

A method to calculate the losses caused by western spruce budworm in uneven-aged Douglas fir forests of British Columbia

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ABSTRACT

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A system was designed for projecting the growth of uneven-aged stands of interior Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) of the Kamloops Region of British Columbia after defoliation by the western spruce budworm (*Choristoneura occidentalis* (Freeman)). The system reads forest inventory files and simulates infestations of varying severity and duration. The system produces the losses in total stand volume (all trees with a diameter larger than 2.5 cm) and in volume of the harvestable trees (all trees with a diameter larger than 30 cm) for every 10 year interval. In a trial consisting of a 20 year projection on 32 stands, assuming a 7 year infestation in the first decade, the system calculated that at the end of the projection, losses in total volume per hectare averaged 6.2%, 23.3% and 32.8% of the total stand volume, for light, moderate and severe infestations, respectively. Reduction in the 20 year periodic annual increment of the total volume averaged 7.1, 39.3 and 51.6%, for light, moderate, and severe infestations. Losses resulting from infestations lasting 1–9 years are also reported.

INTRODUCTION

The western spruce budworm (*Choristoneura occidentalis* (Freeman)), a native defoliator of interior Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), periodically reaches outbreak levels in British Columbia. The infestations extend for thousands of hectares on a variety of forest types, mostly in the interior of the province (Harris et al., 1985).

Budworm defoliation causes tree mortality, reduction of growth rates, and reduced lumber quality. Tree mortality is generally less than that reported for eastern Canadian forests defoliated by the spruce budworm (*Choristoneura*

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fumiferana Clemens) (Schmitt et al., 1984; MacLean, 1988). In western Canada, mortality is more prevalent among trees in the lower canopy than in the dominant or co-dominant strata (Alfaro et al., 1982; Alfaro, 1986).

Defoliation severely reduces tree growth. The width of annual rings produced during the infestation years is progressively reduced with each additional year of defoliation, in a cause-effect relationship that usually has a 1 year lag (Thomson and Van Sickle, 1980; Alfaro et al., 1982). After the infestation collapses, defoliated trees take several years to regain their full foliage; during this period radial growth rates slowly recover.

Because of the budworm's preferential feeding on the current year's buds and foliage, height growth is severely reduced or eliminated during each year that defoliation occurs. In addition, severe defoliation for a number of years often causes mortality of the upper crown in a type of damage known as die back or top-kill; this type of damage reduces the height of the tree by one to several internodes (Van Sickle et al., 1983). Trees which sustain die back resume height growth by means of lateral branches gaining apical dominance or by branches that originate from adventitious buds in the main stem (Van Sickle et al., 1983). This process may result in the formation of stem defects that curtail the merchantability of the stem (Ferrell and Scharpf, 1982).

Determination of the losses caused by budworm requires growth and yield models capable of predicting forest productivity under epidemic conditions. In determining effects of *C. fumiferana*, MacLean and Erdle (1984) included budworm effects in an existing forest wood supply model. A model for predicting losses due to western spruce budworm was developed by the Canada/US spruce budworms program (CANUSA) (Crookston, 1985; Sheehan et al., 1987), as an addition to PROGNOSIS, a stand model widely used in the western US (Stage, 1973; Wykoff et al., 1982). The application of these to British Columbia is thwarted because the basic data for their calibration to the local conditions is incomplete.

In British Columbia, Thomson and Alfaro (1990) developed a method to estimate yield reduction due to budworm defoliation for even-aged stands or for the overstory layer of uneven-aged stands. Budworm impact was expressed as correction factors which could be applied to the expected volume at rotation.

In uneven-aged stands there are differential budworm impacts on the different canopy layers. The objective of this report is to describe a method to calculate losses due to budworm defoliation in all layers of uneven-aged stands and to present results of a test of the system using data from the Kamloops Region of British Columbia.

METHODS

The stand projection system reported here reads data from one or more inventory plots and projects stand development in 10-year steps, yielding the

number of trees per hectare, total stand volume, and harvest volume (i.e. number and volume of logs from trees above a user-defined diameter limit). Two projections are performed. The first projection produces an estimate of forest conditions without budworm. In the second projection, budworm impacts are calculated by applying growth and mortality modifiers (described below) to the first projection. In this paper a set of 32 inventory plots were grown for 20 years. This projection period was selected because it is a common interval between harvests under a selection regime in these interior forests. The projection was started in 1985. Budworm infestations, of varying duration, were simulated to start 2 years after the start of the projection (i.e. in 1987). Detailed results are presented for a duration of 7 years which is a common infestation duration in British Columbia. Separate runs were performed to simulate light, moderate, and severe infestations.

