

**Dendrochronological analysis of balsam fir (*Abies balsamea*) radial tree-ring growth
across edges created by a spruce budworm outbreak**

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Abstract

Outbreaks of spruce budworm can form patches or large expanses of dead trees and surviving trees at the edge of these areas experience a detectable decline in growth. However, we do not know how far this pattern extends from the edge. The growth of trees at budworm-induced edges was evaluated within the boreal forests of Cape Breton Highlands National Park in northern Cape Breton, N.S. The objectives of this study were (i) to analyze radial growth before, during and after the spruce budworm outbreak to see if there was a change over time, (ii) to determine how far budworm-altered radial growth extends into the forest, and (iii) to discern if edge balsam fir experienced more of an increase in radial growth after the budworm outbreak compared with the forest interior. Balsam fir trees were cored at three sites in plots at different distances from either side of the edge. Dendrochronological analysis was performed to observe changes in annual tree growth patterns of balsam fir trees. Each site experienced a significant decrease in growth during the period of spruce budworm outbreak (1974-1984). Surprisingly, decreases in tree growth were detectable far away from the edge. After the budworm outbreak subsided, two sites showed an increase in growth near the edge but not right on the edge. The increase in growth near the edge may have been due to release from light competition modified by local spatial pattern (e.g. gaps), while the lack of a gradient in tree growth reduction into the forest could indicate that a second wave of severe budworm defoliation stopped at the current edge, perhaps due to weather effects.

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1.0 Introduction

Natural perturbations are drivers of change in forest ecosystems. In boreal forests, fire, disease and insect outbreaks are all natural disturbances among which fire is often claimed to be paramount. However, the role of fire may be over-emphasized in boreal systems and alternative types of disturbance, such as insect herbivory, may be more common (Bonan and Shugart, 1989). The study of insect outbreaks has become a major subfield of dendrochronology because forest managers are interested in the historical effects of insect outbreaks on their managed lands (Speer, 2010). Dendrochronological studies have shown that insect outbreaks are an intrinsic, periodic disturbance of many ecosystems (Swetnam and Lynch, 1993; Blais, 1962). Knowledge of these natural disturbances is important to help understand both the trends and periodic occurrences of insect epidemics on forest ecosystems, with important roles in both forest dynamics and succession (Campbell *et al.*, 2005; Blais, 1962).

Eastern spruce budworm (*Choristoneura fumiferana*) outbreaks are one of the main disturbances influencing forest structure and species composition in the boreal forests of eastern North America. Periodic severe outbreaks can cause widespread tree mortality, particularly in mature balsam fir forests. Despite its common name, spruce budworm's preferred species in boreal forests is balsam fir (*Abies balsamea*), but it also defoliates white spruce (*Picea glauca*), black spruce (*Picea mariana*), and red spruce (*Picea rubens*) (Pothier and Mailly, 2006; Simard *et al.*, 2012). Outbreaks are related to forest composition and are most likely to occur when mature stands of balsam fir cover an extensive area. Spruce budworm populations increase gradually, reaching outbreak proportions approximately once every 30 years. During episodes of severe outbreaks, insect populations remain high for several years and usually subside after severe defoliation of balsam fir has taken place (Blais, 1983). Outbreak periods have been known to last for tens of years, depending on forest structure, climate conditions and natural predation (Kumbas *et al.*, 2011). During significant outbreaks, tree mortality and widespread reduction in radial growth is noted in the host species. According to Belle-Isle and Kneeshaw (2007), 75% of balsam firs over 10 cm dbh usually start dying after 5 years of severe defoliation. Defoliated trees that recover health after the outbreak

subsidies will have a historical recording of the outbreak conditions contained within the ring patterns of their annual radial growth. Radial-growth reductions caused by severe spruce budworm infestations are usually easily recognized; radial growth in balsam fir is relatively uniform with no drastic growth fluctuations. The presence of a series of narrow rings occurring amongst regular growth rings is distinguishable and noticeable (Blais, 1962, 1983; Swetnam and Lynch, 1993; Speer, 2010). Dendrochronological analysis can be used to determine the extent, intensity and duration of the outbreak (Blais, 1958; Speer, 2010).

Once budworm population levels are reduced, the outbreak will ultimately create a boundary between the budworm damaged landscape and the undamaged forest. A forest edge is defined as the interface between forested and non-forested ecosystems or between two forest communities of different structure and composition (Harper *et al.*, 2005). Conditions near the forest non-forest edge differ from those in the forest interior (Macdonald and Urban, 2005) and these conditions (microclimate, light, nutrients) will have an influence on the growth of trees growing along the edge. Burton (2002), while studying edge tree growth in sub-boreal spruce forests, concluded that these “edge effects” can extend between 40 and 120 m into the forest and positively or negatively influence tree growth depending on species type (shade tolerant vs. shade intolerant), orientation (south facing or north facing edge) and wind direction. While it is known that changes in these variables will influence growth near the edge, it is not known how far the influence of budworm defoliation on tree growth extends into the forest, nor the response of growth in the years after release from the outbreak.

The boreal forest of northern Cape Breton Island presents a unique study site. Significant moose browsing has maintained the spruce budworm induced edge since the 1974 to 1984 outbreak. The purpose of this research was to evaluate changes in radial growth rates across budworm induced edges in the Cape Breton Highlands created during the 1974 to 1984 epidemic. This research attempted: (i) to analyze radial growth before, during and after the spruce budworm outbreak to see if there was a change over time, (ii) to determine how far budworm-altered radial growth extends into the forest, and (iii) to

discern if edge balsam fir experienced more of an increase in radial growth after the budworm outbreak compared with the forest interior.

