Exploratory Retrospective Analysis of the Interaction Between Spruce Budworm (SBW) and Forest Fire Activity

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Abstract

The dominant types of natural disturbance in Canada's boreal forests are wildfire and outbreaks of spruce budworm, *Choristoneura fumiferana* (Clem.). Carbon budget studies show that changes in the corresponding disturbance regimes may be greatly influenced by climate warming and are critical influences on the net atmospheric carbon exchange. Fire-spruce budworm (SBW) interaction under climate warming is also important because (1) the tendency for SBW-killed stands to burn is expected to increase in warmer, drier climates; (2) in much of Canada's boreal forest, SBW outbreaks occur over much greater spatial extents than do fires, and (3) SBW outbreak frequency and extent, and thus the availability of SBW-killed stands, may increase as the climate warms. These three factors, when considered together, suggest that in a warmer, drier climate, the interaction of SBW and wildfire disturbance regimes may substantially accelerate carbon releases from the boreal forest.

A retrospective analysis of Ontario's historical records from 1941-1995 was conducted as a prerequisite to developing models for forecasting, as a means of filling information gaps in carbon budget studies, and as a baseline for future monitoring. These results begin to quantify the interaction between SBW outbreak and wildfire disturbance regimes on a regional basis, and how climate has influenced this interaction in the past.

1. Introduction

1.1 <u>*Disturbances and the Carbon Cycle*</u>

In their recent assessment of global change research, Steffen and Ingram (1995) identified "our lack of understanding of landscape-scale processes, particularly disturbances" as the major immediate impediment to further advance. The term "disturbance" refers to any biomass-destroying incident that changes resource availability and ecosystem structure (Pickett et al. 1987). Forest disturbances which occur over extensive areas (i.e., at landscape-scales) in Canada can include windthrow, ice storms, wildfire, insect outbreaks, disease epidemics, and logging.

- Table 1 -

Wildfire and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), dominate among natural disturbances, particularly in boreal regions (Fleming, 2000: Weber and Flannigan, 1997). Spruce budworm (SBW) outbreaks and wildfire disturbances have similarities in that both affect large areas of forest on an annual basis, and both often have a cyclical aspect to their occurrence and play a role in forest succession (Bergeron and Dubuc, 1989; Van Wagner, 1978). There are also important differences between the two types of disturbance. Unlike wildfire which characteristically lasts days to weeks, it can take 5-15 years of complete loss of the current year's foliage before widespread tree mortality occurs during a SBW outbreak, and the mortality is often limited primarily to balsam fir, *Abies balsamea*, and secondarily to spruces, *Picea spp.* (MacLean 1985). SBW outbreaks are also often much more extensive than wildfires and in approximate synchrony over large areas (Candau et al., 1998; Hardy et al., 1986; Williams and Liebhold, in press). In addition, even where stand-replacing mortality is not occurring during SBW outbreaks, the damage to trees reduces their growth and consequently their sequestration of carbon. Thus, in contrast to the effects of wildfire which are likely offset by photosynthetic uptake elsewhere in the forest (McNaughton et al., 1997), even at national scales, SBW are capable of imposing the oscillatory signature of their 35 year outbreak cycle on the net carbon fluxes from Canada's boreal forests (compare Fig. 3 of Kurz and Apps, 1999, with Fig. 2 of Candau et al., 1998).

Like other landscape-scale forest disturbances, SBW and wildfire play important roles, both directly and indirectly, in the carbon cycle. Fleming (2000) suggests that the major indirect role appears to arise through the effects of these disturbances on ecosystem succession. He notes that different kinds of ecosystems are generally associated with different disturbance regime complexes (Runkle 1985), and explanations for this association point to the fundamental role that disturbance plays in the development of ecosystem structure and function (Aber and Melillo 1991, Attiwill 1994). In sustaining itself at a site, an ecosystem goes through repeated cycles of maturation and renewal. Disturbances are thought to be the principal agents in these 'renewal' cycles for releasing the tightly bound accumulations of biomass, energy, and nutrients that characterize an ecosystem at maturity (Holling 1986). This sudden release produces a pulse of available resources which opportunistic species exploit as they effectively invade the site and thus launch another successional sequence. This is a critical time. The next successional sequence could retrace previous successional pathways at the site and thus culminate in a mature ecosystem with much the same properties (in terms of species composition, soil qualities [Bever et al. 1997], etc.) as the one which existed on the site immediately before the disturbance. In this sense, the original ecosystem has effectively retained the site. On the other hand, if the original ecosystem is not going to retain the site, this is the part of the 'renewal' cycle when another, radically different form of ecosystem is most likely to begin to assert itself (Holling 1987). Depending on the mix of available resources and micro-environments available at the site, and the variety of species with opportunity to exploit them, the new successional sequence may veer away from the successional pathway leading back to the ecosystem originally situated at the site (e.g., forest) and veer toward a pathway culminating in a totally new form of ecosystem (e.g., grassland) (Bazzaz 1996, Oliver 1980) with its own unique disturbance regime complex (Mack and D'Antonio 1998) and carbon sequestration capacity.

Landscape-scale forest disturbances also affect the carbon cycle directly. In broad terms, the amount of carbon stored by a forest ecosystem is the difference between the amount produced through photosynthesis and the amount lost through total ecosystem respiration (including plant, animal, and microbial respiration) and through direct losses to the atmosphere during wildfire. Outbreaking populations of SBW affect carbon storage by reducing photosynthesis through defoliation and by increasing total ecosystem respiration through their own respiration and through acceleration of microbial respiration. The latter occurs during decomposition in the soil as SBW larvae: (i) convert eaten foliage into frass, (ii) clip off and kill other needles which would normally stay on the tree for up to eight years (Piene and Fleming

1996), (iii) defoliate the canopy which allows more light to reach and warm the forest floor, and (iv) during heavy infestations, cause widespread top-kill and tree mortality. Intense fire has a much more spectacular effect by almost immediately eliminating photosynthesis and releasing large amounts of carbon directly to the atmosphere (Cofer et al. 1996). After a forest fire, total ecosystem respiration usually exceeds the accumulation of carbon through plant re-growth for some time (Woodwell et al. 1998). As Fig. 1 suggests, a less dramatic but otherwise similar pattern can be expected after a spruce budworm outbreak (Szujecki 1987, Haack and Byler 1993).