Development of the uneven-age stand projection system

Database and analysis

In 1987, the British Columbia Ministry of Forests established 32 growth and yield plots in the Kamloops Region in areas defoliated by budworm in 1986 and 1987 (MacLauchlan and Smith, 1987). The objective of the plots was to gather information on the effects of defoliation on tree and stand growth. These plots were circular and occupied 0.015, 0.025 or 0.035 ha, depending on stand density. All living trees 7.5 cm diameter at breast height (DBH) and larger were measured for diameter. The plots also included a subplot (size also variable with density) where all living trees with a DBH of 2.0–7.4 cm were measured. Trees with a DBH less than 2.0 cm and any trees that did not reach breast height but were taller than 0.3 m were also recorded. These trees are referred to later as 'trees without DBH'.

Of the 32 plots, 15 were established in the IDFxh forest biogeoclimatic subzone (very dry submontane interior Douglas fir) and 17 in the IDFdk subzone (very dry montane interior Douglas fir) (Lloyd et al., 1989). Eight of the 15 plots in IDFxh were established on undisturbed stands (not logged in the last 20 years), and seven in stands that had sustained selective logging in the last 20 years. Of the plots in the IDFdk subzone, eight were undisturbed and nine had sustained selective logging. All plots were located on medium sites and in uneven-aged stands.

In the fall of 1988, after radial growth for the season had ended, one increment core was collected from 20 to 25 trees in five to seven plots in each combination of logging regime and biogeoclimatic zone (a total of 462 cores were collected) (Table 1). Trees to be cored were selected from each 5 cm diameter class, in proportion to the percentage that each diameter class contributed to the total number of trees in the stand. Increment cores were collected at breast height from no particular aspect of the tree circumference.

TABLE 1

Mean 10 year periodic growth (standard deviation in brackets) of interior Douglas fir calculated from increment cores collected in two biogeoclimatic zones and two logging regimes in the Kamloops Forest Region of British Columbia

Zone	Management regime	No. trees	Diameter (cm) in 1985	10 Year periodic growth (cm)	
				1976–1985	1966–1975
IDFxh	Not logged	133	17.9	2.6(1.7)	2.4(1.7)
	Logged	80	17.0	2.6(1.9)	2.2(1.4)
IDFdk	Not logged	123	17.6	2.2(1.5)	1.9(1.0)
	Logged	126	18.1	2.2(1.4)	1.9(1.2)
	Total	462			

Annual ring widths in cores were measured to the nearest 0.01 mm using a DIGIMIC measuring instrument and the software described by Alfaro et al. (1984). Sample cores were cross-dated (Stokes and Smiley, 1968; Fritts, 1976) and missing rings were accounted for when detected.

The annual rings for the last 2 years of growth (1986 and 1987) were deleted because the trees were defoliated in these years. Diameters inside bark up to 1985 were calculated. Regression analysis was used to test for differences in increment in the last 10 years (1976–1985) by logging regime and biogeoclimatic subzone. The increment of the previous 10 years (1966–1975) and tree diameter in 1965 were used as covariates. This analysis indicated that diameter increment in the last 10 years was significantly related only to increment on the previous 10 years. When previous 10 year increment was not included in the equation, a very low ($r^2=0.06$) but significant ($F=14.9$, $P<0.01$) correlation was found between increment in the last 10 year period and tree diameter at the start of the period (1975), and with biogeoclimatic subzone. A low correlation between diameter growth and initial diameter for interior Douglas fir was also reported by Clark (1952).

Based on these findings data for all plots was pooled and the following autoregressive model was developed to predict diameter growth:

$$\log(\text{INC}) = 0.1095 + 0.8602 \times \log(\text{PINC}) \quad (1)$$

with $R^2=0.66$; $P<0.01$; $F=859$; where INC is breast height diameter increment inside bark in a decade, and PINC is breast height diameter increment inside bark in the previous decade.

This equation was tested using an independent data set consisting of 24 permanent plots located in interior Douglas fir stands (Bonnor et al., 1991), and which contained two 10-year remeasurements (1968–1977 and 1978–1987). For the test, the trees were sorted by diameter class in 1977 and then the diameter in 1987 was calculated using the 1968–1977 growth in eqn. (1).

The equation predicted the average 1987 diameter of the trees in a diameter class with an accuracy which varied among the classes from -0.9 to $+2.2\%$ of the true diameter.

Growth projection

The system calculates future diameter growth of individual trees in the plots on a 10 year step. Then, using appropriate equations, it calculates diameters outside bark, new tree heights, volumes, and the number of logs of various dimensions. At the end of each step the tree list is sorted into 5-cm diameter classes and factors for mortality and ingrowth are applied to each class. The various components of the system are described below.

