WESTERN HEMLOCK LOOPER: A BIOLOGICAL AGENT OF DISTURBANCE IN COASTAL FORESTS OF BRITISH COLUMBIA

BY

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ABSTRACT

My dissertation examines western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst) as an agent of disturbance in coastal forests of British Columbia. Western hemlock looper populations along coastal British Columbia have undergone seven episodes of outbreak from 1911 to 2004, leading to visible defoliation of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)-dominated forests. My research investigates the causal factors that influence the timing of outbreaks, the impacts the resultant defoliation has on forest structure and composition, and the spatio-temporal dimensions of this biological disturbance agent.

In order to identify the specific antecedent climate conditions that contributed to western hemlock looper outbreaks between 1911 and 2003, I analyzed local meteorological records to develop a moisture stress index of combined temperature and precipitation data. This index included periods of warm, dry climate between 1895 and 2004, and I hypothesized that these warm, dry conditions would improve the survival of western hemlock looper larvae and facilitate population increases. Indeed, a high moisture stress index in June was associated with the onset of visible defoliation by western hemlock looper populations later that year. Furthermore, a high moisture stress index over the entire growing season (May to September) was associated with conditions two years before visible defoliation events, thereby providing a trigger for populations to increase to outbreak levels in subsequent years. Given predicted warmer and drier climatic conditions during the growing season in coastal British Columbia, I anticipate that the frequency of western hemlock looper outbreaks will increase in future.
To quantify the impacts of defoliation on the structure and composition of the coastal forests, I compared the effects of three different levels of disturbance severity on stands with comparable tree composition, density, age and stand structure within the Coquitlam River watershed during a western hemlock looper outbreak from 2000-2003. I hypothesized that defoliation from western hemlock looper would slow the growth of canopy western hemlocks at sites with low levels of defoliation and lead to the death of canopy western hemlocks at sites with more severe defoliation. I found that the degree of canopy openness increased with disturbance severity and resulted in an increase in understory vascular plant diversity. I suggest that these alterations to forest structure and composition will lead to an increase in the number of possible future successional pathways and increase forest heterogeneity at the landscape level.

In a second study of disturbance effects, I analyzed the temporal pattern of tree death and the resulting rates of mortality after the 2000-2003 western hemlock looper outbreak. I hypothesized that mortality of trees in defoliated areas would be influenced by tree diameter, with smaller trees more susceptible to defoliation and dying at a greater rate than larger trees. Using repeated census data, I was able to show species-specific responses in mortality following western hemlock looper outbreaks. Western hemlock had high levels of mortality across all diameter classes, while mortality of western redcedar and amabilis fir was confined to smaller trees.

To determine if the frequency of western hemlock looper outbreaks changed over the past two centuries, I employed dendroentomological methods to reconstruct outbreaks that
occurred on Coquitlam Island, a 75 ha island where three outbreaks had been documented during the 20th century. I used differential rates of tree-ring growth between ‘host’ western hemlock and ‘non-host’ western redcedar to detect periods of radial growth suppression associated with western hemlock looper outbreaks using the program OUTBREAK. I used known periods of western hemlock looper outbreaks in the 20th century to calibrate and verify the reconstruction techniques. I successfully reconstructed four outbreaks over a 135-year period between 1775 and 1910. The dendroentomological method was successful at identifying low, moderate and high severity outbreaks, whereas the written record identified only periods of visible defoliation from high severity outbreaks. Based on the reconstructed outbreaks, I have determined that the frequency of defoliations has not changed significantly over the past 200 years.
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DEDICATION

This dissertation is dedicated to the memory of my brother, Grant McCloskey (1975-2006).

You have never left my thoughts.

I love you.

There was a time I was happy in my life,
There was a time I believed I'd live forever...

Madonna
CO-AUTHORSHIP STATEMENT

This dissertation presents research conducted by Shane P. J. McCloskey in collaboration with Lori D. Daniels (supervisor). The primary investigator and author of the dissertation was Shane McCloskey, who was responsible for research design, field research, statistical analyses, interpretation of results and writing. Editing assistance and consultation was provided by Lori Daniels.