2.0 Methods

2.1 Study Area

Northern Cape Breton is a unique study area comprising three forested ecoregions: Acadian forests in the low lying regions, boreal forests above 330 meters elevation and tiaga ecosystems comprised of wetland bogs and rocky barrens reside on the exposed plateau above 400 m (Parks Canada, 2009). The unique geography and topography of the Cape Breton Highlands creates the physical and climatic conditions necessary to sustain boreal forest vegetation well below its typical circumpolar range. Climate data from the nearest weather station in Chéticamp report mean annual precipitation at 1056 mm. Annual snowfall amounts of 347 cm are typical. The mean annual temperature is approximately 6.2°C. Daily average temperatures of -6.3°C and 18.32°C were recorded in February and July respectively (Environment Canada, 2012). The region has a short growing season of 196 days (Webb and Marshall, 1999). This boreal ecodistrict supports characteristic boreal forest species of balsam fir, white birch, and white spruce. Some less common canopy associates include yellow birch *Betula alleghaniensis* and, occasionally, scattered maples (*Acer pensylvanicum*, *A. saccharum*, *A. rubrus*) (Neily *et al.*, 2010). Northern Cape Breton is home to the Cape Breton Highlands National Park where 20% of the boreal ecodistrict is protected and preserved. The study was carried out entirely within the boundaries of the national park.



Figure 1 – Map of northern Cape Breton with the Cape Breton Highlands National Park shown in light tan. Site 1 is located off Benji's Lake Trail, site 2 is located ~2 km from the road on North Mountain and site 3 is located ~1.5 km in the woods south of the Skyline Trail entrance.

Established in 1936, Cape Breton Highlands National Park covers 948 km² of northern Cape Breton. The park attempts to maintain ecological integrity within its boundaries by allowing natural processes and events to occur without anthropogenic influence. This policy prevents spruce budworm population control measures from being applied within the park (i.e. pesticides), allowing the full extent of a budworm outbreak to be reached and natural edges created. The current state of the historical edge from the 1974-84 outbreak is being maintained by another boreal resident, the western moose (*Alces alces andersoni*). A study by Bridgeland *et al.* (2007) yielded a 1985 population estimate of 1126 moose with a 95% confidence interval ranging from 678 to 1573 moose in the boundaries of the national park. Due to the large resident moose population, forest regeneration has been inhibited. Moose feed mainly on balsam fir and white birch (*Betula papyrifera*). Heavy browsing along the budworm induced edge has led to the replacement

of fir and birch with white spruce and other unpalatable tree species, as well as encouraging encroachment from grass species (i.e. *Calamagrostis*). This selective browsing has maintained the physical presence of the edge and is altering the post-budworm understory structure and succession patterns (Smith *et al.*, 2010).

Evidence of past spruce budworm presence on Cape Breton Island dates back more than 160 years. Historically, there have been 5 major spruce budworm outbreaks; the first outbreak began in 1846, a second between 1891 and 1896, a third between 1911 and 1915 and a fourth between 1951 and 1955 (Parry, 1997). No appreciable budworm numbers were recorded in 1973; however, in 1974 a severe budworm outbreak began (Kettela and Moran, 1975). Severe defoliation continued for 4 to 5 years, with the epidemic lasting until 1984 (MacLean and Ostaff, 1989).

At the time of the 1974-1984 spruce budworm outbreak, the forested plateau of Cape Breton Highlands National Park was primarily made up of mature to late-mature stands of balsam fir. MacLean and Ostaff (1989) reported balsam fir stand ages of approximately 150 years at the start of the outbreak, making it highly vulnerable to attack from the spruce budworm (Johnston, 1987). Maclean and Ostaff (1989) reported an average stand mortality of 87% from 20 sites in Northern Cape Breton's boreal forest.

The intensity of the 1974 to 1984 outbreak, responsible for the current state of the Cape Breton Highlands fir-spruce boreal forests, was a result of the combined effect of budworm migration from distant outbreak areas, large areas of vulnerable mature fir-spruce forest, no control interventions, and, possibly, favorable weather conditions (MacLean and Ostaff, 1989).

2.2 Sampling Design

Site	UTM Coordinates	Elevation (m)	Edge orientation	Average dbh (cm)	Average height (m)
Site 1 (Benji's lake area)	20 T 0667192, 5178624	442	60° (NE)	18.8	8
Site 2 (North Mountain)	20 T 0677648, 5186305	465	292° (NW)	22.03	8
Site 3 (Skyline trail area)	20 T 0660735, 5178802	381	270° (W)	14.4	6.4

Table 1 – Site characteristics including UTM coordinates, elevation, edge orientation, and average dbh and height of balsam fir trees.

Potential study sites were selected based on aerial photographs of budworm induced forest edges within the Cape Breton Highlands National Park. Subsequent ground surveys determined if sites were accepted or rejected, primarily on the condition of easy access to the site. In total six sites were selected and sampled during June, July and August of 2012. However, three sites were omitted due to improper mounting of tracheid cells (making tree-ring boundaries difficult to see), trees too young, or a combination of both. In total three sites were used (Figure 1). Edge orientation was determined using a compass. At each of the three sites, 5 m x 20 m structure plots were set up along a transect at 0 m (the forest edge) and 10, 20, 40, 60 and 100 m into both the forest and the budworm disturbed area. Within the budworm disturbed area, tree mortality was significantly high enough to limit the availability of suitable balsam fir trees. The majority of suitable balsam fir trees in the budworm disturbed landscape had internal rot; hence, structure plots in the budworm-disturbed areas were unsuitable for data analysis. Balsam fir trees within the structure plots were selected based on their apparent age and size with larger diameter trees being preferred. The three largest diameter balsam fir trees in each structure plot were cored at breast height (~1.3 m). Structure plots with suitable fir trees slightly outside the structure plot area were also sampled to increase the sample size. Two core samples were taken from each individual tree at approximately 180° angles unless obstructed by tree growth or the presence of an anomaly (branch, windsnaps, etc.) that would misrepresent the data. Extracted cores were placed into a straw for storage and transportation, with slits in the side of the straws to prevent

molding. Cores were then labeled and mounted on wooden board mounts, bearing in mind that tracheids should be aligned vertically when mounting so individual cells and ring boundaries are visible (United States Department of Agriculture, 1985). Once the cores were mounted they were sanded using progressively finer grain sand paper until the cell structure and ring boundaries were easily recognized.

