Std. Dev.	.198	.353	.380	.342
BAR82	Mean	.77	.75	.81	.77
	Sign. Diff. from RC				
	Std. Dev.	.216	.357	.349	.334
CVPHGT	Mean	.20	.20	.24	.21
	Sign. Diff. from RC				
	Std. Dev.	.150	.163	.169	.162
TOP82	Mean	1.2	1.0	4.2	1.8
	Sign. Diff. from RC				
	Std. Dev.	4.14	6.56	14.42	8.94

Study and Sample Design Limitations

The historical data used in this study provided valuable information about individual host tree, plot and site conditions during a WSBW infestation which otherwise would have been unavailable. However some problems arose from using data collected from a sampling system which was designed for purposes other than this study. In particular, the adherance to a 40 BAF variable plot in all stands insured a large minimum basal area increment for plot measurements, probably artificially increasing variability of plot basal area estimates. These study limitations may have confounded efforts to detect real differences between Recovery Classes for variables describing basal area, for example PHPBA69, PHPBA82, BACHA and BAR.

Variables describing coefficient of variation in plot condition (i.e. CVPCC, CVPDBH, CVPHGT) were calculated using standard deviation of measurements of live plot trees in 1982 with no weighting factor for the number of trees (per acre) each sampled tree represents. Because sampling probability increases with basal area of the tree for variable radius plots, larger trees had a greater probability of being sampled (Beers and Miller 1964), and represented in coefficient of variation calculations. A better approach may have been to wieght each tree parameter (i.e. diameter, height etc..) by the number of trees per acre each sampled tree represents and calculating of coefficient of variation on this value.

Mean values for several variables used to compare dead with live host trees were only calculated from measurements of a subsample of dead trees. Specifically, crown ratios were recorded only for trees which were still alive in 1974 (the first plot measurement), and cumulative defoliation and topkilling were measured only for trees which were alive in 1978. Live and dead host trees had missing values for other variables in some instances, because forest inventory sampling procedures did not require sampling of all plot trees for these variables. The assumption was made that varying sample size did not bias calculations of average values of variables for live and dead trees.

1974 measurements of host tree diameter, height, crown class, and age were selected to compare live and dead host trees because these measurements should best minimize bias introduced by continued growth of live trees after death of the other host trees. However approximately half of host trees which eventually died were dead before the 1974 measurement, so that relative stature of dead versus live trees may still be slightly underestimated. The assumption was made that most host trees which died prior to the 1974 measurement had died after the WSBW infestation began. This is probably a reasonable assumption for the most part, as average host tree CGF curves suggest that the infestation influenced radial growth approximately five years prior to 1974. Alfaro et al. (1982) indicated that mortality of Douglas-fir began as early as three years after the beginning of a WSBW infestation in British Columbia. However because some trees undoubtably died prior to infestation, there is likely some inaccuracy in the data. A comparison of mean diameter of all dead host trees (6.6") with diameter of only post-1974 host tree mortality (6.9") suggests that pre-1974 mortality does not greatly shift average characteristics of the data.

Advantages and Limitations of Methodology Used in the Radial Growth Analysis

There were several advantages to use of the Cumulative Growth Function (Carlson and McCaughey 1982) in the radial growth analysis. The squared annual increment component of this function tends to accentuate growth rate changes, facilitating detection of periods of growth depression and acceleration. Visual examination of CGF curves simplified classification of host trees into Recovery Class 2 or 3 depending on the presence or absence of an upwards curve inflection during the post infestation period. A programmed graphics system, made available by Clint Carlson and Leon Theroux of the Intermountain Forest Science Lab, allowed direct graphical comparison of host and nonhost CGF, annual increment, and other growth functions. Use of this system allowed rapid graphing of large numbers of increment series, facilitated comparison of candidate host and nonhost annual increment series used in the pairing procedure, and eliminated the time consuming process of gaining access to, and programming, an alternate graphics system.