The research design in Chapter 2 was formulated with guidance from John McLean.
CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

Ecosystem Management and Natural Range of Variability

Ecosystem management involves managing ecosystems to ensure the sustainability of their structure, function and processes (Christensen et al. 1996). To be successful, ecological management must be firmly based upon sound models and scientific research that emphasize the interactions and processes that create and maintain ecosystems. Increasingly, this research objective has recognized the dynamic character of ecosystems and a greater understanding of natural range of variation within ecosystems has become necessary. Natural variability can be defined as the ecological conditions, and the spatial and temporal variation in these conditions for a study area. The study area must be specified at temporal and spatial scales that correspond to the research objectives (Landres et al. 1999). The use of natural variability in ecosystem management requires that managers have sufficient knowledge of historical conditions, and the processes that created and maintained them; however, for many ecosystems such fundamental knowledge is lacking. In forest ecosystems in particular, a firm understanding of historical disturbance and disturbance regimes, a fundamental source of natural variation, is tantamount as disturbance-driven spatial and temporal variability is a vital attribute of these systems (Landres et al. 1999).
In the coastal temperate forests of British Columbia, large-scale, stand-replacing disturbances by fire, wind or geomorphic events are rare (Wong et al. 2003). The dominant trees are long-lived with amabilis fir (*Abies amabilis* Doug. ex Forbs) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg) living up to 500 years and western redcedar (*Thuja plicata* Donn ex D. Don) and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) living more than 1000 years. In these old-growth forests, the ecosystem is maintained by the interplay of many spatially and temporally discrete disturbances, including fine-scale gap dynamics and stand-level disturbances by insects and pathogens that contribute to the structural diversity of the forest. In the past two decades, substantive research has focused on gap dynamics in old-growth forests (Lertzman and Krebs 2001, Arsenault 1995, Gavin et al. 1996, Daniels and Gray 2006). In contrast, little research has been conducted on insect disturbance regimes, so that the historic range of variability and the impacts of defoliating insects on the composition, structure and function of coastal old-growth forests remain poorly understood.

In British Columbia, there are approximately 140 species of defoliators known to feed on native conifers (Ministry of Forests and Range 1995). Most of these insects are moths and butterflies (Lepidoptera), although aphids (Homoptera) and sawflies (Hymenoptera) are also common defoliators. In terms of size of area and severity of impacts to the forest, the western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst), Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), western blackheaded budworm (*Acleris gloverana* Tortricidae) and the western and eastern species of spruce budworm
(Choristoneura occidentalis Tortricidae and C. fumiferana Clemens) are the most destructive in British Columbia (Ministry of Forests and Range 1995).

The Western Hemlock Looper

Hemlock looper is a defoliating insect of the family Geometridae. Two subspecies of hemlock looper exist in Canada, Lambdina fiscellaria fiscellaria (Gueneé) east of the Rockies and Lambdina fiscellaria lugubrosa (Hulst) west of the Rockies, although recent genetic analyses have questioned this distinction (i.e. Sperling et al. 1999). In western Canada, the preferred host for Lambdina fiscellaria lugubrosa is western hemlock, although during outbreaks they will feed on almost any foliage, including broad-leaved deciduous trees and shrubs (Jardine 1969).

Details of the life cycle of the western hemlock looper help explain the particular pattern of its folivory and the resulting defoliation of western hemlock dominated forests. The larvae of western hemlock looper emerge in late May from eggs laid in moss, lichen or bark on the upper trunks of trees. The larva is a looper, 5-33 mm long with six instar stages before pupation. The early instars are black with light grey bands while latter instars are mottled grey-to-brown with two pairs of dark spots on each abdominal segment (Figure 1.1). New larvae preferentially feed on new foliage, but as larvae mature they feed on old foliage and even small twigs (Jardine 1969). Larval feeding initially takes place in the upper crown, but the larvae move down to lower sections of the tree during later stages, when feeding can be described as ravenous. During outbreaks, the feeding larvae can defoliate a tree in its entirety by August (Figure 1.2). They are not
efficient feeders, often leaving browning needle remnants that give defoliated trees a
distinct rust colour. The last of the six instar stages occurs in late July or early August
producing a looper about 33 mm long. This is followed by pupation on remaining foliage,
tree trunks or duff that typically lasts 10 to 14 days after which adult moths emerge.
Mating takes place soon after, with adults in flight from September to October (Edmonds