- Fig. 1 here -

Therefore an important concern is how climate change, which is taken to include increasing levels of atmospheric CO_2 as well as climate variables other than temperature, will affect the disturbance regimes (frequency, extent, duration, and intensity) of SBW outbreaks and, especially, of forest fires. Since forests accumulate biomass (carbon) as they age, and since increasing the rate of (stand-replacing) disturbance results in younger stands, it follows that generally the greater the disturbance rate, the lower the amount of carbon stored in forests, and the greater the amount left in/released into the atmosphere where it can accelerate climate warming. (Release of carbon can occur almost immediately when severe wildfire vaporizes dead foliage and fine branches, or it can occur very slowly during the decomposition of coarse woody debris). Thus carbon budget studies (Kurz and Apps 1996) "show that changes in these disturbance regimes - changes that may be significantly influenced by human activities, including modification of the climate - are critically important in determining the net atmospheric C exchange."

The SBW and wildfire disturbance regimes in Ontario have been described by Fleming et al. (2000) and Thompson (2000), respectively. Efforts are also underway to understand how climate warming might affect the regimes of both SBW outbreaks and wildfires individually (Fleming and Volney, 1995; Stocks et al. 1996). However, since many areas have experienced both SBW outbreaks and wildfire, it is important to consider the possibility that these two types of disturbance might affect each other. If they do, this interaction must be understood in order to gain a thorough understanding of either disturbance regime (Furyaev et al. 1983).

1.2 *Spruce Budworm (SBW) Outbreak-Wildfire Interaction*

Spruce budworm researchers (e.g., Graham, 1923; Swaine et al., 1924; Prebble, 1950; Baskerville, 1975) have long suggested that SBW-damaged stands represent an increased risk of wildfire. There are also records of major forest fires occurring in areas shortly after SBW outbreaks. Notable examples include New Brunswick's 'Miramichi' fire in 1825 (Flieger, 1971), Minnesota's 'Isle Royale' fire in 1936 (Hansen et al., 1973), and Ontario's 'Mississagi' fire in 1948 (Stocks and Walker, 1973). Nonetheless, many fire managers remained skeptical of the importance of this interaction so a joint Canadian Forest Service-Ontario Ministry of Natural Resources series of experimental burns was undertaken near the Aubinadong River (latitude 46°53'N, longitude 83°24'W) from 1976-1982 (Stocks, 1985; 1987). The burns occurred in mixedwood stands typical of Canada's Great Lakes - St. Lawrence and boreal forest regions (Rowe, 1972) where balsam fir grows in the understory in a heterogenous mix of tree species which often includes spruce, pine (*Pinus spp.*), and birch (*Betula spp.*). Unfortunately, only 5 of the 13 established 2-ha experimental plots were successfully burnt leaving a sample size (n=5) too small to statistically identify patterns among plots with acceptable power (Cohen, 1988). Nonetheless, these burns clearly showed that SBW-damaged stands can become an extreme fire risk (Stocks, 1985; 1987).

Previous workers have recognized the importance of the fire-insect interaction but have lacked the data to examine it. For instance, in their carbon budget work, Kurz and Apps (1996) lamented "the paucity of data from which to infer whether fires occurred in stands previously affected by insects." In summary, the available information suggests that forest fire activity and spruce budworm outbreaks interact and that this interaction is important to understanding past, present, and forecasting future carbon storage rates in Canada's forests.

In this paper, we begin to quantify the wildfire-SBW interaction on a regional basis by combining geographic information system (GIS) and statistical randomization techniques to compare historical maps of fire and SBW defoliation occurrence. This provides a different perspective on the wildfire-SBW relationship than that of Stocks' (1985): between 1976-1982 he manipulated the time of ignition of his 5 successful experimental burns which were all located at a single site; we search for temporal correlations between the occurrence of SBW defoliation and large ($\geq$ 2 km^2) wildfires throughout Ontario from 1941-1996. We consider whether historical frequencies of SBW defoliation are related to the probability of an area being burnt and characterize the temporal relationships between SBW defoliation and wildfire for areas which have experienced both.

2. Methods

2.1 *Data*

The analysis brings together data from a number of sources. The fire occurrence data comes partly from an extensive GIS-based data set of all fires exceeding 2 km^2 in area that have occurred since 1980. The data set was built through detailed analysis of individual fire reports collected from all Canadian fire management agencies (Stocks et al., 1996). The Ontario aspects of this large fire data base have been augmented by digitizing the fire history maps produced by Donnelly and Harrington (1978) for Ontario for 1921-1976, inclusively. Ontario Ministry of Natural Resources (OMNR) has filled in gaps by digitizing other data to produce an extensive and thorough database for all large (> 2 km^2) fires that occurred in Ontario since 1921. The rationale for focussing on only the largest fires comes from an analysis of the records of all wildfires in Canada from 1980-1989 (Stocks et al., 1996). These records show that only 3.5% of wildfires grew larger than 2 km^2 but that these large fires were responsible for 97% of Canada's total area burned. (Presumably this low percentage reflects the success of control efforts).

The main limitation to the wildfire database arises from the likely presence of some fire location errors and the possibility that a few fires in remote northern regions may have been overlooked altogether (Stocks et al., 1996). This last limitation is of questionable relevance here since our analysis focuses more on the southern regions of Ontario where SBW outbreaks are recorded (Fig. 2).

- Fig. 2 here -

The SBW defoliation data comes from survey data collected by the Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service. FIDS has been conducting aerial reconnaissance of large-scale SBW defoliation in Ontario's productive and exploitable forests since 1941. Reconnaissance flights are planned annually to begin as soon as the current season's defoliation is completed, generally in mid- to late-July. During survey flights, the observer relies on the telltale signs (Sippell 1983) of SBW infestation to delineate defoliation on maps, usually with an error under 500 m. During their most active feeding stages (i.e., 4th-6th instars), budworm larvae lay down a fine silk thread as they crawl about the foliage of their host conifer, and when they stop to feed, the larvae tie up the surrounding needles in their silk. As this silk dries, it contracts, pulling the needles together to form a sort of shelter for each feeding larva. The larvae feed on the new shoots, cutting off needles near their base rather than consuming all the green tissue. The severed needles are prevented from falling by the silken webbing which attaches them to the tree. These severed needles slowly develop the brick red colour which provides the distinctive tinge to trees defoliated by the spruce budworm that is so evident from the air.