The use of nonhost trees to determine WSBW influence on host radial growth involved adaptation of methodology developed by Carlson and McCaughey (1982), but differed from their procedures in some respects. Carlson and McCaughey (1982) analyzed WSBW infestation severity at the stand level, and therefore compared mean stand CGF of dominant and codominant host trees with mean stand CGF of nonhost. In contrast, WSBW influence on individual host trees was analyzed in this study, and individual CGF of host trees of all crown classes were examined.

Pairing procedures also differed between the two studies. Carlson and McCaughey (1982), minimized variation by pairing three or four host and nonhost trees of similar diameter and crown class on each plot. In contrast, host and nonhost trees were not paired in the field in this study, because of limitations imposed by the pre-established plots. For example, some plots contained several potential host/nonhost pairs, whereas other plots contained only host trees. The office procedure for pairing host and nonhost trees was devised using the assumption that the best host/nonhost pairs were those trees with the most similar annual radial growth fluctuations during a defoliation free period. Such pairs would respond most similarly to environmental influences but would show greatest separation of WSBW effects.

Several assumptions made during the radial growth analysis, if erroneous, could have resulted in misclassification of host trees into Recovery Classes. In particular, the equation used to determine Recovery Class 1 membership made no allowance for potential release of nonhost trees. If a host tree was paired with a released nonhost tree, the host tree could have been rejected from Recovery Class 1 membership when in fact growth was not reduced from WSBW defoliation.However subjective evaluation of CGF curves indicated no obvious release of nonhost trees used in the pairing process.

The procedure whereby individual host and nonhost trees were paired was vulnerable to error due to individual tree variability. Misclassification of host trees into Recovery Classes could have occurred if: 1. a host tree was paired with a nonhost tree growing abnormally due to microsite influences, damage to the nonhost tree, or other unknown causes, 2. use of several species of nonhost trees in the pairing procedure resulted in classification inconsistencies due to differing species response to climatic fluctuation, or 3. the period when host and nonhost growth was compared was not defoliation free, or host trees had not entirely recovered from a previous defoliation period.

The three to four year period after cessation of WSBW infestation is a relatively short period to assess radial growth recovery. Some trees classified into Recovery Class 3 may begin to show growth rate recovery at a later date. Thus temporary differences between Recovery Classes could potentially change over time.

An advantage of assessing WSBW influence on host radial growth at the individual tree level is that individual tree characteristics, as well as average plot or stand characteristics, may be compared between Recovery Classes and importance of these different levels of resolution determined. However, a disadvantage is that between tree variation associated with the individual tree approach may disguise broad relationships more easily discernable at the stand level.

One source of between tree variation that is uncontrolled in this study is genetic variation of host trees. McDonald (1981) observed phenotypic variation in the degree to which Douglas-fir are defoliated by WSBW, suggesting that genetic mechanisms influence individual tree resistance to WSBW defoliation.

Summary of Results

Analysis of these data suggest relationships that tend to be supported by other research. These relationships are presented in a hypothetical context context because low predictive power of descriminant models, and lack of consistently significant differences of descriptive variable means between Recovery Classes, reduced conclusiveness of results.

1. Smaller host trees in densely stocked areas are more likely to die during WSBW infestations. Such trees tend to be lower in vigor, as evidenced by low crown ratios prior to death than surviving trees.

2. Host trees which survive, but do not recover after WSBW infestations (RC3), tend to be in areas where proportion of maximum average basal area (BAR) is high at onset of infestation, and remains high after infestation cessation. Host percentage of basal area (PHPBA69) is also high in these areas. High BAR associated with these trees probably precludes growth recovery. Continued high BAR and PHPBA69 values associated with RC3 trees after infestation cessation suggests that these trees and areas may remain vulnerable to WSBW in subsequent infestations.

3. A combination of slightly greater vigor, as suggested by higher mean crown ratios and lower frequencies of other biotic and abiotic damage (OD82), and a tendency of trees to be in areas with slightly lower BAR, tends to increase likelihood of recovery of host trees (RC2). The presence of OD82 in discriminant models suggests that post-infestation tree condition is a better predictor of growth recovery than defoliation intensity during infestations.