Figure 1.1 The larval stage of the western hemlock looper.
Western hemlock looper outbreaks tend to be quite punctuated, with populations increasing rapidly to a single peak, which usually lasts three to four years before collapsing to pre-outbreak levels. Density-independent factors may facilitate looper population growth; however, to my knowledge no relationship has been established between such factors and the onset of western hemlock looper outbreaks in coastal forests. Populations of western hemlock looper cannot be maintained at outbreak levels and are reduced by density-dependent and independent factors (Turnquist 1991). The populations of predators, parasites, and diseases often increase in an exponential pattern as the western hemlock looper population becomes more abundant, though there is a lag.
time as in most predator-prey systems (Moran 1953). A number of bird species prey on the larval and pupal stages, yet their impact on the population density of looper, especially during outbreaks is unknown (Otvos 1979). Telenomus dalmani and Trichogramma minutum are common egg parasites of the western hemlock looper and are thought to lead to population collapse when the rate of parasitism is above 30% (Turnquist 1991). There are also numerous larval and pupal parasites associated with western hemlock looper, including Trachinid flies, braconid wasps and ichneumoid wasps (Turnquist 1991). Disease also may contribute to population collapses of western hemlock looper. The most common disease is Endomorphthora species, which were isolated from western hemlock looper populations in the Coquitlam River watershed in 1972. Nuclear polyhedrosis virus (NPV) was associated with a collapse in the Kamloops Region in the mid 1980’s (Turnquist 1991). Interestingly, during the most recent outbreak on the coast, 43% of pupae were infected and contributed to low levels (38%) of adult moth emergence (Burleigh and Gustafsson 2003). In severe outbreaks, food may become limiting for western hemlock looper and larval starvation becomes a factor in terminating outbreaks (Koot 1994). Additionally, density-independent factors, such as heavier than normal precipitation and cooler weather, especially during the adult flight and egg hatching periods, may contribute to a population collapse (Koot 1994).

There have been several attempts to control western hemlock looper populations in British Columbia when outbreaks have occurred. The earliest large-scale attempt to control the population of any forest insect in BC was the dusting of almost 325 ha of coastal forest within Stanley Park and the Vancouver watersheds with calcium arsenate
during 1929-1930 (Richmond 1986). The success of the program was questionable. Later attempts included the use of DDT, an organochlorine, in 1959 within Stanley Park and the use of phosphadimion, an organophosphate, during 1962-1963 for parts of southern Vancouver Island (Richmond 1986). Today, *Bacillus thuringiensis* var. *kurstaki* (Btk) is registered for use against western hemlock looper, and just over 10,000 ha were sprayed in 2003 on affected stands in the interior of BC (Burleigh and Gustafsson 2003). Outbreaks in the coastal region are generally considered to crash more easily than those in the interior, and coastal trees are thought to be more resistant to defoliation (Burleigh and Gustafsson 2003). For these reasons, the economic threshold for implementing a control program on the coast is much higher, and little action was taken against coastal western hemlock looper populations during the most recent (2000-2003) outbreak.
Defoliation Impacts of Western Hemlock Looper Outbreaks

Disturbances such as insect outbreaks will affect growth and vigour at the level of the individual tree. The length and severity of the defoliation by western hemlock looper determines the level of impact on individual trees. Because the larvae of western hemlock looper feed on all ages of needles, severe outbreaks can completely defoliate a tree in one season, producing distinct patches of defoliated trees over the landscape (Figure 1.3).

Figure 1.3 Defoliated patch of coastal forest on Coquitlam Island following a western hemlock looper outbreak from 2000-2003.