To calculate the diameter increment in the next 10 years, Model (1) requires an estimate of the previous 10 year increment (inside bark) for each tree in the plot, a datum which was not available for every tree. Therefore, the previous 10 year increment of each plot tree was estimated from the increment core data as follows. Cored trees were sorted into 5-cm DBH classes (inside bark) and the mean increment and standard deviation for the last 10 years of growth was calculated (Table 2). Separate calculations were done for

TABLE 2

Mean inside bark diameter increment (cm) and standard deviation for the last 10 years of growth in Douglas fir trees from the Kamloops Region, British Columbia in two biogeoclimatic subzones, tabulated by inside bark diameter class at the end of the period. Based on a sample of 462 increment cores

Diameter class ¹ (cm)	Zone IDFxh		Zone IDFdK	
	Mean increment (cm)	Standard deviation	Mean increment (cm)	Standard deviation
0	0.64	0.31	0.76	0.22
5	1.56	0.90	1.24	0.78
10	2.12	1.23	1.68	1.12
15	2.76	1.53	2.19	1.38
20	2.90	1.72	2.27	1.32
25	2.75	1.67	2.76	1.53
30	2.91	2.05	2.77	1.31
35	2.90	2.13	2.84	1.43
40	2.43	1.56	2.88	1.00
45	1.93	1.22	2.82	0.93
50	2.44	0.13	1.75	0.53
55	1.34	0.40	— ²	—
60	0.65	0.13	—	—

¹Numbers in this column represent the mid-point of the class, except for Class 0 which includes trees with DBH from 0.1 to 2.4 cm.

²No trees sampled in these classes.

each biogeoclimatic subzone. The tree diameters outside bark were read from the inventory file, converted to diameters inside bark, and sorted into 5-cm diameter classes. Then, each tree was assigned a previous 10 year increment selected randomly from a normal distribution with mean and standard deviation corresponding to the diameter class in Table 2. The previous increment was limited to being larger than zero. Once all trees were assigned a previous increment, the future 10-year and 20-year diameters inside bark were obtained using successive runs of Model (1). Outside bark diameters (DBHob) were calculated from the following model which was based on the increment cores collected for this study:

$$\text{DBHob} = 1.19 \text{ DBHib} \quad (2)$$

with $r^2 = 0.94$, $P < 0.01$. At the end of each 10 year cycle, every tree with a DBH was assigned a height based on the equation used by Bonnor et al. (1991):

$$\text{HT} = 1.3 + a(1 - e^{b\text{DBH}^c}) \quad (3)$$

where a is 24.992 in IDFxh and 27.499 in IDFdK; b is 0.027 in IDFxh and -0.021 in IDFdK; c is 1.115 in IDFxh and 1.134 in IDFdK; DBH is breast height diameter inside bark.

Volume calculation

Tree volumes between stump and 10 cm top diameter, and volume of the logs were calculated using Smalian's formula and Kozak's variable-exponent taper equation (Kozak, 1988) to calculate upper stem diameters. Summing over all trees in the stand yielded a total volume. To obtain the harvestable volume, every tree larger than 30 cm in DBH was sectioned into 5-, 10- and 15-m logs. These log sizes were considered by the authors a reasonable representation of log sizes in the British Columbia interior. Sectioning followed an optimization procedure where all possible 15-m logs were obtained first, then the remaining portions were cut into 10-m logs, and the leftovers into 5-m logs. Summing the volume of all logs yielded the harvestable volume.

Ingrowth and juvenile suppression

No reliable data on levels of ingrowth exist for interior Douglas fir in British Columbia (see Bonnor et al., 1991 for a discussion on the limitations of the British Columbia database). Ingrowth was assumed to occur into DBH Classes 0 cm (0.1–2.4) and 5 cm (2.5–7.4), as trees below breast height grow and acquire a DBH. Diameter growth of the trees below breast height was simulated in two steps. It was assumed that all plot trees without a DBH had a height just below breast height and that all will grow a 10 year increment at breast height in the first 10 years. For these trees, a random number from a normal distribution of mean equal to 2.94 cm and standard deviation of 1.45

was assigned as their first 10 year diameter increment. These values are the mean and standard deviation of the first 10 years of growth at breast height for the trees cored in this study. Then, a selection of 85% of these trees (those with the largest increment) were allowed to pass into the upper DBH classes. The remaining 15% were assumed to be suffering juvenile suppression and their breast height increments were reset to zero. The rejected trees have a chance to become ingrowth in the next cycle. The 85% figure corresponds to the percentage of trees that reached breast height in the first decade of life in a sample of 75 interior Douglas fir trees subjected to stem analysis in a previous study. In order to maintain a stock of candidate trees for ingrowth, once a tree below DBH grew and obtained a DBH, a new tree with no DBH was created by the program.