There are a number of potential sources of error in FIDS' aerial surveys of SBW defoliation (Sippell 1983). Heavy rain can wash away dead foliage causing defoliated trees to lose their distinctive reddish brown hue before the survey plane flies over. Underestimating defoliation also occurs in the first year of heavy defoliation on white spruce when the proportion of the total foliage that becomes discoloured is so small that it is barely detectable from the air. The scale of the infestation also affects survey accuracy. Observers typically map with less relative, but greater absolute, error when an infestation is extensive (e.g., over 100,000 km^2) than when it is small (e.g., under 200 km^2). The phase of an outbreak also has an influence on survey accuracy. Budworm damage is more conspicuous during the peak than during either the build-up or the collapse: large flower or cone crops and injuries caused by other pests and frosts can all create difficulties.

FIDS also reports the presence of spruce budworm-caused tree mortality. Observers look for totally grey trees from the air. Subsequent ground checks (for brown cambium on both sides of some boles) are needed for confirmation, however, because trees appearing grey from the air are not necessarily dead - they may have only dead crowns (Sippell 1983). In many years, tree mortality was not reported so it was often difficult to determine when FIDS first noticed tree mortality in a particular area.

While fire control has clearly had an effect on the wildfire data (Donnelly and Harrington, 1978), there is reason to suspect that, as Hardy et al. (1986) imply, spraying generally has had little effect on the large-scale patterns of spruce budworm defoliation in

Ontario. The largest spray program occurred in 1986 (Howse et al. 1995) but this amounted to only 1.7% of the 8.75 x 10^4 km^2 of moderate and severe defoliation that year (Howse 1995). Furthermore, Lysyk's (1990) analysis of Ontario survey data from 1968-1988 indicated that "sprays ... overall, did not confer a high level of foliage protection". Similar results have been reported for some other jurisdictions (e.g., Fleming et al. 1984).

2.2 *Analysis*

The 56 annual survey maps (from 1941 to 1996), which delineate areas of Ontario within which SBW caused defoliation occurred that year, were digitized. Each map was represented by a "layer" and in each layer, areas experiencing moderate or severe defoliation were depicted by polygons. Various arithmetic manipulations were performed on the digitized SBW defoliation maps (Candau et al., 1998). Summing the areas of the polygons of defoliation in a layer gave the total area defoliated that year for the entire province or within specified zones of the province. The frequency of defoliation from 1941 to 1996 for each small area was also calculated. This involved determining the union of the 56 layers of annual defoliation in the database. The result was a new data layer of many small polygons, with a number associated with each polygon indicating the cumulative frequency of defoliation for the corresponding area.

Using this approach, Candau et al. (1998) showed that from 1941-1996, SBW defoliation in Ontario has occurred in a belt running east-west between 45° and 52°N latitude (Fig. 2a). The northern and southern fringes of this belt have rarely been defoliated. Within this belt, these researchers distinguished three somewhat autonomous zones of relatively frequent SBW defoliation separated by two narrow corridors running approximately north-south in which SBW defoliation was less frequent (Fig. 2a). Part of our analysis compares the SBW-wildfire interaction in these different zones.

Since SBW-caused tree mortality is the cumulative effect of years of defoliation (MacLean, 1985), tree mortality is reported as a net value resulting from each outbreak. To calculate this value, the total area within which tree mortality occurred during and following an outbreak, we summed the areas within which SBW-caused tree mortality was reported up to the start of the next outbreak. In doing so, we took care not to count any areas more than once.

The data set of digitized SBW defoliation maps was combined with the digitized maps of the large wildfire data set for Ontario described above. GIS methods were applied to these digitized maps to perform various manipulations and rearrangements of the data relevant to SBW-wildfire interaction. A wildfire-SBW combined data set emerged which identified every non-contiguous (ploygon) area with a unique combination of wildfire and SBW defoliation histories. The forward (and backward) lags between the time an area was burned and the next (and closest previous) incidence of reported SBW defoliation in the same area were of particular interest. The frequency of each lag was calculated for all Ontario and for stratifications based on SBW defoliation zone and on historcal defoliation frequencies. The lag frequencies were weighted by the total area over which they occurred to provide a measure of relative importance. Histograms were then constructed showing spectra of these area-weighted frequencies of occurrence against the time lag.

Regression analysis (Draper and Smith, 1981) and null models (Gotelli and Graves, 1996) were applied to support statistical inferences. In regression analysis, when parameter estimates were not statistically significant (α=0.05) we removed the one with the largest P-value according to the partial F-test (Draper and Smith, 1981) and refitted the reduced model. This procedure was continued until only parameters with statistically significant estimates remained. In this process certain parameters (e.g., exponents, divisors) were tested against 1.0, others (e.g., linear coefficients) were tested against zero. Residuals were examined to verify that the regression assumptions were adequately satisfied and the Anderson-Darling normality test (Anderson and Darling, 1954) was applied to test the assumption of normally distributed residuals.

In general, null models provide frameworks for generating the patterns expected in non-experimental data when a particular effect, or relationship between variables, is not present. Thus, in the terminology of inferential statistics, these patterns can be thought of as manifestations of the ‘null’ hypothesis. We used null models to test whether the time lags between wildfire occurrence and the most recent (or next) occurrence of SBW defoliation in the same area were explainable by chance alone. Computer-intensive statistical methodology, specifically ‘bootstrapping’ (Efron and Tibshirani, 1991), was used to generate these patterns. In ‘bootstrapping’, we randomly assigned (with replacement) time-series of wildfire occurrence(s) and, separately, time-series of SBW defoliation reports to the different non-contiguous polygon areas in the combined wildfire-SBW data set. The forward and backward time lags were then calculated for each area. All areas experiencing a given time lag were then summed. When this was done for all time lags, a histogram resulted with its height representing cumulative area and its horizontal axis denoting the time lag. This process was repeated 300 times to produce a frequency distribution reflecting natural variability in the cumulative area at each time lag. The 2.5 and 97.5 percentiles of these distributions were calculated as non-parametric estimates of 95% confidence limits for the pattern expected if the null hypothesis were true (i.e., that wildfire events are completely independent of the occurrence of SBW defoliation).

