Estimation of tree growth losses caused by pest activity

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An improved method of quantitative evaluation of pest-caused reduction of tree growth is described. Radial and height growth rates were measured from discs along the bole of the tree, and growth losses were evaluated by a computer program (IMPACT). The method is independent of site characteristics or competition effects. Use of the method was demonstrated for growth losses in *Pseudotsuga menziesii* attributable to defoliation by *Choristoneura occidentalis*, and with slight modification it may be applied to a range of tree–pest systems. A three-dimensional graphical procedure was used to display the growth pattern.

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Les auteurs décrivent une méthode améliorée pour évaluer quantitativement les pertes de croissance des arbres causées par les ravageurs. Il s'agit de mesurer les taux de croissance radiale et en hauteur, à partir de disques le long du fût de l'arbre, puis d'évaluer les pertes de croissance au moyen d'un programme informatisé (IMPACT). La méthode n'est pas reliée aux caractéristiques de la station ni à l'influence de la concurrence. L'utilisation de la méthode est démontrée quant aux pertes de croissance du *Pseudotsuga menziesii*, mais avec de légères modifications, elle peut s'appliquer à une gamme de ravageurs forestiers. Un procede de graphiques tridimentionnels est employé pour étaler les effets de l'impact des ravageurs.

[Traduit par le journal]

Introduction

A prerequisite of pest-control policy decision making is an estimate of losses attributable to the pest. Mott *et al.* (1957) investigated the effect of insect defoliation on radial growth of forest trees, using a system developed by Duff and Nolan (1953) for describing the patterns of radial growth increment in trees. While actual radial increments could be accurately measured and the change in patterns resulting from defoliation described, this method did not lend itself to quantitative assessment of potential growth and timber losses. Quantitative evaluation of losses is further complicated if dieback and reduction of height growth are considered. Other attempts to quantify growth losses, based on the approach of Mott *et al.* (1957), have met with only limited success (Stark and Cook 1957; Williams 1967; Miller 1977).

An epidemic of western spruce budworm (*Choristoneura occidentalis* Freeman) has persisted in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in British Columbia since 1968 (Shepherd *et al.* 1977). Trees in some areas had been subjected to up to four budworm outbreaks prior to the current outbreak. Radial increment was reduced in each outbreak and height growth was curtailed. Varying degrees of top killing were also associated with each outbreak. Estimation of growth losses in such situations is complex.

In British Columbia, the major budworm infestations of Douglas-fir occur over large areas. Unattacked trees are usually found only at considerable distances from infested stands and usually with significantly different age, density, aspect, elevation, topography, or site characteristics. It is therefore of questionable validity to evaluate losses from a study of unattacked trees. In addition, it may be misleading to estimate the growth of Douglas-fir from growth rates of nonhost species in the stand, as such trees may increase their growth rates in response to reduced competition resulting from defoliation of the Douglas-fir. Even lightly defoliated host trees may be released by defoliation of adjacent hosts (Williams 1966).

In the absence of other valid and practical alternatives, the approach used in the present study is to modify growth increments during outbreak and recovery years based on the growth increments of host trees between infestations.

This method is applicable to pest-caused growth losses that occur as a consequence of clearly delineated episodes of pest damage followed by growth recovery. Abnormalities such as multiple tops or where the growth loss period is prolonged, as in dwarf mistletoe infestations, will be considered in future papers.

Sampling methods

Annual ring width varies at different heights along the stem (Duff and Nolan 1953). Similar patterns have been observed in tussock moth defoliated trees (Wickman 1963). In addition, failure of defoliated trees to produce one or more annual rings, par-

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ticularly near the base of the bole, has been reported (Evenden 1940; O'Neil 1963). A single sample of radial growth, such as an increment core at breast height, is therefore inadequate for accurate evaluation of growth losses over the whole bole.