Natural mortality

At the end of every 10 year cycle, trees were removed from the stand by natural mortality (i.e. died from causes other than budworm); the probability of a tree being removed by natural mortality varied by diameter class of the tree and the biogeoclimatic subzone of the plot (Table 3). These probabilities were derived from a set of permanent plots from the Kamloops Region. However, no mortality of trees in DBH classes greater than 40 cm was recorded in these plots. This is possibly due to the fact that mortality in these classes, which contain the dominant trees, is relatively infrequent and was not

TABLE 3

Percentage mortality in a 10 year period among interior Douglas fir trees sorted by diameter class (outside bark) at start of the period

Diameter class ¹ (cm)	Percent mortality	
	Zone IDFxh	Zone IDFdk
0	16.2	5.5
5	9.7	2.9
10	4.1	2.9
15	2.0	2.9
20	2.0	1.2
25	2.0	1.2
30	2.0	1.2
35	2.0	1.2
40	2.0	1.2
45	0.5	0.5
50	0.5	0.5
55	0.5	0.5
60	0.5	0.5

¹Numbers in this column represent the mid-point of the class, except for Class 0 which included trees with DBH from 0.1 to 2.4 cm.

observed with just one remeasurement period. Mortality for these classes was assumed to be an arbitrary 0.5% of the trees every 10 years.

Budworm infestation simulation

Budworm effects consist of tree mortality, top-kill, and diameter and height growth reduction. Top-kill induces stem defects which reduce lumber recovery. The severity of these effects depends on the duration and severity of the defoliation. The system was developed to allow the simulation of infestations of variable duration and severity. Infestations can last up to 10 years but in the model they must start and end within a 10 year cycle. Most damage factors used here are based on unpublished observations of damage on file at the Pacific Forestry Centre. The loss factors for top-kill and for diameter growth reduction are modifications of similar factors reported by Thomson and Alfaro (1990). Where no data could be found, factors based on the best judgment of the authors were used. These loss factors can be easily updated as new data become available. The definitions of a light, moderate or severe infestation follow those used by the Forest Insect and Disease Survey of Forestry Canada (Harris et al., 1985).

Budworm-induced tree mortality

For each tree the probability of mortality due to budworm is dependent upon the severity and the duration of the outbreak and upon the diameter class of the tree (Alfaro et al., 1982) (Table 4). These probabilities are based on observations from three stands severely defoliated for 6 years (1980–1986) near Cache Creek, British Columbia. Mortality in severe infestations lasting 7–10 years was assumed to be the same as with 6 years of defoliation. Mortality from moderate defoliation was assumed to be one-half of the mortality that would occur in a severe infestation. Light infestations cause no mortality. In the absence of data, the same mortality probabilities were used for both biogeoclimatic subzones in this study.

Growth loss

The program reads the file containing the future decadal increments in height and diameter for every plot tree, without budworm. These increments are then transformed into annual increments by dividing them by ten and are reduced to reflect budworm impacts as follows.

Because of the bud mining habits of the budworm and its preference for feeding on new foliage, defoliated trees usually do not increase their height during years of active feeding (Van Sickle et al., 1983); therefore, during feeding years, annual height increments are set to zero. Usually, in trees that survive the infestation, height increment resumes immediately after the infestation collapses; however, growth rates are reduced. In this projection, trees

TABLE 4

Probability of Douglas fir tree mortality due to severe western spruce budworm defoliation in the Kamloops Region of British Columbia

Diameter class ¹ (cm)	Duration of infestation (Years)					
	1	2	3	4	5	6
0	0.00	0.00	0.25	0.50	0.75	1.00
5	0.00	0.00	0.20	0.41	0.61	0.81
10	0.00	0.00	0.15	0.30	0.45	0.60
15	0.00	0.00	0.11	0.22	0.33	0.45
20	0.00	0.00	0.08	0.16	0.25	0.33
25	0.00	0.00	0.06	0.12	0.18	0.24
30	0.00	0.00	0.04	0.09	0.14	0.18
35	0.00	0.00	0.03	0.07	0.10	0.13
40	0.00	0.00	0.02	0.05	0.07	0.10
45	0.00	0.00	0.02	0.04	0.06	0.07
50	0.00	0.00	0.01	0.03	0.04	0.05
55	0.00	0.00	0.01	0.02	0.03	0.04
60	0.00	0.00	0.01	0.01	0.02	0.03

¹Numbers in this column represent the mid-point of the class, except for Class 0 which includes trees with DBH from 0.1 to 2.4 cm.

lose 50% and 25% of their normal height increment in the first and second year after the outbreak collapses, respectively. Increments are not affected thereafter.

Diameter loss was simulated by reducing the increments by a factor which depended on the duration and severity of defoliation (Table 5). These factors were derived from stem analysis of one stand defoliated in the 1970s at Railroad Creek, near Pemberton, British Columbia. This stand contained trees in a variety of defoliation classes. These factors probably vary by diameter class but, in the absence of data, the same factors were applied to trees in all diameter classes.