Initially, the analysis of null model results produced one extremely anomolous outlier. According to the data, moderate-severe SBW defoliation occurred in almost 3000 km^2 just 5 years after wildfire swept through the same areas. This result was both highly statistically significant (the upper bound for the 95% confidence interval was about 1600 km^2) and biologically atypical (stands usually take considerably longer than 5 years to recover from fire before they can support SBW populations large enough to cause aerially visible defoliation). Closer examination showed that much of this 3000 km^2 originated from areas reported burned in 1980 and defoliated in 1985. In many cases, these were isolated reports of defoliation even though much of the surrounding area was reported as defoliated by SBW in the immediately following years. This suggested that in 1985, FIDS may have inadvertently assessed some areas that were burned in 1980 as defoliated in 1985. In a few rare cases this seeming mis-classification was also repeated in 1986 before correction in 1987. Reclassifying these areas as “not defoliated” in years of supposed mis-assessment reduced the data set from 25354 to 23262 km^2. The recomputed the 95% confidence intervals for the null model, which reflects the hypothesis that histories of fire occurrence and of SBW defoliation are completely independent, indicated that the frequency of occurrence of the 5-year time lag for SBW defoliation following wildfire in the same area was no longer statistically significant. Because this seemed biologically reasonable, corresponding corrections were made to our data and these corrections are reflected in the results reported below. After further error-proofing and data verification, statistical methods were applied to reveal general, large-scale patterns of the interaction of wildfire and SBW defoliation.

To determine the effects of SBW defoliation zone on the spectrum of time lags between SBW defoliation and wildfire, the data were stratified by zone (Fig. 2a). Histograms of area-weighted frequencies of different time lags were developed from the data in each strata. Null models were used to design 'bootstrapping' computer algorithms for estimating 95% confidence limits for the spectrum illustrated in each histogram individually.

A non-parametric procedure was developed to compare histograms among strata. In each histogram, each time lag was given a value from 1-3, respectively, depending on whether its area-weighted frequency was significantly low, was not significant, or was significantly high. This produced an ordinal representation of the occurrence of statistical significance in the time lag spectrum for each strata. Cross-correlation time-series analysis (Chatfield, 1989) provided comparisons of these patterns of statistical significance among strata over specific ranges of time lag.

3. Results

Over half of the area burned in Ontario from 1941-1996 was north of the SBW belt (Fig. 2b; Fleming et al., 2000, Fig. 8.11). Time series of total area defoliated by SBW and of large burns within the SBW belt are illustrated in Fig. 3. Wildfire activity, particularly in the western and central zones, decreased after 1941 when FIDS became fully operational. Both the decrease in wildfire activity and assemblage of FIDS signalled increasing efforts to sustain and understand Ontario's timber resources through monitoring and control of natural disturbances.

- Fig. 3 here -

Figure 4 shows the general relationship between the defoliation frequency of an area and its tendency to experience wildfire from 1941-1996. The fitted model is

$$Y = a X^2 + b X + c,$$

where Y is the percentage of the total burnt out of all areas that were recorded by FIDS as experiencing the indicated frequency of moderate-severe SBW defoliation, and X is that frequency. This model explained $R^2 = 55.4\%$ of the variance in percent burnt, its fit was statistically significant ($F_{2,21} = 13.05$, $P < 0.0005$), and the precision of the estimated regression curve, as indicated by the standard error of the estimate, was 2.76%. Application of the Anderson-Darling normality test revealed no statistically significant deviations ($A^2 = 0.315$, $P = 0.521$) of the residuals from a normal distribution. The parameter estimates (and their associated standard errors and P-values, respectively) were $a = -0.0542$ (0.0132, $P < 0.0005$), $b = 1.11$ (0.339, $P = 0.004$), and $c = 10.5$ (1.84, $P < 0.0005$).

- Fig. 4 here -

3.1 *Time Lag Analysis*

Figure 5 concerns those areas of the SBW belt which have been both burned and defoliated at least once between 1941-1996. Positive lags are calculated as the time between the last incidence of defoliation before a fire, and the occurrence of that fire. The lags are negative when fire preceeds defoliation. Zero lags indicate that fire and SBW defoliation were reported in the same year for the same area. The histogram gives the area-weighted frequency with which various time lags occurred. Null models were used to calculate the thin, vertical bar which approximates the 95% confidence interval of no statistically significant ($\alpha = 0.05$) effect at each lag. (At lag = 0 years the lower 95% confidence limit is 5597 km^2). Time lags at which the height of the histogram falls outside the 95% confidence interval cannot be easily explained by random variation and hence are considered statistically significant. Time lags of significantly high frequency, where the histogram's height exceeds the upper 95% confidence limit, are designated by the small, vertical, block arrows.

- Fig. 5 here -

Figure 6 provides histograms of the area-weighted frequencies with which various time lags occurred between the occurrence of wildfire and the closest incidences in time of SBW defoliation in the same area. These histograms are exactly analogous to the histogram in Fig. 5 except that they pertain separately to the individual defoliation zones (Fig.2). Because null models have been applied separately to each zone, there is variation among confidence intervals at a given time lag.

- Fig. 6 here -

Cross-correlation time-series analysis revealed statistically significant differences between SBW defoliation zones in the patterns of statistical significance within each zone (Fig. 6) over time-lags of 1-16 years for fire following defoliation. In each zone to zone comparison, only one lag's correlation exceeded the critical value (Chatfield, 1989) of $2N^{-1/2} = 0.5$. The western zone's pattern lagged 2 years behind that of the central zone (R = 0.599), and 3 years behind that of the eastern zone (R = 0.611). The cross-correlations between the central and eastern zones were logically consistent with these results: the central zone lagged 1 year behind the eastern zone (R = 0.680).

For each zone of SBW defoliation and for all Ontario, Table 2 reports general indicators of the extensiveness and severity of the 1941-1963 and 1967-1996 outbreaks. The Table also reports the prevalence of wildfire in each zone and indicates the amount associated with each outbreak.

- Table 2 here -

4. Discussion

A key question is whether climate warming will induce a positive feedback, or as Woodwell et al. (1995) bluntly put it: "will the warming speed the warming?" There are at least three mechanisms which lead to increased plant growth through photosynthetic and 'fertilisation' effects (Woodwell et al. 1998) and thus work against this suggestion: (1), increasing mobilisation of nitrogen due to a variety of human activities (Kauppi et al. 1995, Moffatt 1998, Vitousek et al. 1997), (2), faster growth rates and longer growing seasons in a warmer climate, and (3), increasing atmospheric levels of carbon dioxide (Bazzaz et al. 1990), which are also largely responsible for climate warming itself (Keeling 1960, Houghton et al. 1996). Recent analyses (Cao and Woodward 1998, Woodwell et al. 1998), however, suggest that as climate warming continues, other mechanisms will begin to predominate. First, after prolonged exposure to an elevated CO_2 concentration, plant growth rates gradually revert back towards their slower, pre-exposure rates (Eamus and Jarvis 1989, Hattenschwiller et al. 1997, Wullschleger et al. 1997). Second, respiration and decomposition rates are quite sensitive to temperature (Lindroth et al. 1998) so climate warming can be expected to reduce the carbon contained in soils and dead organic matter. Third, since carbon release typically exceeds the carbon accumulation in plant regrowth on a site after disturbance (Fig. 1), a major concern is that if climate warming leads to more frequent disturbances, then the warming may indeed speed the warming. The results reported above constitute an initial exploration of this last issue in the context of how SBW outbreaks affect subsequent fire potential and of how increases in fire potential following SBW outbreaks may respond to climate change. (While it is recognized that climate change is just one aspect of the larger issue of global change which also involves changes in land use/land cover, biological diversity, atmospheric composition in general, and their interactions with each other and with climate change [Walker and Steffen, 1997], these other changes are largely beyond the scope of this paper).