In a preliminary study to determine the minimum number of discs and minimum sample effort required from a tree for satisfactory estimate of volume, data from five healthy western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) which averaged 42.6 m in height and had been sectioned with discs taken at 1-m intervals were examined. Volumes from a decreasing subsample of equidistant discs were calculated using Smalian's formula, and the results were compared with the volume estimated from the total sample (Table 1). A sample of 11 discs per tree was selected as a practical compromise between accuracy, sampling effort, and subsequent processing effort in the field and laboratory. This sampling intensity will result in greater accuracy with shorter trees and reduced accuracy in taller trees than is indicated in Table 1.

Subsequent sampling of 42 Douglas-fir trees affected by western spruce budworm included a disc 2 to 4 cm thick at stump height (0.30 m), a second disc at breast height (1.30 m), and the distance between the remaining nine discs was obtained from (tree height − 1.30)/10. Discs were cut as close to these distances as possible, avoiding branch nodes, and the bark was peeled off before removal to the laboratory and cold storage at 0°C.

Use of discs instead of increment cores facilitated examination for discontinuous rings, allowed measurements to be made perpendicular to the annual rings, and provided a larger, less fragile sample for more accurate observation and measurement. To reduce sample weight and bulk for storage and to minimize variability caused by asymmetric growth of the tree bole, two average radii were determined (Chapman and Meyer 1949), marked on the disc, and the disc segments containing these radii were removed by cuts 2 cm on either side. All segments were retained in the event reexaminations were necessary. Two radii were measured to reduce variation arising from the irregularities of bole growth; with this method of disc preparation, only two segments containing the pith and early growth rings could readily be obtained. Any further increases in precision did not seem to warrant the time required for preparation and measurement.

The radial segment was sawn along the cross section using a planer or plywood blade on a tablesaw to provide a clean, smooth, even surface easily examined on the Swedish Addo-X tree ring measuring machine, described by Ecklund (1969). Ring contrast could usually be enhanced by surface wetting the sample with water. Ring widths were measured to ±0.01 mm and automatically punched on computer cards. All measurements from the two radii of each disc were computer plotted for all discs on a tree and compared for anomalies indicative of missing rings or inconsistent age counts, and the samples were reexamined, if necessary. Such anomalies will be discussed in a separate presentation. The mean of the increments on the two radii was used as input to the computer program for evaluating the volume loss. Designation of years of outbreak, recovery, and "normal growth" may be influenced by corroborating observations, if available, for any infestation or by relative comparisons with growth patterns in other nonhost tree species. However, precise relationships between duration and severity of defoliation, tree age, site, etc., and tree growth will only be determined through careful, long-term monitoring preceding stem analysis.

The vertical distance between discs is partitioned among the intervening internodes to estimate annual height growth. To guide this partitioning process, 10 Douglas-fir with 21 externally visible bole disturbances arising from three previous infestations were dissected in detail. Node ages were compared to annual ring counts at a minimum of 11 intervals in each tree and discrepancies were traced to discontinuities in the boles and probable causes determined. A separate paper is in preparation describing the absence of height growth and dieback which may result from budworm defoliation.

Methods of analysis

General description

A computer program (IMPACT), written in standard FORTRAN for use on PDP-11 computer, was developed to carry out volume analyses based on the measured growth increments. Volume is obtained by summing the volumes of the individual internodes, calculated as in the standard Smalian's formula where the bole segment is considered a truncated cone. Losses from pests are estimated by resetting the radial and height increments during affected years to an expected potential growth and comparing the volume to that estimated from the observed growth rates. The program carried out the following operations. (*i*) The mean annual radial growth increments on each disc, the year of formation of the internode from which the disc was

TABLE 1. Accuracy of tree volumes calculated by Smalian's formula using varying numbers of discs compared to a total sample size of 43 discs in each of five trees

No. of discs in subsample	Percentage volume difference from maximum sample size in each of five trees		
	$\bar{X}$	$SE_{\bar{X}}$	Range
22	−0.33	0.26	−1.0 to 0.6
15	1.01	0.38	0.0 to 2.0
12	0.35	0.43	−0.8 to 1.8
10	0.94	0.74	−0.9 to 2.3
8	1.50	0.66	−0.5 to 3.1
6	2.09	1.08	−1.7 to 4.4
4	5.39	1.10	1.9 to 7.8
2	11.58	2.17	8.4 to 19.4

cut, and the height interval to the next disc were entered. (*ii*) The distance between discs was partitioned among the internodes between the discs to provide estimates of annual height growth. (*iii*) Radial increments on internodes where no discs were taken were estimated by interpolation of the observed increments on the discs taken on the internodes above and below. These data, together with the height increment of each internode obtained in (*ii*) above, comprise the observed growth rates representing the actual growth of the tree. (*iv*) Some of these radial and height growth increments remain unaltered and some are reset to reflect alternative or assumed growth conditions in certain years.