2.3 Data analysis

Tree cores were examined using the Velmex Stage system at the Mount Allison Dendrochronology lab. Cores were individually measured for annual ring widths using the stage system in combination with a microscope. The width between the rings, measured in microns (0.001mm) per year, was assumed to represent annual growth rate per year. Annual rings were counted backwards from 2011, the final year of growth prior to data collection. Field data were collected during July and August of 2012, therefore, that year was not used during the analysis as the ring width would not represent a full year's growth. Data from each individual tree core were compiled for each structure plot within each site and cross-dated using the freeware program COFECHA. Ring width data was standardized using ARSTAN to develop the ring width index (RWI) of each site that removes seasonal growth trends. Data was analyzed by using graphs and not statistically because of low sample sizes and variability among sites.

3.0 Results

All sites experienced a decline in growth during the period of budworm outbreak; however, site 1 was not affected to the same degree as sites 2 & 3 (Figure 2). The period of budworm suppression varied; site 2 experienced the most significant growth reduction and the longest period of suppression and post-budworm recovery. Prior to the start of the budworm outbreak, site 2 experienced significantly higher radial growth rates than the other study sites.

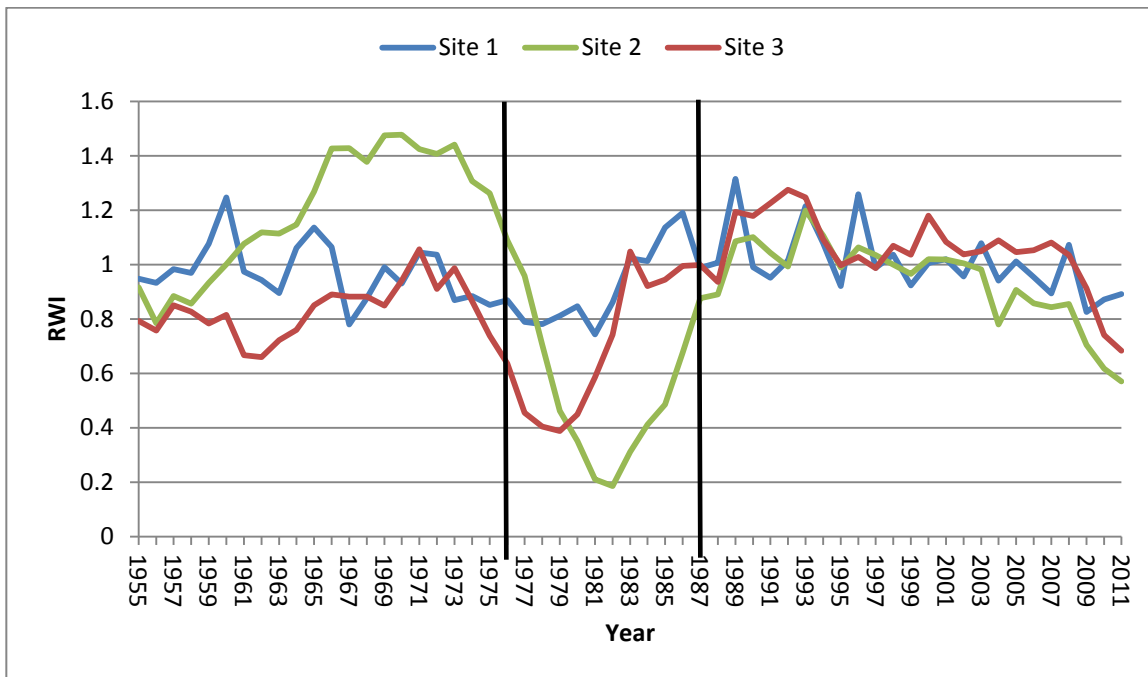


Figure 2– Ring Width Index (RWI) for all study sites. Sites 2 and 3 experienced significant reductions in radial growth during the 1974 to 1984 budworm outbreak (shown between the two vertical lines). However, site 1 did not experience as significant a reduction in radial growth when compared with the other sites.

Average RWI was significantly reduced during the budworm outbreak for all sites and RWI during the post-outbreak years (1985-95) did not recover to pre-outbreak growth values (Figure 3). However, site 1 & 3 did experience increases in average growth rates after the budworm outbreak (Figure 4). Only site 2 did not recover to pre-outbreak levels of radial growth after release from the budworm outbreak.

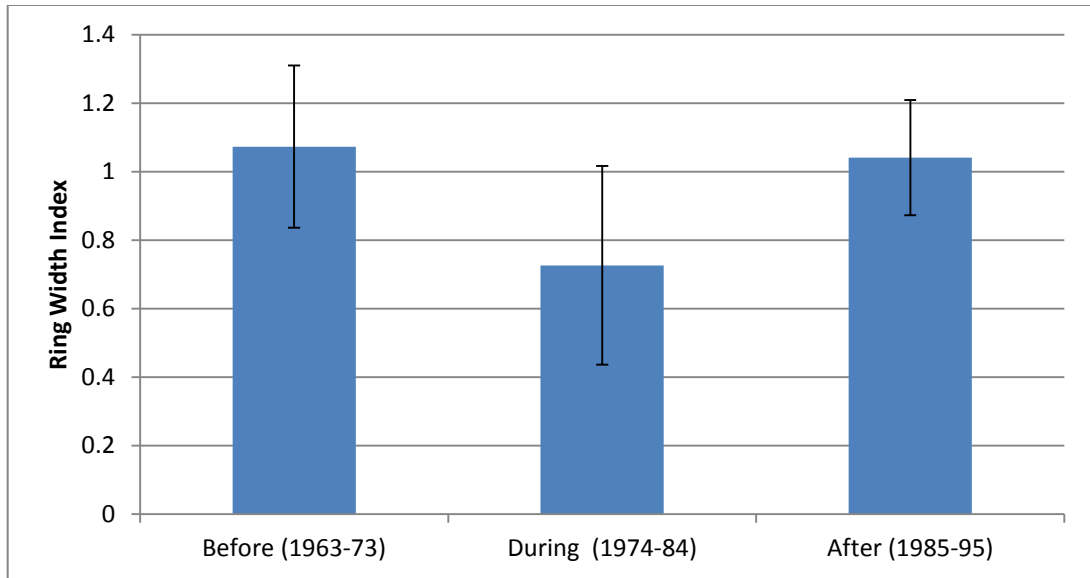


Figure 3 – Average ring width indices at all sites before, during and after the spruce budworm outbreak with standard deviation bars.