Typically, mortality of trees begins after a tree has been defoliated for at least two consecutive seasons. However, structural differences between individuals will lead to differences in the impacts of defoliation and variation within forest. For instance, larger
trees will have more starch reserves and should be able to withstand a longer period of defoliation, and loss of new photosynthates. Hoggett and Negrave (2001) found that mortality caused by western hemlock looper outbreaks in the interior of BC was related to tree diameter, with smaller diameter classes exhibiting the highest rates of mortality.

Mortality rates vary among tree species, with a study in the BC Interior noting a higher proportion of host subalpine fir dying than other species (Alfaro et al. 1999) and another study on Vancouver Island noting higher levels of mortality among western hemlock and Douglas-fir (Kinghorn 1954). With differing tree species responding differently to defoliation events, the composition of the forest may change following a looper defoliation event (Alfaro et al. 1999). Most outbreaks in the coastal Pacific region have occurred in mature or old-growth hemlock or hemlock-cedar stands (Ministry of Forests and Range 1995). In the Coastal Western Hemlock biogeoclimatic (CWH) zone, the effects of western hemlock looper defoliation, especially tree recovery rates and associated impacts on forest stand dynamics, are poorly understood due to the practice of emergency salvage logging of affected stands. Thus, the long-term effects of hemlock looper defoliation events on the forests of coastal BC remain poorly documented and the species-specific responses and resulting compositional change of coastal forests after looper outbreaks have not been quantified.
1.2 Objectives

I hypothesize that western hemlock looper, an endemic biological agent of disturbance, has important impacts on forest dynamics and ecosystem function. The main objective of my dissertation is to examine the role of western hemlock looper as an agent of disturbance in forest ecosystems of coastal British Columbia. My specific objectives are to investigate the causal factors that contribute to outbreak commencement, to quantify the impacts of the resultant defoliation on forest structure and composition, and to determine if the frequency of this disturbance has been consistent through time.

To address these objectives, I examined western hemlock looper activity at a variety of spatial scales ranging from individual trees to stands to the south-coast region and at temporal scales ranging from seasonal variation in climate to historical reconstructions over 200 years. I completed four inter-related studies of western hemlock looper outbreaks. I examined historical monthly and seasonal temperature and precipitation, as well as insect population records from the south coast and lower mainland of British Columbia to investigate the role that antecedent climatic conditions play in driving western hemlock looper outbreaks (Chapter 2). I determined how the forests in the Coquitlam River watershed were affected by differing severities of defoliation following an outbreak of western hemlock looper in 2000-3 by quantifying canopy openness and composition of the understory (Chapter 3). I quantified the temporal patterns of mortality following western hemlock looper defoliation (Chapter 4). Species-specific logistic regression models were developed by repeated census data from approximately 1000 individual trees over a four-year period to quantify the probability of tree death following
a western hemlock looper defoliation event. To assess historical outbreaks, I concentrated on Coquitlam Island where western hemlock looper outbreaks had been previously documented over the past half-century (Chapter 5). In this study, I employed dendroentomological techniques to detect periods of radial growth suppression corresponding to western hemlock looper outbreaks. The final chapter provides a summary of the main findings and concludes that a greater understanding of the natural variability in disturbance by western hemlock looper in coastal British Columbia will aid in the ecologically management of these forests.
1.3 LITERATURE CITED


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CHAPTER 2: EVALUATION OF THE ROLE OF CLIMATE IN DRIVING WESTERN HEMLOCK LOOPER POPULATION OUTBREAKS