The observed growth rates

The detailed tree dissections indicated that height growth was zero during years of heavy feeding and that during the 4 or more years of the recovery period following the penultimate outbreak (Fig. 3), average total height growth was approximately equivalent to 2 years of postrecovery growth. In addition, the pest activity resulted in dieback of two preoutbreak internodes during each outbreak, on the average. These killed internodes are not included in the distance between discs as the new growth of the tree bypasses the killed section. These data have been assumed to be representative for development of the program but can be altered as new data become available.

During program initiation, the years of formation of the internodes killed by dieback are specified, as are the 1st year of effect of the outbreak and the year of complete recovery of normal radial growth (Fig. 3). To estimate annual height increments, the distance between discs of known age was partitioned equally among the intervening internodes, excluding dieback years and all but the last 2 years of the recovery period; i.e., all growth during the recovery period is represented by the last two internodes. In excluded years, a zero increment was assigned. In other sites and with other pests, alternative methods of partitioning the distance between discs might be required.

Annual radial increments on internodes between two discs were estimated by linear interpolation between the corresponding increments on the discs above and below the internode. The innermost increments on an internode, which must be estimated from the increments on the disc below the internode, were treated as a special case, contingent on the method of partitioning the distance between discs among the intervening internodes and an assumption of linearity of the outer bole surface between the discs.

The basal disc lies within the butt flare region of the bole and growth increments on this disc were often anomalous. The increments on this disc were therefore extrapolated from those of the breast-high disc.

Exact measurements of ring widths made on the discs, and estimates of growth rates by interpolation as described above, are treated with equal weight in the subsequent operation of the program.

Graphical display of growth data

Duff and Nolan (1953) demonstrated the value of graphical techniques in describing patterns of radial increment as discussed by Mott *et al.* (1957). These authors identified three growth sequences: type 1 (oblique), type 2 (radial), and type 3 (vertical). In the present study, the value of graphical techniques has been enhanced by use of computer graphics systems. The radial and oblique sequences were combined using a three-dimensional computer graphics system originally developed for display of topography (Thomson and Moncrieff 1979). The radial growth of a tree subjected to four budworm outbreaks is illustrated in Figs. 1 and 3*a*. For clarity, radial growth is illustrated only for every fifth internode. Periods of budworm outbreaks are indicated by shading on the diagram.

During outbreaks, radial growth is reduced along the entire bole, but reduction is greatest in the upper levels of the tree (Fig. 1). The start of the effect of the outbreak and the end of the recovery period may be clearly defined, at least in this tree, which was a 96-year-old (at stump) dominant Douglas-fir cut near Pemberton, B.C. on July 21, 1977. The height and diameter at breast height over bark (dbhob) were, respectively, 28.3 m and 47.0 cm. When felled, a dead top 1.4 m long with a basal diameter of 3.0 m was found, although in 1973 as much as 5 m of the top had been bare, and it was estimated that 65% of the tree's foliage had been lost through annual defoliation commencing in 1970. A single new leader had not become dominant.

A second graphics program (GINC) was developed to display the combined effects of radial and height increment (Fig. 2). During outbreaks, there may be no height growth in severely defoliated trees and there is also the added possibility of dieback. These periods are indicated by the discontinuities and the close spacing of the annual layers of wood formed over the surface of the tree.