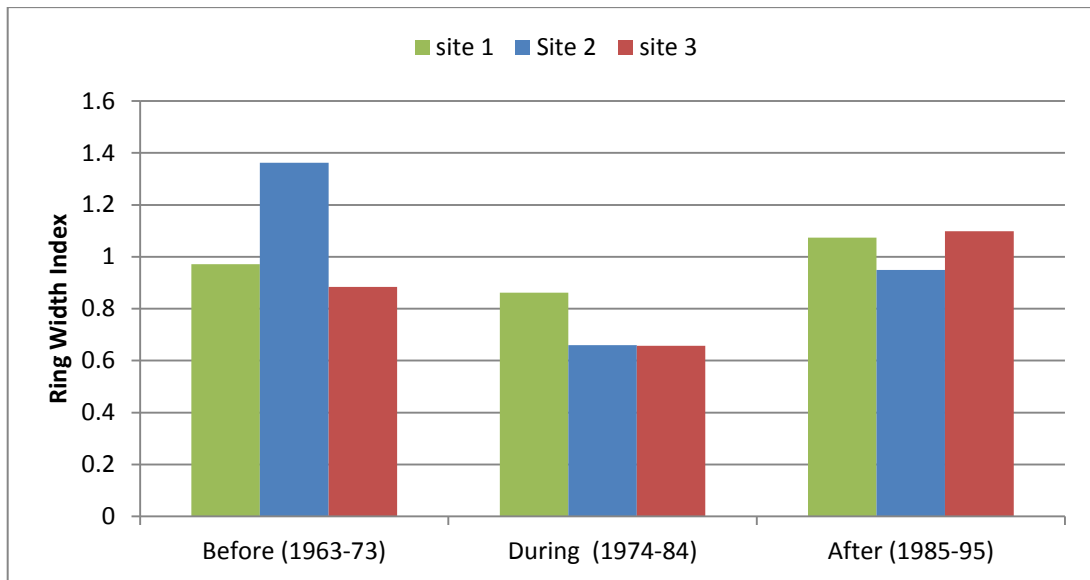


Figure 4 – Average ring width indices (RWI) for individual sites before, during and after the spruce budworm outbreak.

Radial growth was affected by the budworm outbreak at all distances from the edge; however, the effects varied among sites. Average radial growth for all sites indicates that growth was reduced during the budworm outbreak at all plots including 100 m from the forest edge (Figure 5). Post-budworm growth did not usually recover to pre-budworm

growth values. Only at 10 m distance were average post-budworm growth rates higher than pre-budworm growth rate, with sites 2 and 3 both showing an increase in radial growth at the 10 m mark (Figure 2A& 3A).

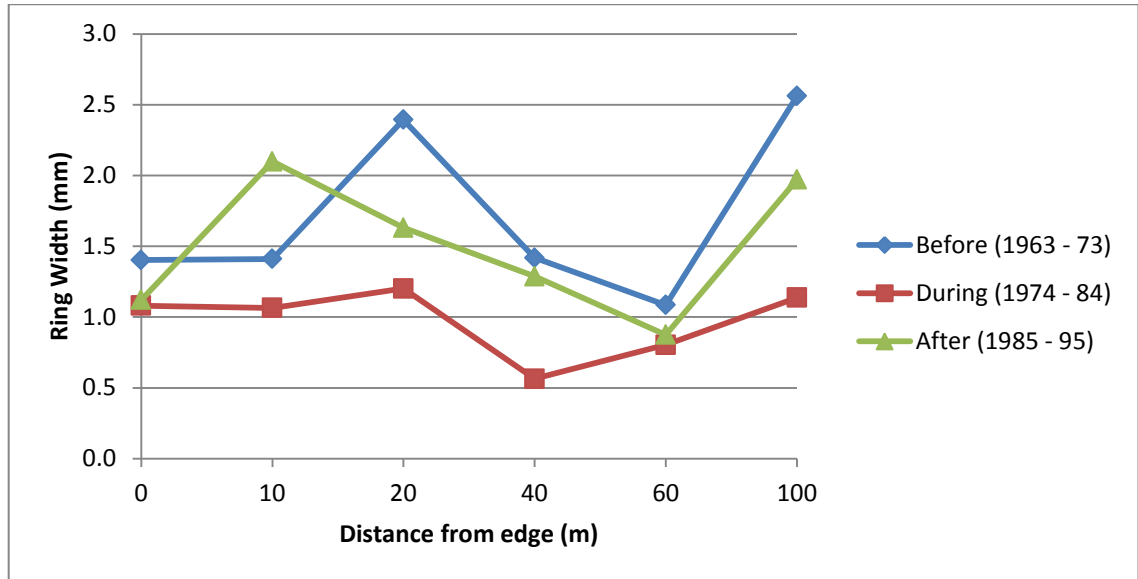


Figure5 – Average radial growth at different distances from the edge for all sites comparing growth rates in 10 year intervals before, during and after the outbreak (1963-1995).

4.0 Discussion

Although site 1 was affected, there was not as much of a radial growth reduction compared with sites 2 and 3. There is a noticeable decrease during the outbreak years at site 1; however, sites 2 and 3 appear to have been more affected by the budworm outbreak. The percentage canopy cover suggests that the budworm pandemic was abruptly stopped at the edge of site 1 (Figure6) perhaps due to changing weather conditions or high mortality. The close proximity of Benji's Lake may have influenced budworm reproduction and dispersal by influencing the air temperature and humidity at this site, both of which have been shown to affect budworm dispersal (Royama, 1984). If spring conditions were not favorable during the early stages of the budworm outbreak, survival of emerging budworm larva may have decreased and moth emigration, predation or parasitism may have reduced populations to a state where a recovery to pandemic

numbers of larva was not possible. Site 2 had the highest average height and dbh (table 1), perhaps indicating that this stand of fir trees was more mature, and, therefore, more likely to be affected by the spruce budworm. It may also be that population levels and local oscillations at each site were different; with site 2 experiencing higher numbers of budworm larva per unit area than sites 1 and 3.