Figures 2 and 3 indicate that the areal extent of SBW disturbances greatly exceeds that of wildfire. In Fig. 2a, some of the areas have been reported defoliated as much as 25 times, while few of the areas reported burnt in Fig. 2b have experienced more than one wildfire. The relative maximal extents of SBW and wildfire disturbances are indicated roughly by the corresponding axes maxima in Fig. 3: in each zone, the maximum area defoliated is over 20 times the maximum area burnt, and the fire data goes back 20 more years than the SBW defoliation data.

Within the SBW belt, SBW outbreaks also caused tree mortality over larger areas than wildfire. Analysis of the GIS data bases indicates that from 1941-1996 fires burned 27.4 x 10^3 km^2 within the SBW belt. The GIS data bases also report the occurrence of trees killed by SBW within 148 x 10^3 km^2 and within 241 x 10^3 km^2 in association with the 1940s-1950s and the late 1960s-1996 outbreaks, respectively (Table 2). Thus, even if all fires in the SBW belt occurred in SBW killed stands, only about 7% of such stands could have possibly been burnt. Manipulations of Table 2's data show that this percentage falls as one uses ever more rigorous specifications of what constitutes a SBW-wildfire interaction. It is not clear which specification is most appropriate, however, because data is missing for both outbreaks. (The beginning of the first outbreak was missed altogether; in the second, defoliation ceased in 1996, but we currently lack data for subsequent years to study for ensuing wildfire).

Figure 3 illustrates the unique history of disturbance in each defoliation zone within the SBW belt. Candau et al. (1998) showed statistically that the outbreak patterns in the western and central zones are synchronized but that they both lag the eastern zone’s pattern by 5-6 years.

The statistical significance of the fitted regression curve in Fig. 4 indicates that areas within the SBW belt that suffered moderate frequencies (9-11 years) of defoliation were the most likely to be burnt. Further analysis is needed to identify the reasons for this pattern definitively, but some likely causes can be suggested in the meantime. First, Fig. 2 indicates that a large area of rarely defoliated and rarely burnt forest occurs near urbanized, south-eastern Ontario. Here farms and large pockets of dense deciduous forest prevent the continuity of SBW host tree species that is found further north (Perera and Baldwin, 2000, Figs. 5.5b, 5.10, 5.12) and this fragmentation may contribute to the relative rarity of reports of SBW defoliation. In addition, the proximity of the area to urban centres calls for vigorous fire control. Hence, this area may be largely responsible for the tendency, highlighted in Fig. 4, that those parts of the SBW belt which are seldom defoliated are also, on average, seldom burnt.

Support for this reasoning comes from summing the areas burnt each year from 1921-1996 in areas defoliated infrequently (i.e., 1-8 years) by SBW from 1941-1996. North and south of 47^{o}N (Fig. 2b) these sums respectively represent 16.7% and 4.1% of the total area infrequently defoliated. Thus the percentage of infrequently defoliated area that is burnt was 4 times less below the 47th parallel, in urbanized southeastern Ontario, than above it. In addition, north of 47^{o}N the percentages for defoliation frequencies 1-5 (13.6%, 15.2%, 21.4% 18.5%, and 18.7%) are sufficient to largely eliminate the statistically significant drop in the Fig. 4's curve at these low frequencies.

Four observations suggest a more complex explanation for the tendency of frequently defoliated parts of the SBW belt to be seldom burnt by large fires (Fig. 4). First, areas that experienced high frequencies of SBW defoliation (Fig. 2a) tend to have high percentages of forest cover (Perera and Baldwin, 2000, Fig. 5.5a), much of it with a large coniferous component (Perera and Baldwin, 2000, Fig. 5.10). Second, work from just east of the Ontario-Québec border suggests that the size of this coniferous component, particularly that of the principal SBW host species, balsam fir, increases with time since fire (Gauthier et al., 1996; Bergeron and Leduc, 1998). Third, the longer the time since fire, the greater the mortality of SBW host species in attacked stands (Bergeron and Leduc, 1998). Fourth, it takes a number of years of SBW defoliation to kill a tree (MacLean, 1985). Taken together, these four observations suggest that SBW host tree species are very well represented in areas experiencing high frequencies of defoliation (and hence presumably also experiencing substantial SBW-caused tree mortality). The last three observations indicate that it takes some time after a large fire for these tree species to succeed to predominance of the forest in those areas. Thus, the tendency for frequently defoliated parts of the SBW belt to be seldom burnt (Fig. 4) partly corroborates the cause-effect relationships suggested by Gauthier et al. (1996) and Bergeron and Leduc (1998): as time since fire increases, SBW host trees become an increasing proportion of the forest, and forests dominated by these species often support SBW populations capable of causing aerially visible defoliation.

4.1 *Time Lag Analyses*

Figure 5 shows a histogram for all Ontario of the spectrum of area-weighted frequencies of various time lags between the occurrence of wildfire and the closest incidences in time of SBW defoliation. According to the 95% confidence interval estimated at each lag, the frequency of occurrence of many lags is statistically significant. In most of these cases, the height of the histogram does not reach the lower 95% confidence limit, indicating a significantly low frequency of occurrence. There are two almost continuous intervals of such lags: from -11 to +1 year, and from +11 to +15 years, with lags at -8, -5, and -3 years in the former interval being non-significant. The vertical block arrows indicate significantly frequent lags at -20 years, and in the interval from 3-9 years (with lags at 4, 5, 7, and 8 years lacking statistical significance). The pattern for the negative lags suggests that stands of SBW host species need about 17-20 years to recover from large fires before they are capable of supporting SBW populations large enough to cause aerially visible defoliation. The 11200 km^2 shown with lags between -17 and +1 were probably not actually defoliated, but rather fell within larger areas mapped and classified by FIDS as “areas within which defoliation occurred”.