Discontinuities in the bole may be grown over, but such abnormal growth contributes an insignif-

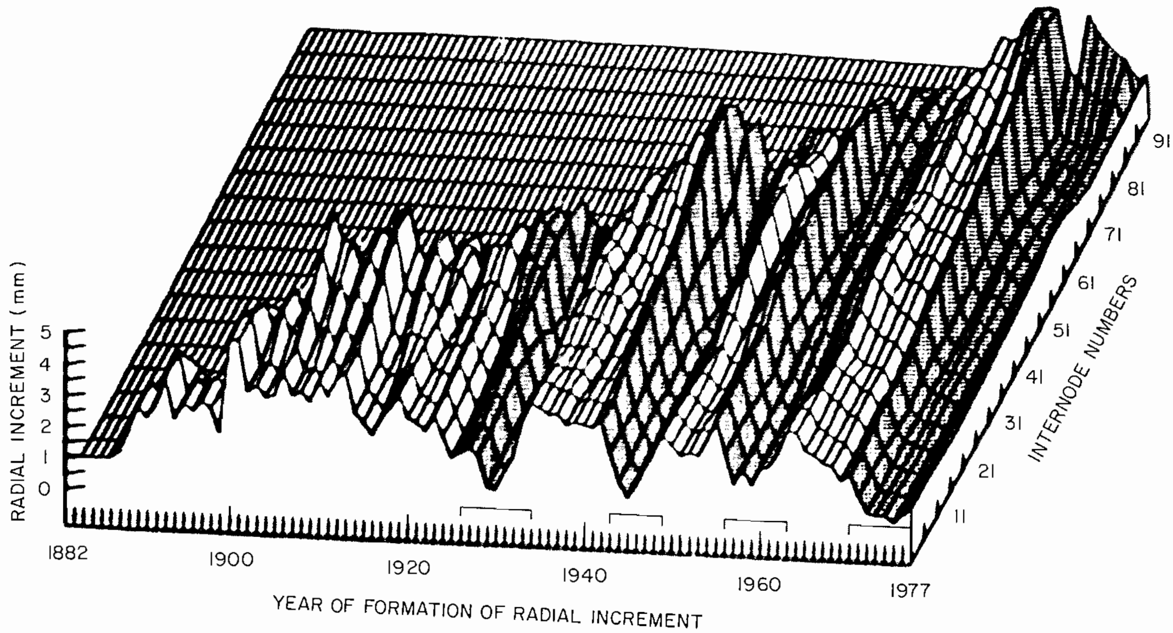

FIG. 1. Computer-drawn figure showing the radial growth increments formed on every fifth internode up the bole of a Douglas-fir tree during each year of growth. Increments formed in years of reduced radial growth resulting from western spruce budworm outbreaks, delineated in Fig. 3, are shaded. The start of the outbreaks and end of the recovery periods, inclusive, are indicated by the bars on the x-axis.

icant amount to the total volume and has not been quantified or included in the analysis. The case of multiple stem development is not considered in the present study.

Modification of the radial growth increments

Potential growth, in the absence of outbreak effects, was estimated by setting the increments in outbreak years to "normal" growth values. These values were estimated from growth increments before and after the outbreak and recovery period based on two alternative methods.

The first method was based on the observation by Duff and Nolan (1953) that in the type 2 sequence of radial growth increments, i.e., the series of ring widths laid down on a given internode in successive years, growth increment generally rose to a maximum in the first few rings, then declined toward the periphery. This trend was repeated on all discs (Fig. 1) and has been indicated for tree species other than that studied by Duff and Nolan (Mott *et al.* 1957; O'Neil 1963; Stark and Cook 1957). For each disc on the tree, separate lines were fitted by a least-squares method through the points before the maximum and from the maximum to the termination of growth (Fig. 3*b*). Increments formed in years designated as outbreak or recovery years were excluded from the line-fitting method. The equations of these lines were used to estimate the potential radial growth increment on a disc during the outbreak years. The increments on intervening internodes during outbreak years were then obtained by linear interpolation.