The factors used to reduce diameter increments during outbreak years reflect the gradual decline in ring width which occurs with each year of defoliation and the equally gradual recovery after defoliation ceases (Alfaro, 1985; Thomson and Alfaro, 1990). The loss of diameter increment after the end of defoliation is the mirror image of losses that occurred during the infestation. For example, for a 3 year outbreak, the program would use the following factors for each corresponding year of infestation: Table 5, factors for Years No. 1,2,3,2,1. The recovery period is limited to 5 years so the following factors would be used for an outbreak that lasted 8 years: 1,2,3,4,5,6,7,8,5,4,3,2,1. The percent diameter increment loss reaches a maximum with a duration of 6 years.

TABLE 5

Loss factors used to modify the annual diameter increment in Douglas fir trees under defoliation by the western spruce budworm (e.g. 0, no loss; 100, 100% increment loss in the year)

Outbreak Year number	Severity of outbreak		
	Light	Moderate	Severe
1	0	10	10
2	0	50	70
3	0	60	80
4	10	70	90
5	50	80	96
6	60	85	100
7	60	85	100
8	60	85	100
9	60	85	100
10	60	85	100

Top-kill

Top-kill or die back consists of the destruction of height increments or internodes grown prior to the onset of an infestation. This is simulated by re-setting height increments from years prior to the outbreak to zero. The probability that a tree will sustain top-kill and the number of internodes killed depend on the duration and severity of defoliation. Again, very little data are available. The probabilities of top-kill used here (Table 6) were derived from data presented by Alfaro (1986) which is based on 65 plots observed in the

TABLE 6

Probability of die back (top-kill) in Douglas fir trees defoliated by the western spruce budworm in the Kamloops Region of British Columbia

Duration of infestation (years)	Severity of outbreak		
	Light	Moderate ¹	Severe
1	0.00	0.00	0.00
2	0.00	0.01	0.02
3	0.00	0.04	0.08
4	0.05	0.10	0.20
5	0.09	0.18	0.36
6	0.14	0.28	0.56
7	0.14	0.39	0.80
8	0.14	0.50	0.80
9	0.14	0.50	0.80
10	0.14	0.50	0.80

¹Based on Alfaro (1986).

Fraser river area in the 1970s. These data were mostly from plots moderately defoliated; the probabilities of top-kill were halved to simulate light infestations and were doubled for severe infestations. When top-kill occurred, the number of internodes killed in a tree was 2, 4, and 5, for light, moderate and severe infestations (all durations).

Stem defects

Upon collapse of the infestation, surviving trees recover by forming a new leader and resuming height growth. Depending on whether top-kill has occurred, on the severity of the top-kill (number of internodes destroyed), and on the branching habits of the tree, a stem defect may develop at the point of injury. Trees that have sustained bud destruction but no top-kill have a lower probability of developing a defect than trees with top-kill (Table 7).

During recovery from severe top-kill, trees form four types of defects: scars, minor crooks, major crooks and forks (for defect definitions, see Alfaro, 1989). The volume of damaged trees was calculated as for undamaged trees if they had no defects or if the trees contained scars or minor crooks. If the tree stem contained a major crook, a section 0.3 m below and 1.0 m above the point of injury (the base of the top-kill that caused the crook) was removed from the stem and considered waste. The remaining stem sections above and below the crook were partitioned into logs as described for undamaged trees. If the tree contained a fork, the entire stem section above the fork was wasted.

The probability that a defect will be formed if only bud destruction occurred was not dependent on infestation severity. However, if top-kill occurred, the probability of defect formation depended upon the severity of the infestation. Virtually no information exists on the probability to defect formation after defoliation, and future work should concentrate on this question. The probabilities in Table 7 are based on the judgment of the authors.

TABLE 7

Probability of defect formation in Douglas fir trees defoliated by the western spruce budworm in the Kamloops Region of British Columbia

Top-kill status	Defect type			
	Scar	Minor crook	Major crook	Fork
Bud destruction with no top-kill	0.05	0.05	0.00	0.05
Bud destruction with top-kill				
Light infestation	0.09	0.45	0.07	0.03
Moderate infestation	0.10	0.34	0.10	0.10
Severe infestation	0.10	0.24	0.15	0.15