At site 1 radial growth returned to pre-outbreak growth rates after the pandemic subsided. At site 3, radial growth was higher after release from the outbreak than before the outbreak began. Edge orientation at site 3 may have influenced the growth rate by allowing insolation to penetrate further into the forest than sites 1 and 2 (table 1). Individual tree conditions at site 3 may have also been a factor, as most trees were young at the time of the outbreak and annual radial growth is more vigorous in young balsam fir trees than mature, slow growing trees (United States Department of Agriculture, 1985).

Surprisingly, the distance of budworm-altered growth extended up to 100 m at all sites. Perhaps this is due to a first wave of budworm infestation defoliating trees in the forest but did not reach high enough numbers to inflict significant mortality. After this first wave subsided, another wave of severe defoliation may have caused high mortality of fir trees up to the current edge where the budworm population plummeted and the pandemic finished. Site 2 was significantly defoliated at all distances into the forest. The percentage of canopy cover into the forest of site 2 is lower at all distances than sites plots at sites 1 and 3 (Figure 6). These canopy “gaps” into the forest were most likely caused by light budworm defoliation causing the mortality of weaker, individual trees (Pardy, 1997). The canopy gaps compliment the assumption that site 2 experienced severe defoliation.

Budworm-altered growth near the edge was expected to increase after release from the budworm outbreak due to less competition for resources such as light, water and nutrients. However, no site experienced increased growth after the budworm outbreak directly on the edge. This may be due to individual tree characteristics or changing weather conditions at the edge (e.g. high winds), but this can only be speculated. Only at the 10 m plot was average post-outbreak growth greater than pre-outbreak growth. Perhaps right at the edge there was too much wind, but at 10 m trees received the benefit of extra light while being shielded from the wind. However this result may be inaccurate

as the 10 m plot at site 1 did not have trees that were old enough (or cores were unusable) to provide an average value for pre-budworm growth.

Budworm altered growth during the outbreak years between 1974 and 1984 was noted in the chronology of all sites as expected. However, it was surprising that budworm altered growth extended into the forest up to and including the 100 m plots. After the budworm outbreak subsided, radial growth on the edge did not experience more of an increase compared with the forest interior, perhaps as a result of changing weather conditions along the edge but this is not conclusive. The results of this study acknowledge the complexity of budworm-fir interactions and the resulting forest mosaic.

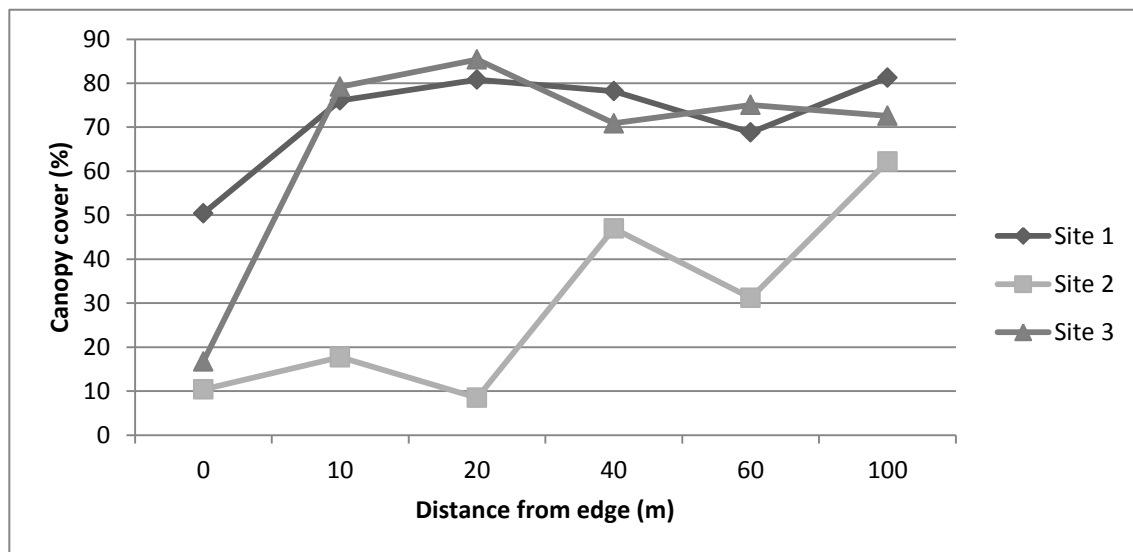


Figure 6 – Percentage of canopy cover at the edge and at different distances into the forest interior (Caroline Franklin, unpublished data).

5.0 References

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6.0 Appendix A

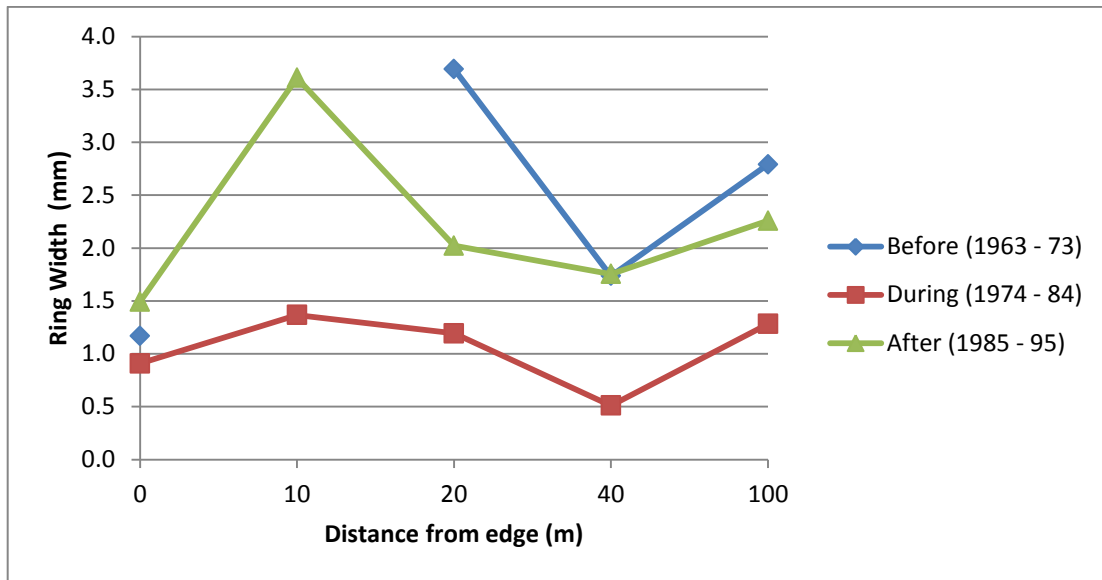


Figure A1– Site 1 average radial growth before, during and after the outbreak at different distances from the edge. Note that at 10 m trees were not old enough to provide data for the 10 years prior to outbreak (1963-73).