The second method established the mean increment for 5-year periods before and after the outbreak effects, around the year of maximum increment described above, and for the initial growth of the disc (if the period is not in an outbreak). These mean values were used to define line segments representing normal growth periods. Interpolation of the line segments across an outbreak gave an estimate of the expected potential growth during that outbreak (Fig. 3*c*). In cases where there were fewer than 5 years of normal growth, the program determined the number of years available.

The relative merit of either approach depends on the degree to which the estimating procedure reflects the normal growth trends, which was tested as follows: (*i*) all radial increments (except for the increments during outbreak years) were set to the estimated values using each of the above methods; (*ii*) the observed height increments were used, and the volume of the tree was calculated; and (*iii*) this volume was compared to the volume calculated using observed increments in all years.

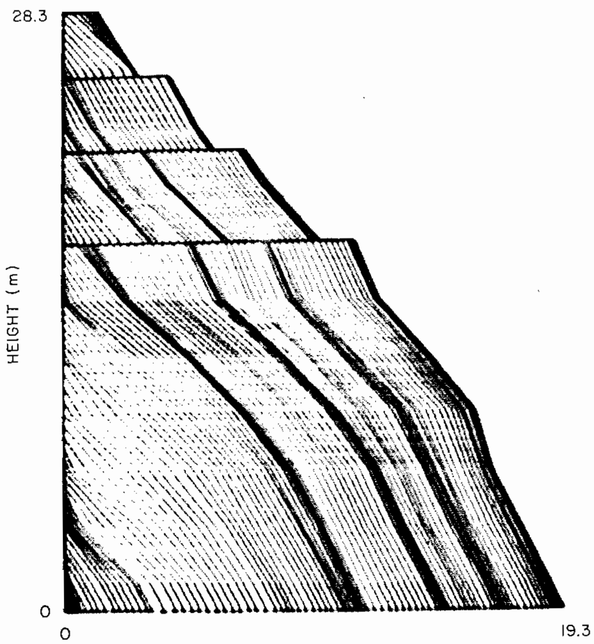

FIG. 2. Computer-drawn figure showing the relationship of height and radial growth increment for each year of growth on each internode of the Douglas-fir tree indicated in Fig. 1. The dense bands result from reduced radial increment during budworm outbreaks and the discontinuities result from suppressed height growth and dieback at these times. The y-axis (height) is partitioned into internodes by the intersection of the annual tree outlines with the axis.

Volume and dbh were calculated in this way for 42 trees of varying defoliation class and compared with the observed values. The least-squares line-fitting method estimated average dbh to within 0.01 mm, the limit of numerical accuracy of the method, and volume to 0.1% of the observed value. The use of line segments based on 5-year means estimated dbh to a 2% and the volume to a 1.1% difference from the observed values.

Having established the validity of the two alternative procedures for estimation of radial increment during normal growth conditions, these procedures may be used to estimate potential radial increment values during outbreak years. If this is done during all outbreaks, the potential volume, in the absence of radial growth reduction, may be estimated. Figure 4 illustrates the resetting of all outbreak radial increments using the means of the 5-year pre- and post-outbreak periods. The altered values during the outbreak years are indicated by shading.

By setting to normal the increments during all outbreaks except one, an estimate may be obtained of the significance of that outbreak as if it had been the only outbreak affecting the tree. Alternatively,