- Fig. 7 here -

The pattern in Fig.5 can be compared with the explanation Stocks (1985, 1987) offered for the results of the Aubinadong experimental burns. He based this explanation on the notion that fire potential follows different time courses after SBW-caused stand mortality (Fig. 7) depending on whether the understory vegetation has undergone its annual flushing. According to this notion, ‘spring’ fires, fires which occur before flushing, are so volatile in SBW-killed stands that fuel arrangement is not a decisive factor. However ‘summer’ fires, fires which occur after the understory flushes, are a different matter. SBW defoliation opens the tree canopy, letting more light penetrate to the moist understory vegetation which proliferates in response. Usually the understory needs only a couple of weeks in early June to “green up”. This moist layer of vegetation separates dry crown and ground fuels and thus effectively dampens fire spread for the rest of summer. (No experimental burns were conducted in autumn, but Stocks (1985, 1987) reasons that after curing of the understory vegetation in the early autumn, fire potential probably increases again). Windthrow and crown breakage gradually add to ground fuel accumulations and build up connections between crown and ground fuels so that by 4-5 years after stand mortality, 'summer' fire potential increases sharply (Fig. 7). After another 4-5 years, however, 'summer' fire potential begins to decline as understory vegetation proliferates and balsam fir fuel on the ground begins to rot and decompose. 'Spring' fire potential seems less affected by stand decomposition and stays high for 10-15 years after stand mortality (Stocks 1985).

The data in Fig. 5 reflect variations in the cumulative annual effects of fire potential throughout the year. That the patterns in Figs. 5 and 7 don't match exactly is expected: besides 'spring' and 'summer' fire potential, Fig. 5's results also reflect 'autumn' fire potential and the additional stochastic effects of temporal shifts in weather and spatial variation in climate, forest composition, and topography throughout the SBW belt. What is remarkable is how closely Fig. 5's interval of significantly frequent lags (3-9 years) coincides with the timing of 5-10 years for the bulge in total fire potential that can be inferred from Stock's reasoning (Fig. 7). This coincidence is all the more remarkable in that positive lags in Fig. 5 are the number of years by which fire follows the last episode of SBW defoliation in the area, whereas the horizontal axis in Fig. 7 counts the years by which fire follows stand mortality.

Figure 6 illustrates time lag spectra (analogous to Fig. 5) from each zone of the SBW defoliation belt (Fig. 2a). Compared to Fig. 5, the sample sizes (areas) are smaller and this increases the likelihood of spurious significance. Accordingly, the small relative amount by which the histogram height exceeds the upper confidence limit for lags of 16 years in the western and -15 years in the eastern zone leaves their statistical significance questionable. The lags at 6 and 9 in the western, 4 in the central, and 3 years in the eastern zone are more convincing. Cross-correlation analyses were used to compare spectra over time lags of 1-16 years, a range which includes all statistically significant positive lags and which is comparable to the horizontal axis of Fig. 7. This analysis showed that over this range of lags, the western spectrum followed the central by 2 years and the eastern spectrum by 3 years, and that the central followed the eastern by 1 year. These results suggest the presence of geographical effects: specifically a trend from west to east for wildfire to follow a period of SBW defoliation more quickly and over a shorter range of time lags.

4.2 *Climatic Change Impacts*

This tendency can be associated with climatic characteristics of the SBW belt. Most temperature related variables have gradients which increase fairly regularly from north to south (Baldwin et al., 2000, Fig 2.4), and because the eastern zone extends further south (Fig. 2a), it has a sligthly warmer (area-weighted) average climate than the other zones. In addition, because of its extended border with Lake Superior, the central zone's climate is slightly cooler than that of the western zone (Baldwin et al., 2000, Fig 2.4). Ontario's SBW belt also has a somewhat irregular gradient of generally increasing precipitation from west to east (Baldwin et al., 2000, Fig 2.5). In the drier climate of the western zone, large fires happen often (Fig.3), especially north of the SBW belt where control efforts are weak (Fig. 2b). In the eastern zone, large fires are rarer, especially since the late 1950s when active fire suppression became widely practiced within Ontario's commercial forest lands (Thompson, 2000). In the northern part of this zone, wet soils and common intrusions of damp, cool air from Hudson Bay limit wildfire (Fig. 2b). Nonetheless, drought and large fuel loads have produced extensive fires in the eastern zone. With respect to climatic effects, the historical trends related directly above suggest that the fire retarding influences of moisture and precipitation have had a greater impact on fire activity than the fire promoting influence of warmer temperatures.

Considering the reasoning diagrammed in Fig. 7 in the context of these climatic gradients leads one to expect differences in the wildfire-SBW interaction across the SBW belt. In the wetter climate of the eastern zone of SBW defoliation, decomposition of ground fuel likely proceeds more quickly than in the western zone. Such an increased rate of decomposition would have two likely effects: shortening the length of time after tree mortality at which fire potential remains high and reducing the likelihood that a SBW killed stand will be burnt at all before it regenerates. The results in Fig.6 and the cross-correlation analyses of these results reported above provide evidence supporting the first of these inferred effects. Some evidence for the second comes from the data in Table 2 which shows that from 1941-1996, the ratios of area burnt in the SBW belt relative to the area within which tree mortality occurred was 0.0568, 0.0886, and 0.0950 in the eastern, central, and western zones, respectively.

The climate change implications are that SBW outbreaks will likely promote wildfire in a drier climate. A number of researchers also suggest that SBW outbreak frequencies may increase in a drier climate (Fleming and Volney 1995). In this case, the increased availability of insect-killed stands as climate change proceeds may further accelerate increases in fire frequency. It remains to be seen if such increases could compare with those due to possible direct effects of climate change on fire disturbance regimes. These results also emphasize the need for reliable estimates of future precipitation patterns in climate change predictions.