4. Host trees which do not suffer radial growth reduction during infestations (RC1) tend to be on plots with lower percentages of host basal area (PHPBA69) and lower proportion of maximum average basal area (BAR) at the onset of infestation. Lower BAR probably increases vigor of host trees and lower PHPBA69 decreases vulnerability of these trees. By the post-infestation period however, BAR for RC1 trees approached mean BAR for RC2 and RC3 trees, and mean PHPBA82 though lowest for RC1, was not significantly different from RC2 and RC3. This suggests that

RC1 trees may be on plots that will grow into a more vulnerable condition over time, although slightly lower PHPBA82 of RC1 trees may indicate that they will remain less vulnerable than RC2 and RC3 trees despite high mean BAR for all Recovery Classes in 1982.

5. Low mean CVPCC associated with RC1 trees may indicate that these trees tend to be on plots with greater uniformity in competitive status, suggesting high vigor of these trees. Lower CVPCC is probably also associated with lower PHPBA and BAR for RC1 trees. Though nonsignificant, mean CVPDBH and mean CVPHGT tend to be highest for RC3 trees, perhaps supporting the contention (Wulf and Carlson in press) that vulnerability increases with variability in stand height structure. Including nonhost trees in the calculation of CVPHGT and CVPDBH may have confounded the relationship of these variables to the Recovery Classes.

6. Discriminant models indicate that crown ratio is the single best predictor of host tree growth recovery, albeit a weak predictor, as were all discriminating variables tested. Crown ratios measured in 1974 showed the same relationships across Recovery Classes as did crown ratios measured in 1982, suggesting that similar relationships for this variable are maintained during and after WSBW infestations. Analysis of individual trees may have enhanced the apparent importance of crown ratio because this variable is sensitive to individual tree variation.

7. Stepwise entry of plot variables such as PHPBA69 in discriminant models (versus individual tree variables such as crown ratio), reinforces the hypothesis that the different Recovery Classes have a tendency to be spatially clustered. Presence of these variables in discriminant models also indicates that plot and site condition may be as important to host tree recovery as individual tree characteristics. In particular, entrance of PHPBA69 and BACHA indicate that several variables describing different facets of basal area are related to growth recovery.

Biological and Silvicultural Implications of Results

Although this study does not conclusively define relationships between tree, site and stand conditions and host tree recovery from WSBW infestations, it is none-the-less important to state results in the context of silvicultural strategies and to make recommendations for further research.

1. Maintenence of vigorous trees and stands increases likelihood of host tree radial growth recovery after WSBW infestations. Higher average crown ratios and lower incidence of generalized damage symptoms of RC2 trees suggest these conclusions.

2. Reduction of the host complement of stands minimizes the effect of WSBW infestations on host tree radial growth, as suggested by lower percentage of host basal area associated with RC1 trees. Carlson and McCaughey (1982) recommended reduction of host basal area during development of young stands.

3. Plots or stands composed of high proportions of host trees at high densities are particularly prone to mortality during WSBW infestations. Williams et al. (1971) noted heavier mortility in dense, stressed Douglas-fir stands. In young developing stands, Carlson et al (1982) suggested maintaining basal areas with the minimum number of seedlings practical when considering other management objectives. They also suggested maintaining low proportions of host basal area (relative to nonhost basal area) in growing stands.

4. More mature stands with high percentages of host trees at high proportions of maximum average basal area are prone to growth stagnation after WSBW infestations. Infestations may not reduce total basal area and host tree portion of basal area in these areas, so that vulnerability to subsequent WSBW infestations remains high. Such stands may need to be prioritized for timber harvesting and subsequent silvicultural treatment.

5. Attainment of maximum average basal area may not be a desireable management objective in stands with high proportions of host basal area. High basal areas should only be maintained when there is adequate proportion of nonhost on the site to minimize vulnerability to WSBW.

Further research should investigate:

1. The relative vulnerability of stands at, or near, maximum average basal area, but with different percentages of host basal area.

2. The relative vulnerability of different aged stands at or near maximum average basal area.

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