RESULTS

At the start of the projection, the average volume per plot (all trees, between stump and 10 cm top diameter) in the 32 plots was $134.8 \text{ m}^3 \text{ ha}^{-1}$ (range $42.6\text{--}227.9 \text{ m}^3 \text{ ha}^{-1}$). Volume after 10 and 20 years averaged $171.1 \text{ m}^3 \text{ ha}^{-1}$ (range $72.3\text{--}265.5$) and $213.3 \text{ m}^3 \text{ ha}^{-1}$ (range $106.4\text{--}320.7$), respectively. The harvestable volume (logs obtained from trees 30 cm DBH and larger) averaged $83.4 \text{ m}^3 \text{ ha}^{-1}$ (range $4.6\text{--}193.4$) at the start of the projection, increasing to $111.9 \text{ m}^3 \text{ ha}^{-1}$ (range $13.5\text{--}221.5$) and $144.6 \text{ m}^3 \text{ ha}^{-1}$ (range $17.4\text{--}271.0$) after 10 and 20 years, respectively. The periodic annual increment (PAI) for the total volume averaged $3.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (range $1.6\text{--}6.5$) in the first 10 year period and $4.2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (range $2.1\text{--}7.3$) in the second decade. The corresponding PAI values for the harvestable volume were 2.9 and $3.3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$.

When an infestation lasting 7 years was simulated in the first decade, budworm losses in total volume per hectare at the end of the first decade averaged 5.9, 19.5 and 28.2% for simulations of light, moderate and severe infestations (Table 8). At the end of the 20 year projection, total volume losses averaged 6.2%, 23.3% and 32.8% of the total stand volume, for light, moderate and severe infestations, respectively. Percentage losses in harvestable volume were very similar to those of total volume (Table 8) due to the fact that most of the volume of the stand is concentrated in the harvestable trees. Figure 1 shows the plot-to-plot variability in total volume losses.

Reduction in the PAI of the total volume in the first decade averaged 26.9, 86.4 to 125.8% for light, moderate and severe infestations (Table 9). Losses higher than 100% indicate negative growth due to tree mortality i.e. that stands not only lost all the potential growth, but had a lower volume than at the start of the projection. In the second decade, reduction in the PAI of total volume

TABLE 8

Average percentage losses (standard deviation in brackets) in total volume (volume of all trees, between stump and 10 cm top diameter) and harvest volume (volume of logs from trees with a DBH of 30 cm or greater) in 32 Douglas fir stands in interior British Columbia after simulated western spruce budworm infestation. Infestations were simulated to last for 7 years and varied in severity from light to moderate to severe, and occurred in the first decade of a 20 year projection

Loss		Severity of outbreak		
Type	Period	Light	Moderate	Severe
Total volume	10 years	5.9(1.8)	19.5 (6.1)	28.2 (9.4)
Total volume	20 years	6.2(2.1)	23.3 (7.1)	32.8(10.2)
Harvest volume	10 years	8.3(5.6)	18.9(11.0)	25.4(13.8)
Harvest volume	20 years	6.1(3.5)	24.0(12.4)	31.8(14.9)

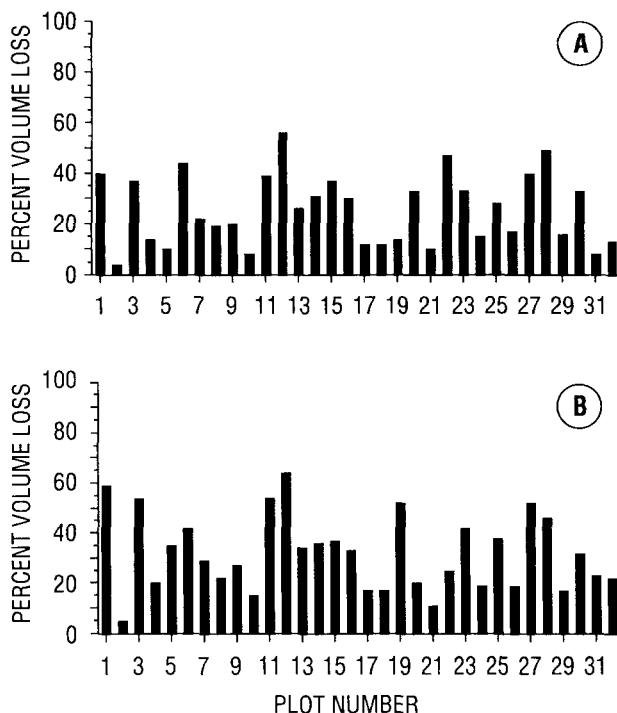


Fig. 1. Percentage loss of the harvestable volume (volume of the logs obtained from trees with a DBH of 30 cm or greater) in 32 uneven-aged Douglas fir stands of the Kamloops Region after a simulated budworm infestation lasting 7 years occurring in the first decade. (A) Losses at the end of the first decade, (B) losses at the end of the second decade. Defoliation intensity was 'severe'.