4.3 *Estimates for Carbon Budgeting*

Finally, it is possible to suggest some approaches for improving carbon budget estimates. To initialize the forest age structure in 1920 for their carbon budget model, Kurz and Apps (1996; 1999) used FIDS records of insect damage plus records of fire and harvesting disturbances to work backwards from 1970 inventory data. Graphs of these records (e.g, Kurz and Apps 1996, Fig. 14.2; Walker and Steffen 1997, Fig. 4) show peaks in the extent of all insect disturbances which are synchronized in their timing with those of the spruce budworm's outbreak cycle (e.g., Candau et al. 1998, Fig. 2A). These graphs imply that the total area disturbed by insects each year has increased many times over since the 1920s. This implication, however, is probably misleading (Fleming, 2000). The virtual absence of any insect damage prior to 1938 in these graphs seems to reflect the initiation of Canada's first large-scale aerial survey programs around that time (Hardy et al. 1986). The fact that the amplitude of the most recent (1978) peak is about twice the size of the next largest peak (1948) in these graphs may reflect the initiation and subsequent build up of aerial survey capabilities in many areas of the country from the late 1930s to the mid 1940s, largely in response to an extensive spruce budworm epidemic (Hardy et al. 1986). Therefore, the aerial survey data alone (e.g., Fig.3) are insufficient for determining long term trends in the total annual extent of all insect disturbances in Canada.

A more accurate approach to deriving historical insect damage might assume that spruce budworm represented about half of the total insect damage during outbreaks (Fleming, 2000,

Table 1) and that the timing (and perhaps even the extent and severity) of outbreaks before 1940 could be crudely estimated by backwards extrapolation of regional time series models (e.g., Candau et al., 1998). Ultimately this approach should improve estimates of the 1920 forest age structure, but whether any substantial difference to Kurz and Apps' (1996; 1999) carbon budgeting for Canada's boreal forests would result is uncertain.

Because of data gaps at the time they developed their budgeting process, Kurz and Apps (1996; 1999) rely on a number of simplifying assumptions. Table 2 provides information for testing some of them. For instance, Kurz and Apps (1999, Table 5) assume that the area of SBW-caused stand mortality (or of at least "significant impact on the age structure of stands") can be estimated as 0.08 of the area of moderate-severe SBW defoliation. The range, mean, and standard deviation of the 6 'independent' ratios of tree mortality to defoliation that can be calculated from Table 2 are 0.0714 - 0.115, 0.0916, and 0.0179, respectively. Hence, 0.08 may be reasonable for Ontario (although FIDS' measure of the "area within which tree mortality occurred" may overestimate the "area of at least significant impact on stand age structure").

Another simplifying assumption made in the absence of specific information, was that SBW and fire disturbances do not overlap (Kurz and Apps, personal communication). Since they worked from historical records in developing their carbon budget, this assumption overestimates the area disturbed by the amount of overlap in the records. Our analysis revealed 3 sources of overlap. First, as explained under 'Methods', 2090 km^2 reported as burned in 1980 and defoliated in 1985, were reclassified as not defoliated in 1985. Second, 11200 km^2 shown with lags falling in the unlikely range of -17 to +1 in Fig.5 were probably not actually defoliated, but rather fell within larger areas mapped and classified by FIDS as "areas within which defoliation occurred".

Third, we found wildfire reported in 13300 km^2 of SBW-killed tree mortality during the same outbreak (Table 2). These 13300 km^2 are presumably a consequence of wildfire-SBW outbreak interaction. This overlap amounts to 49% and 3.4%, respectively, of the total areas attributed to wildfire and SBW caused tree mortality in the SBW defoliation belt. In terms of the Kurz and Apps' (1996; 1999) carbon budget, this overlap is equivalent to an area of 13300/0.08 = 166 x 10^3 km^2 of SBW defoliation. Summing overlaps for the 3 sources described above gives a total overlap of approximately 181 x 10^3 km^2 of SBW defoliation (or equivalently, 14.5 x 10^3 km^2 of

SBW caused tree mortality) in the unmodified historical records. Only about 8.3% of this overlap appears to result from misclassification. Failing to account for this 14.5 x 10^3 km^2 of overlap produces overestimates of the total (fire + SBW-caused) tree mortality from 1941-1996 by 100% x 14.5 / (148 + 241 + 17.0 + 10.4 - 14.5) = 3.6%. This small percentage is largely due to the dominance of SBW which is credited with killing trees over areas 14 times larger than wildfire within the SBW belt. Thus we conclude that failing to account for spatial overlap of SBW outbreaks and wildfire in carbon budgeting incurrs little error, at least in (all) of Ontario.

5. Summary

In Ontario as a whole, spruce budworm (SBW) disturbances are typically much more extensive than wildfire: from 1941-1996 fires were reported in approximately 70.4 x 10^3 km^2 while SBW caused whole tree mortality within 389 x 10^3 km^2. Most of our analyses pertain to the 417 x 10^3 km^2 defoliated by SBW at least once in 1941-1996. This area is contiguous and crosses Ontario in an east-west strip termed the "SBW belt". Within this strip, the maximum total area recorded as defoliated in any year from 1941-1996 is over 20 times the maximal area burnt from 1921-1996. The eastern, central, and western parts of the SBW belt each have unique histories of wildfire and SBW disturbance.

Within this belt, areas that suffered moderate frequencies (9-11 years) of SBW defoliation were the most likely to be burnt. That a large part of the rarely defoliated area occurs near urbanized south-eastern Ontario where fire control is vigorous explains the reduced proportion burnt at low defoliation frequencies. At the other extreme, high fire frequencies prevent the development of extensive areas of forest heavily populated by SBW host tree species. It is these areas which are most capable of supporting frequent defoliation.

In areas experiencing both wildfire and SBW defoliation, analysis of the spectra of time lags between the two types of disturbance indicated that an area generally takes 17-20 years to recover from large (over 2 km^2) fires before it is capable of supporting SBW populations large enough to cause aerially visible defoliation. The analysis also showed that fires occurred 3-9 years after a SBW outbreak disproportionately often ($P<0.05$). The timing of this 'window of opportunity' for wildfire has consistencies with Stocks' (1985; 1987) reasoning. After a SBW outbreak, breakage of dead tree tops and windthrow of dead trees gradually build up an accumulation of ‘ladder fuels’ which provide surface fires access to crowns where fire becomes much more serious. Later, as the balsam fir fuel on the ground begins to rot and decompose, fire potential declines.

The data suggest that this ‘window of opportunity’ for wildfire begins longer after SBW outbreak and is wider in western than in eastern Ontario. In addition, 9.5% of the areas containing SBW killed trees were burnt in western compared to 5.7% in eastern Ontario. Both of these geographical differences may result from slower decomposition of dead fuels in the drier climates of the western SBW belt compared to the eastern SBW belt. Thus in stands attacked by SBW, one can expect increases in the proportion subsequently burnt in drier future climates. If SBW outbreak frequencies also increase in drier climates as some have suggested, this may further accelerate increases in fire frequency.