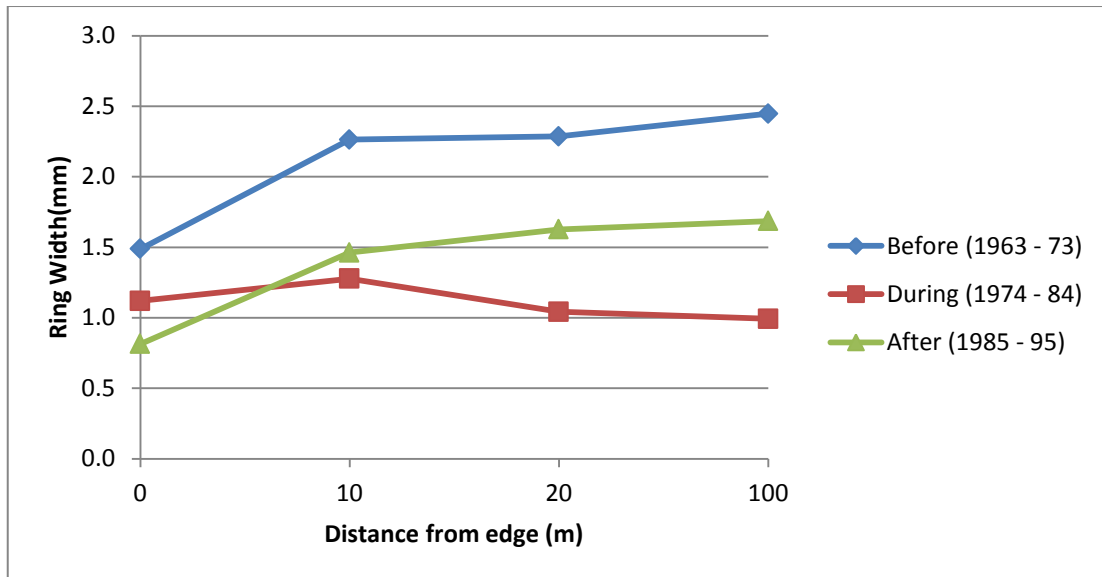


Figure A2 - Site 2 average radial growth before, during and after the outbreak at different distances from the edge.

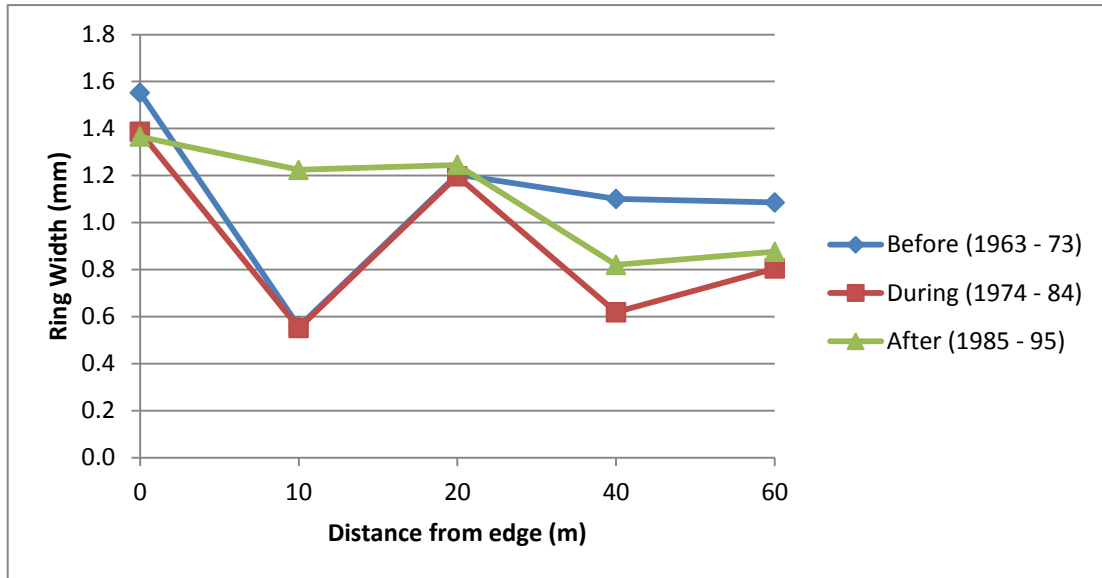


Figure A3 – Site 3 average radial growth before, during and after the outbreak at different distances from the edge. Note that 60 m is the maximum distance into the forest as 100 m was unavailable for data analysis.