2.1 INTRODUCTION

Many forest insect populations are predisposed to exponential growth and, given suitable conditions, populations can increase dramatically. White (2004) argues that changes in populations are ultimately driven by factors that influence the survival of the young. For many populations, it is density-independent factors such as climate that determine the survival of the young, and thus climate has a determining influence in population dynamics (Stenseth et al. 2002). The determination of inter-annual variation in climate as a driving mechanism for population cycles is not easy however, owing to lags and buffers and the difficulty in establishing cause and effect between climate events and population responses. However, the link between climate and population cycles is understood for some species. For instance, White (1969) hypothesized that suboptimal climatic conditions result in plant ‘stress’ which leads to an increase in the concentrations of mobile nitrogen in leaves and nitrogen availability to herbivores. For defoliating insects, the increased availability of nutritious forage results in increased growth, accelerated development, and increased survivorship and fecundity of individuals. Therefore, insect populations can quickly increase in abundance during periods of plant stress. To demonstrate this relationship, White (1969) calculated a ‘stress index’ that combined temperature and precipitation records to identify periods of climate that caused stress in native plants. He compared climatic stress to recorded outbreaks of the psyllid

\[ A \text{ version of this chapter will be submitted for publication.} \]
*Cardiaspina densitexta* which live on *Eucalyptus fasciculosa* in southern Australia and found that the combination of wet winters and dry summers produced conditions of prolonged stress for the trees, which increased the amount of nitrogenous food available for the psyllids and greatly aided their reproductive success.

**The Western Hemlock Looper**

The western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst) is a defoliating insect that exhibits population cycles in mature forests of western North America (Otvos and Vanderveen 1993). Western hemlock looper is found in areas corresponding to the range of its preferred host western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), which extends from northern California to southeastern Alaska (Duncan 2006), although the insect is less prevalent north of 56°N. Western hemlock looper is one of the most destructive defoliators in British Columbia (Ministry of Forests and Range 1995). During outbreaks they will feed on almost any foliage, including broad-leaved deciduous trees and shrubs (Jardine 1969). Western hemlock looper outbreaks usually last 2 to 4 years before collapsing. Populations of western hemlock looper cannot be maintained at outbreak levels and several density-dependent and density-independent factors contribute to the collapse. Often populations are limited by parasitism by wasps or an epizootic of a nucleopolyhedrosis virus (Edmonds et al. 1999). In severe outbreaks, foliage may become limiting and larval starvation becomes a factor in terminating outbreaks (Koot 1994). Density-independent factors, such as heavier than normal precipitation and cooler weather, especially during the adult flight and egg hatching periods, may also precede a population collapse (Koot 1994).
Western Hemlock Looper Outbreak Records

Insect outbreaks have been documented in British Columbia for almost 100 years. The Forest Insect and Disease Survey (FIDS) section of the Pacific Forestry Centre (PFC) in Victoria, BC and its predecessor agencies have conducted ground surveys since 1909 and routine aerial surveys since the 1960s. Data on western hemlock looper outbreaks were compiled by Parfett et al. (1995) from 1911 to 1995. They used a geographical information system to compile cartographic historical data and illustrate the spatial and temporal patterns of outbreaks in the province. Aerial overviews were discontinued by the Canadian Forest Service in 1995. Since then, the B.C. Ministry of Forests and Range has conducted annual aerial overview surveys of the majority of forested land in the province. These surveys yield comparable data to the FIDS monitoring surveys. Details of the most recent outbreak (2000-2003) in the Greater Vancouver Regional District, including size and severity, were also documented by PheroTech Inc. (Burleigh and Gustafsson 2003).

Noncontiguous and spatially independent outbreaks of western hemlock looper tend to develop over a wide area of the province during the same years (Parfett et al. 1995). Outbreaks have occurred someplace within the province during 39 of the 84 years between 1911 and 1995, with outbreaks in the interior, south of 56° latitude, within the Interior Cedar Hemlock (ICH) biogeoclimatic zone occurring most frequently, and outbreaks in coastal forests, within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Turnquist 1991) less frequently. Outbreaks in the interior of BC cover a much larger area than outbreaks that occur along the coast (Parfett et al. 1995).
Little is known about the factors that facilitate western hemlock looper population growth and ultimately drive populations to outbreak levels. No study has yet demonstrated a link between inter-annual climate variation and western hemlock looper populations within coastal forests. We hypothesize that climate has a significant influence on the timing of historic western hemlock looper outbreaks. In this study, instrumental temperature and precipitation records are combined to develop a moisture stress index similar to that used by White (1969) and used to examine correlations among impacts of monthly, seasonal, and annual climate variation on western hemlock looper outbreaks that have occurred along the south coast and lower mainland of British Columbia during the 20th century.