Our analyses also led to some suggestions and support for recent forest oriented carbon budgeting exercises (Kurz and Apps, 1996; 1999). First, we note that most FIDS aerial surveys began in the 1940s; this may account for the very small areas reported insect-disturbed from 1920-1940 (Kurz and Apps, 1996, Fig. 14.2; 1999, Fig. 3). We suggest backwards extrapolation of regional time series models (e.g., Candau et al., 1998) would provide a useful alternative for estimating the missing 1920-1940 data. On a positive note, we found that the multiplier of 0.08 that these authors used accurately represented the “area within which tree mortality occurred” as a proportion of the area with moderate-severe SBW defoliation. We also found that these authors’ omission of overlaps of SBW and wildfire disturbances in their estimation of historical disturbance impacts incurred an error of only 3.6%, at least for Ontario.

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Figure Captions

Figure 1: Schematic comparing expected impacts of SBW outbreak and wildfire on stand carbon, C, reservoirs from the (indicated) start of disturbance until stand maturity. Depending on disturbance intensity, much C stored in living tree biomass is quickly converted to dead organic matter, including dead trees and breakage from surviving trees. Shortly after the disturbance is over, tree biomass C increases through uptake by growing trees as the stand regenerates, and dead organic matter C declines due to decomposition and reduced transfers from living tree biomass. These transfers increase later as the regenerated stand matures. The ecosystem is a net C source until uptake by the regrowing stand exceeds losses from dead organic matter.

Figure 2: Spatial patterns in Ontario from 1941-1996 of (a) the frequency (see legend) of moderate to severe SBW defoliation recorded by FIDS aerial survey; (b) the occurrence of forest fire (black) overlaid on the 'belt' experiencing SBW defoliation at least once (grey). Two vertical lines on each map separate the western (W), central (C), and eastern (E) zones of SBW defoliation identified by Candau et al. (1998). In (b), the circled 'X' and the dashed line running it through respectively indicate the location of the Aubinadong River experimental burns (Stocks, 1985; 1987) and 47^{o} N. (after Fleming et al., 2000).

Figure 3: Time series of total area defoliated by SBW (dashed line, right axis) and of total area of large (> 2 km^2) burns (solid line, left axis) within the SBW belt's (a) western, (b) central, and (c) eastern zones (Fig. 2).

Figure 4: The horizontal axis indicates the number of years that different areas of the SBW belt were defoliated from 1941-1996 (Fig. 2a). The vertical axis shows the total area -years burnt from 1921-1996 as a percentage of the total area at each defoliation frequency. (Areas were counted every time they were burnt). Observations (●), a fitted regression curve (solid line), and the curve's 95% confidence limits about the mean (dashed lines) are shown.

Figure 5: Histogram of the total area in Ontario from 1941-1996 that experienced various time lags between the occurrence of wildfire and the closest incidences in time of SBW defoliation in the same area. A thin, vertical bar at each lag shows the 95% confidence interval of no statistically significant ($\alpha = 0.05$) effect. Small, vertical block arrows point out lags of significantly high frequency.

Figure 6: For each zone in the SBW belt (Fig. 2), a histogram gives the total area from 1941-1996 experiencing various time lags between wildfire and defoliation (as in Fig. 5). A thin, vertical bar at each lag shows the 95% confidence interval of no statistically significant ($\alpha =$ 0.05) effect. Small, vertical block arrows point out significantly frequent time lags.

Figure 7: Schematic of the potential for wildfires in the fuel complex of SBW-killed balsam fir stands occurring before and after flushing of the understory vegetation (i.e., in 'spring' and 'summer', respectively). There is potential for summer fires when contributions from crown breakage and windthrow exceed the fire-retarding influences of understory vegetation and rotting ground fuel (after Stocks, 1987).

Table 1. Average annual depletions (10^6 m^3/year) of Canada's productive wood volume in 1977-1987 with focus on the major insect disturbance agents in Canada's boreal forest (after Fleming, 2000).

Disturbance Type	Average Annual Volume Depleted
Harvest	160.0[a]
Insects	56.6
Disease	48.3
Fire	36.0[a]

Total	298.8[b]

MAJOR BOREAL FOREST INSECT DISTURBANCE AGENTS

Insect Species	Growth Loss	Mortality	Total Annual Depletion
Spruce Budworm	6.5	28.6	35.1
Forest Tent Caterpillar	4.9	0	4.9
Jackpine Budworm	0.4[c]	0.9[c]	1.3

[a] estimates from Hall and Moody (1994) for 1982-1987

[b] by comparison, annual 1982-1987 growth[a] = 244.3 - 346.0 x 10^6 m^3/year

[c] ratio of growth loss to mortality in jack pine budworm depletions in 1982-1987 was pro-rated from Ontario data[a].

Table 2. Indicators of the extensiveness of the 1941-1963 and 1967-1996 spruce budworm (SBW) outbreaks and their associated wildfires in each defoliation zone (Fig. 2), and for all of Ontario's SBW belt. Units of km^2 x yrs indicate that areas were counted each time they experienced the disturbance during the given time period.

	ZONE OF SPRUCE BUDWORM DEFOLIATION			
	East	Central	West	whole SBW belt
Area (10^3 km^2):	255	66.0	96.0	417
Defoliation (10^3 km^2 x yrs)				
1941-1963	769[a]	187[a]	426[a]	1380[a]
1967-1996	1780	392	610	2780
Tree Mortality (10^3 km^2)				
1941-1960	85.2[b]	14.0[b]	48.9[b]	148[b]
1973-1996	159[c]	28.0[c]	53.8[c]	241[c]
Wildfire (10^3 km^2 x yrs)				

1941-1966	12.2	1.94	2.87	17.0
1967-1996	1.68	1.78	6.89	10.4
Wildfire in areas where defoliation reported during the same outbreak (10^3 km^2 x yrs)				
1941-1966	11.1	1.65	2.53	15.3
1967-1996	1.68	1.19	4.08	6.95
Wildfire in areas where tree mortality reported during the same outbreak(10^3 km^2 x yrs)				
1941-1966	7.46	0.805	1.71	9.97
1967-1996	1.15	0.261	1.90	3.31
Wildfire following 2-16 years after the area's last defoliation ended [d] (10^3 km^2 x yrs)				
1941-1966	6.87	0.889	2.20	9.96
1967-1996	0.778	0.0773	0.359	1.21

[a] underestimated because the first outbreak was already underway in 1941 when the data begins

[b] undersetimated because records are incomplete

[c] underestimated because the data ends as defoliation collapses in 1996?

[d] allocated to time period based on the last reported defoliation (before wildfire)