Appendix B

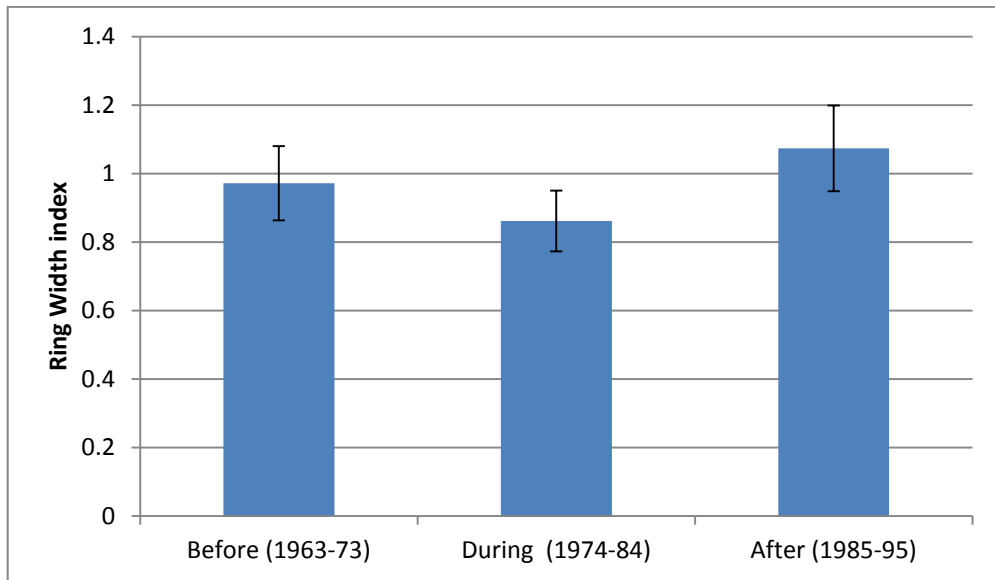


Figure 1B – Site 1 ring width index (RWI) before, during and after the spruce budworm outbreak with standard deviation bars. Growth after the outbreak exceeded growth during and prior to the budworm outbreak.

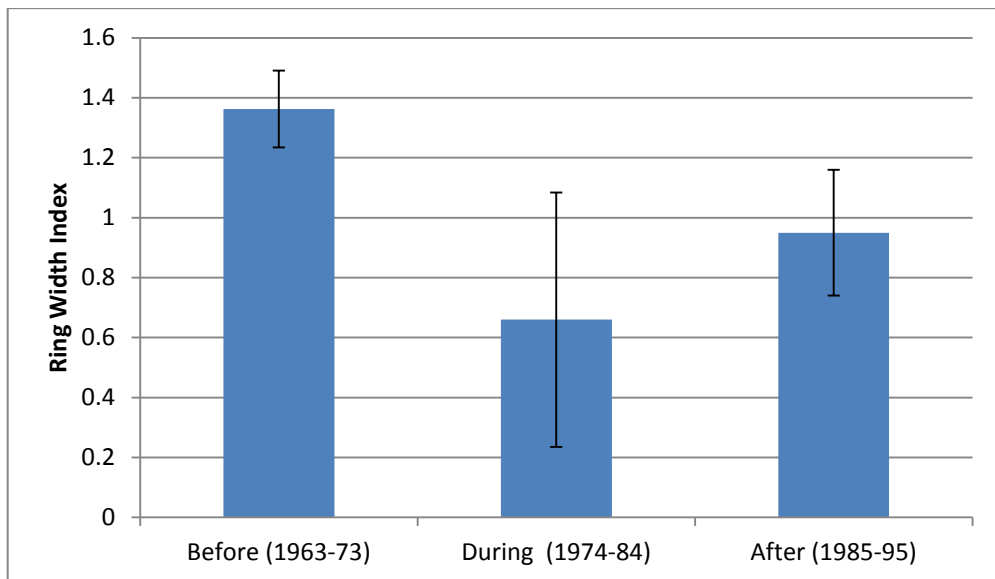


Figure 2B – Site 2 ring width index (RWI) before, during and after the spruce budworm outbreak with standard deviation. RWI values after the outbreak exceeded growth during the outbreak, but did not return to growth rates pre-outbreak growth.

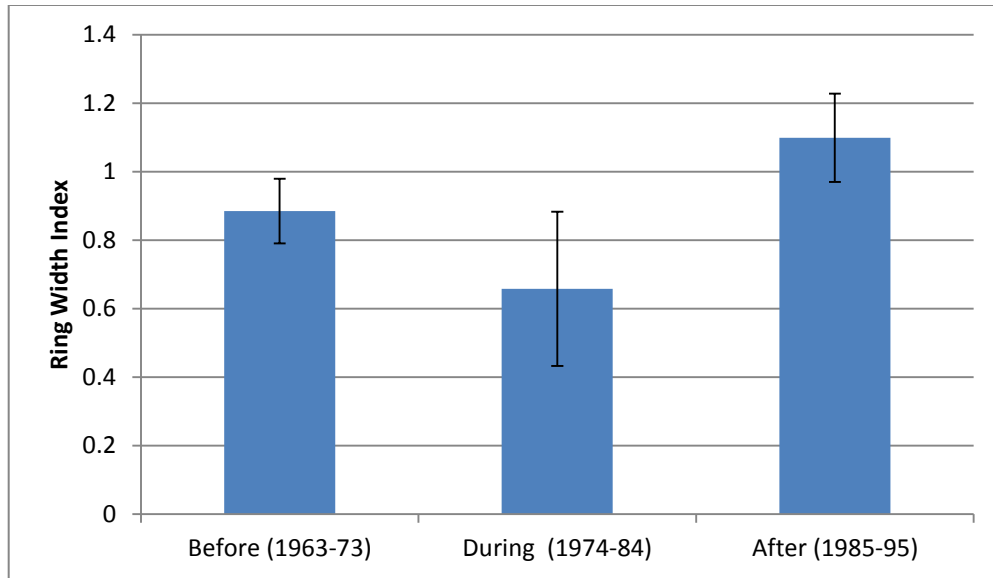


Figure 3B - Site 3 ring width index (RWI) before, during and after the spruce budworm outbreak with standard deviation bars. Post-budworm growth exceeded pre-budworm growth.