TABLE 9

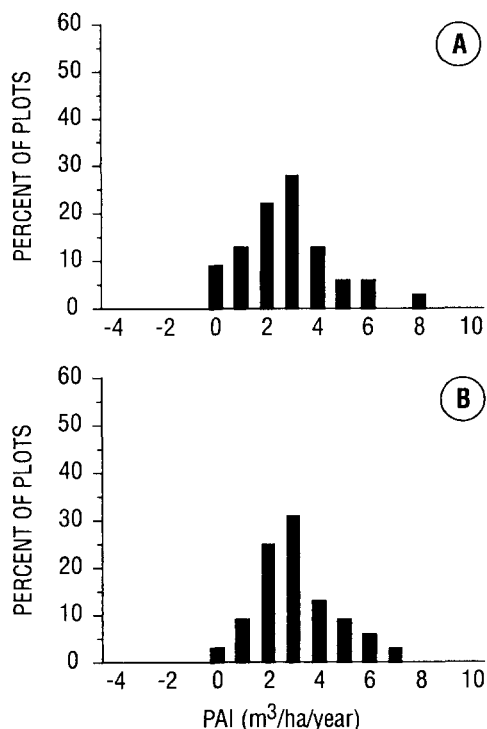
Average percentage losses (standard deviation in brackets) in periodic annual increment (PAI) of total volume (volume of all trees, between stump and 10 cm top diameter) and of harvest volume (volume of logs from trees with a DBH of 30 cm or greater) in 32 Douglas fir stands in interior British Columbia after simulated western spruce budworm infestation. Infestations were simulated to last for 7 years and varied in severity from light to moderate to severe, and occurred in the first decade of a 20 year projection

Loss		Severity of outbreak		
Type	Period	Light	Moderate	Severe
PAI total volume	10 years	26.9 (3.2)	86.4(16.0)	125.8(21.0)
PAI total volume	20 years	7.1 (3.9)	39.3 (8.2)	51.6 (9.6)
PAI harvest volume	10 years	27.1(11.5)	67.6(23.7)	93.7(44.1)
PAI harvest volume	20 years	0.4(16.6)	38.3(48.6)	46.8(27.7)

averaged from 7.1 to 51.6% depending on the severity of the outbreak. Reductions in the PAI of harvestable volume varied with the severity of the outbreak from 27.1 to 93.7% in the first decade and from 0.4 to 46.8% in the second decade (Table 9). Figure 2 shows the plot-to-plot variation in PAI.

It was estimated that at the end of 20 years, in the absence of budworm, the number of harvestable logs (i.e. from trees with a DBH of 30 cm or greater) accumulating over all plots was 710 5-m logs, 172 10-m logs and 5094 15-m logs (Table 10). With an outbreak duration of 7 years the numbers of 15 m logs were reduced from 4.6 to 30.5% depending on infestation severity (Table 10). The numbers of 5- and 10-m logs decreased by 0 to 28.0% except for the 10-m logs under light defoliation which increased by 23.8% due to proportional reductions in the numbers of 15-m logs.

Repeated runs of the program in which the duration of the infestation was varied from 1 to 9 years for each severity class (Fig. 3) indicated that light defoliation lasting 1–9 years created a loss of 0–8.9% of the total stand volume over the 20 year projection. For similar durations, moderate and severe infestations created a loss of 0.3–27.1% and 0.3–36.1% of the total volume, respectively. The percentage losses of harvestable volume resulting from outbreaks of the same severity and duration were similar.



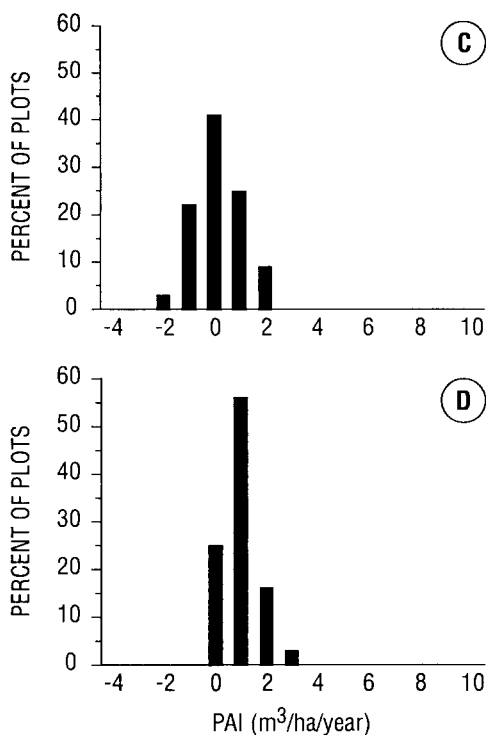


Fig. 2. Percentage of total number of plots sampled tabulated by periodic annual increment classes in: (A) first decade, no infestation; (B) second decade, no infestation; (C) first decade, severe 7 year infestation in first decade; (D) second decade, severe 7 year infestation in first decade.