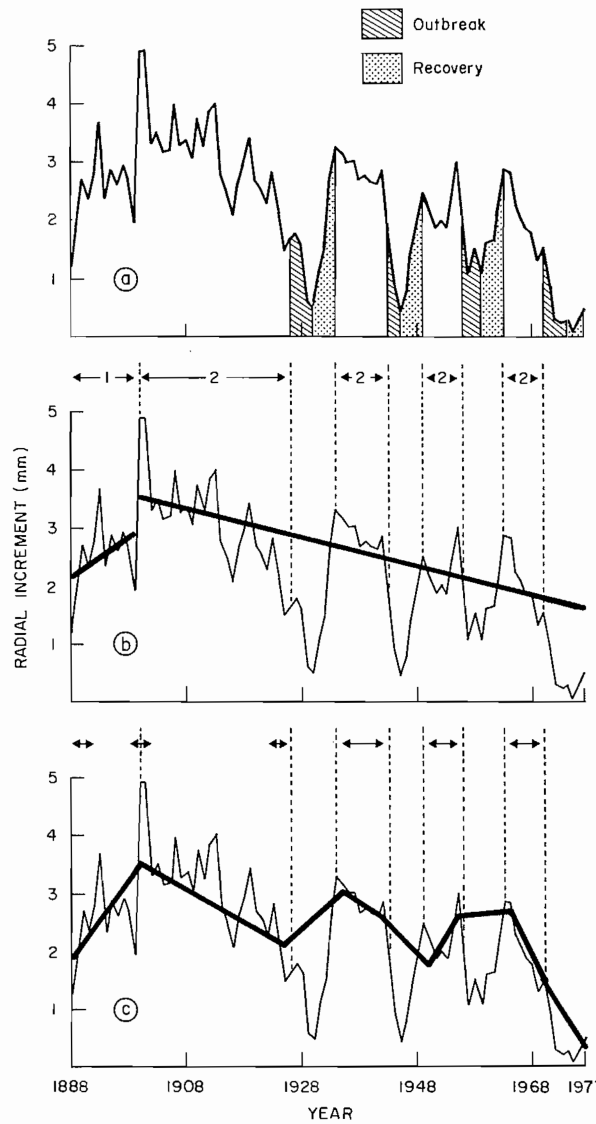

FIG. 3. Estimation of growth trends for extrapolation to outbreak conditions. (a) Mean annual radial increment from two radii on the disc taken at breast height showing the years designated as outbreak and recovery years, inclusive. (b) Lines used to estimate normal radial increment, using those points between the arrows in the evaluation of the line before the maximum increment (arrow 1), and from the maximum to the termination of growth (arrow 2). (c) Lines used to estimate normal radial increment, using line segments based on the 5-year means of normal growth during the years included within the arrows, immediately preceding the outbreak or following recovery.

by setting to normal the values for a single outbreak, an estimate may be made of the effect of controlling that outbreak.

Modification of the height growth increments

The original height growth data were in the form of distances between discs. Distances were parti-