Appendix C

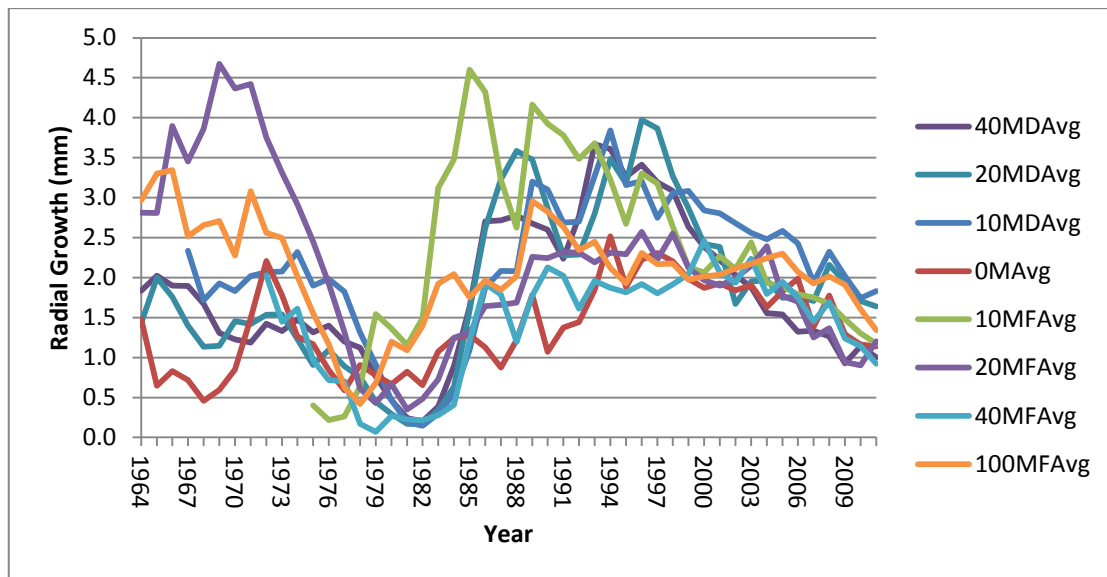


Figure 1C – Site 1 Average Radial Growth in each structure plot from 1964 – 2011. In the legend DA means disturbed area and FA stands for forest area. For example, 40MDAvg is 40 meters into the budworm-disturbed area while 40MFAvg is 40 meters into the forest.

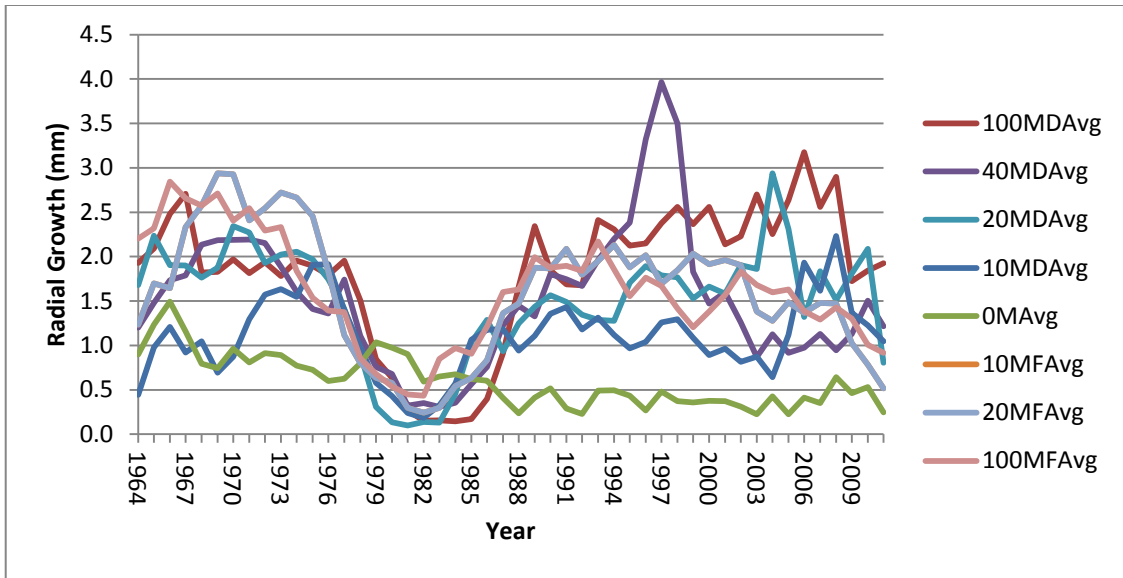


Figure 2C - Site 2 Average Radial Growth in each structure plot from 1964 – 2011. In the legend DA means disturbed area and FA stands for forest area. For example, 40MDAvg is 40 meters into the budworm-disturbed area while 40MFAvg is 40 meters into the forest.

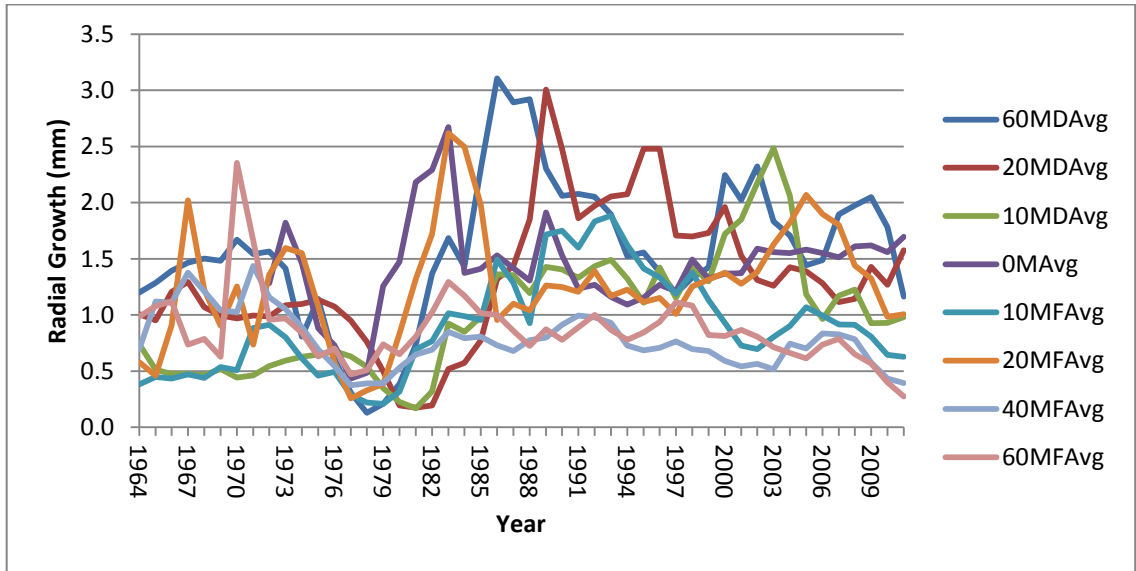


Figure 3C –Site 3 average radial growth in each structure plot from 1964 – 2011. In the legend D means disturbed area and F stands for forest area. For example, 40MDAvg is 40 meters into the budworm-disturbed area while 40MFAvg is 40 meters into the forest.