TABLE 10

Total number of logs obtained from 32 Douglas fir stands at the end of 20 years and percentage change due to simulated western spruce budworm infestation. Logs tabulated by log size and infestation severity. Length of the projection was 20 years starting in 1985. Budworm infestations were simulated to start in 1987 and lasted 7 years

Level of infestation	Log size (m)		
	5	10	15
Non-infested (No. of logs)	710	172	5094
Infested (% reduction)			
Light	8.2	-23.8 ¹	4.6
Moderate	19.1	0.0	23.6
Severe	28.0	18.6	30.5

¹A negative reduction means that the number of logs in this class actually increased.

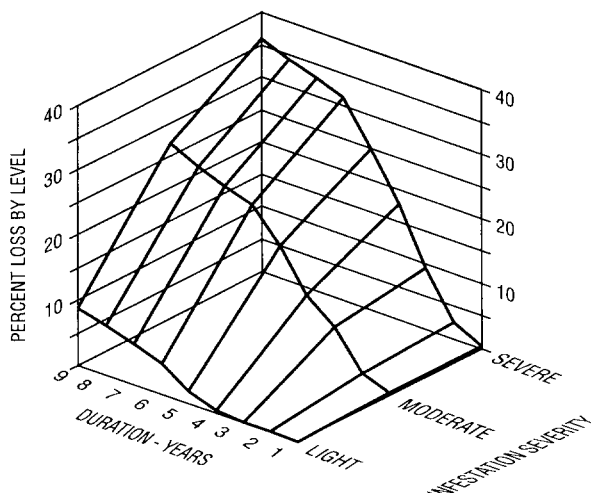


Fig. 3. Percentage of the total stand volume lost after simulations of budworm infestations of varying duration and severity.

DISCUSSION

The PAI rates for uninfested Douglas fir reported here ($3.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ and $4.2 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ in the first and second decade, respectively) are within the range of PAI values reported by Bonnor et al. (1991) for interior Douglas fir (mean $3.3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$, range -1.7 to 9.54). This suggested that the projections of the uninfested stand were reasonable.

No accurate data on ingrowth or natural mortality (i.e. not caused by budworm) was available for the development of the uninfested stand model. However, in a 20 year projection such as this, errors in the estimation of ingrowth are probably of no consequence because the ingrowth trees contribute little to the stand volume due to their small size.

We suspected that the estimates of natural mortality used here (Table 3) are probably an underestimation, particularly among the large diameter classes. To determine the effect of an underestimation of the natural mortality on the loss calculations, the program was run again with the mortality rates reported in Table 3 multiplied by four. These adjustments increased the percentage losses reported for a moderate infestation of 7 years in duration by 2.5%. This small change suggested that, because the objective was to calculate relative or percentage losses, the error in the estimation of undamaged volumes was unimportant.

Budworm defoliation affects all layers of uneven-aged stands, but damage is most severe in the lower canopy. Here tree mortality, growth loss, and top-kill are at a maximum. The losses caused by budworm will materialize at various times in the future as trees in different layers reach harvestable sizes and

are harvested in future cutting cycles. The losses calculated for this short-term 20 year projection represent mostly losses from the trees in the upper layers of the stands. In these large trees the losses are due mostly to tree mortality and growth reduction. In trees from the lower layers, which will reach maturity in subsequent cycles, the losses from top-kill and related stem defects will be added.

The loss factors presented in this report are derived from a highly simplified model of budworm outbreaks. Here, a single defoliation intensity level has been used for the duration of each outbreak. However, in nature, budworm infestations vary in duration and severity both in time and in space, i.e. during the course of an infestation, a single stand may sustain a combination of severities. Typically, for any given stand, infestations are light for 1 and 2 years then increase to moderate or to severe levels. Stands located in other parts of the same outbreak may have a different pattern. However, we lack the data to simulate the consequences of the many possible combinations.

Long-term projections were not performed because of the limitations in the database; accurate estimates of tree mortality or ingrowth in the absence of budworm were not available. Also unknown is the long-term response of a defoliated stand after the collapse of an infestation. Two opposite scenarios are possible. In some situations defoliated trees may take many years to develop a full and vigorous crown and resume their full growing potential. This may happen due to a combination of poor site and severe crown damage. In other situations, where sites are better but moisture is not a limiting factor, the surviving trees may undergo a release and grow better after the budworm has killed the understory. Future research should focus on obtaining the missing information on the growth of interior Douglas fir and on the various components of the damage caused by western spruce budworm. Meanwhile, simulations of budworm infestations are the only avenue open to gauge the relative importance of budworm as a pest of Douglas fir.

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