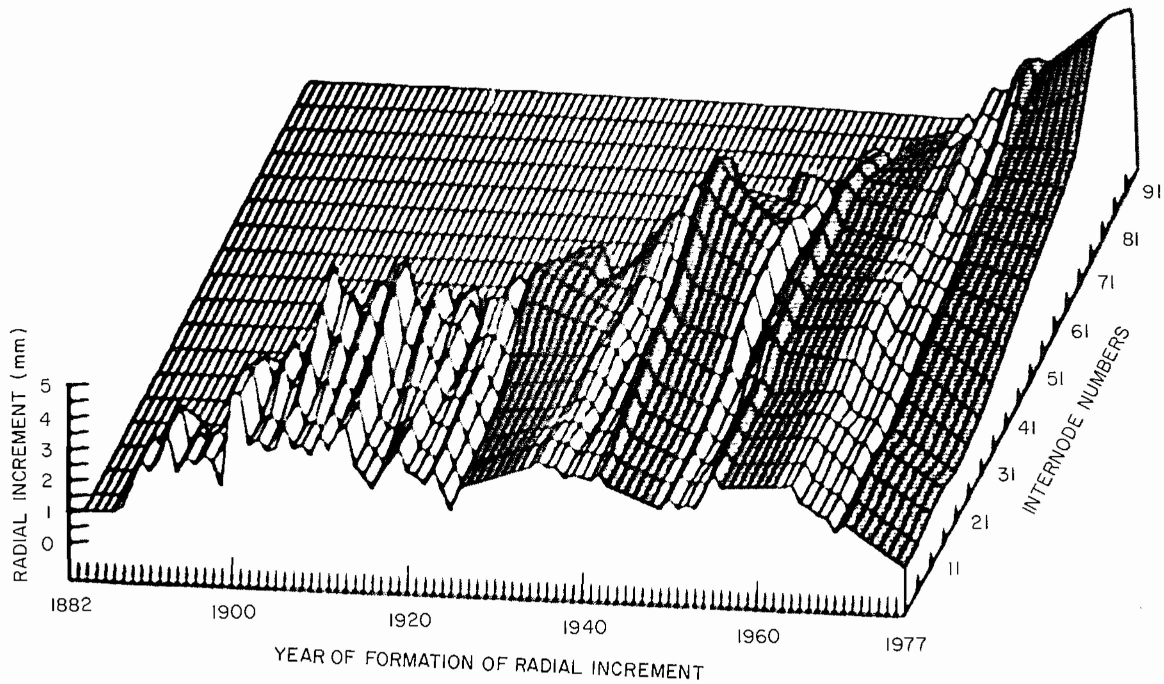

FIG. 4. Computer-drawn figure, similar to Fig. 1, but with the increments during the outbreak years set to the values estimated from line segments derived from the 5-year means of normal growth indicated in Fig. 3*c*.

tioned among the nonoutbreak, nondieback years as prveiously described, the increment in dieback internodes and all but the last two internodes of the recovery period being zero.

The program permitted the annual height increment during a specified time interval to be set to a specified value. Detailed examination of height increments in ten 87-year-old Douglas-fir trees during pre- and post-outbreak years indicated a mean increment of 43 cm during these periods. Thus, during outbreak and dieback years in this stand, the height increment may be reset to 43 cm to evaluate the potential growth.

Discussion

This paper describes the development and use of a method for obtaining and analysing tree growth data to better enable quantitative estimation of potential growth in the absence of pest effects, and thus losses attributable to the pest. The method is species independent insofar as it depends upon data consisting only of measurements of radial increment and height growth. Species-specific growth patterns and the effects of site and competition indices are implicit in these data.

Use of the method has been demonstrated for Douglas-fir growth and illustrates some effects of defoliation by western spruce budworm. The computer program enables one to examine the effects of single or multiple infestations in terms of actual and potential height and diameter, and gross volume, throughout the life of the tree. Studies of the effect on merchantable volume are in progress.

Tree height-age relationships are widely used to assign site growth indices. Such indices may greatly underestimate the tree growth conditions if the effects of previous pest damage on dieback and suppression of height growth, especially during the immature period before height increments decline, are ignored. The method developed here permits consideration of such pest effects in site index calculations.

In comparing the relative merits of the two methods of estimating the radial increment used here, it must be remembered that it is only growth during the outbreak which must be estimated. Although the use of the first method (Fig. 3*b*) gives a better estimate of the actual volume, the second method (Fig. 3*c*) may give a better estimate of potential growth during outbreaks, especially if the long-term trend of interoutbreak radial increments is nonlinear. On the other hand, the second method does not utilize all the available data, notably the period from 1900–1925, in filling in the outbreaks.

Drought conditions preceding outbreaks may also result in reduced increments (Silver 1960).

This reduction lowers the endpoints of the lines estimated from the 5-year means and is a possible cause of the reduced accuracy of the second method in estimating the actual volume. However, as continuation of drought conditions into the outbreak years might result in lower potential growth, the second method, being based on adjacent values, may give a better estimate of these short-term effects. As the relative merits of the two methods to estimate potential growth have not been fully established, options for selecting either method in the program are at the user's discretion.

Potential volumes estimated from the observed data are conservative as the estimating procedures assume that radial growth returns to normal after the outbreak, neglecting the possibility that long-term effects of several outbreaks indicated could result in a general decrease in host vigor. The post-outbreak levels are therefore probably somewhat reduced. While data are not presently available to decide this issue, its effect could be simulated by adjusting the postoutbreak radial increments by fixed percentages. No "rebound" effect, where radial growth following the period of pest activity was greater than normal, was exhibited by the trees examined in the present study. To evaluate potential growth in situations where such an effect was found, these abnormally large increments would be excluded from the determination of the normal growth trend in the same manner as the reduced increments during the recovery period are excluded.

The current report describes only the basic approach of the method, which is currently being used to evaluate the effect of defoliation by budworm on timber volume losses. Results of this investigation will be reported when the analyses are complete.

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