The objective of this study is to identify the specific climate conditions that contribute to outbreaks of western hemlock looper in coastal forests and to consider the impacts of predicted climate change on the timing and frequency of future outbreaks.

2.2 METHODS

Study Area

The study area includes the south coast of mainland British Columbia, extending from Hope to the head of Jervis Inlet on the Sunshine Coast (Figure 2.1). In this area, the prime habitat for the western hemlock looper includes forests dominated by western hemlock in the submontane (elevation < 900 metres above sea level) variants of the Very Wet to Moist Maritime Coastal Western Hemlock biogeoclimatic subzones (Parfett 1995). In these forests, western hemlock (Tsuga heterophylla (Raf.) Sarg) is the most common tree species but other frequently occurring species are western redcedar (Thuja plicata Donn ex D. Don), Douglas-fir (Pseudotsuga menziesii var. menziesii (Mirb.) Franco) and
amabilis fir (*Abies amabilis* Dougl. ex Forbs) (Klinka et al. 1991). The understory of these stands typically is characterized by a well-developed shrub layer of ericaceous species such as Alaskan blueberry (*Vaccinium alaskaense* Howell) red huckleberry (*V. parvifolium* Smith) and salal (*Gaultheria shallon* Pursh); ferns, and a well-developed moss layer (Acres et al. 1999). There is also a pervasive layer of advance regeneration of western hemlock and, to a lesser extent, amabilis fir.

![Map showing the location of defoliation by western hemlock looper along the south coast of British Columbia, 1911-present, adapted from Parfatt et al. (1995) and aerial overview surveys from the BC Ministry of Forests and Range. Recurrent defoliations have been most common in the Coquitlam River watershed (1927-1929, 1944-1947, 1969-1973 and 2000-2003). Meteorological stations used in calculating the moisture stress index are shown.]

**Figure 2.1** Location of defoliation by western hemlock looper along the south coast of British Columbia, 1911-present adapted from Parfatt et al. (1995) and aerial overview surveys from the BC Ministry of Forests and Range. Recurrent defoliations have been most common in the Coquitlam River watershed (1927-1929, 1944-1947, 1969-1973 and 2000-2003). Meteorological stations used in calculating the moisture stress index are shown.
The study area lies along the south coast of British Columbia, within the Marine West-Coast Climate (Csb) of the Köppen classification in the mid-latitude zone where upper air westerlies predominate throughout the year (Geiger and Pohl 1953). Largely influenced by the positions of the Pacific anticyclone and the Aleutian low, the position of the jet stream shifts latitudinally so that high- and low-pressure synoptic weather patterns alternate between the seasons along the south coast of BC. From October to April, the area is under the influence of low pressure systems 66% of the time, and under high pressure systems 29% of the time. These patterns reverse throughout the growing season (May-September), with high pressure systems dominating 50% of the time, and low pressure systems only 39% percent (Maunder 1968).

Annual precipitation totals for the area are large, exceeding 1700 mm, yet there are strong seasonal variations in precipitation patterns due to the alternations in synoptic weather (Figure 2.2). Only 24% (424 mm at Agassiz, BC - 49.25 N 121.77 W, 1895-2004) of the annual precipitation falls during the five-month growing season, leading to moisture deficits in the summer months as evapotranspiration exceeds precipitation. In soils without large water-holding capacities, the soil water balance is in deficit and plants often experience water deficiency (Bertrand et al. 1991).
At lower elevations, the annual temperature range in the area is small, with winter temperatures rarely below freezing. The average January temperature at Agassiz is 1.5 °C while the average July temperature is 17.9 °C (Environment Canada 2005). Less than 5% of total annual precipitation falls as snow. A moderate temperature regime is due to the location near the coast and the moderating effect of the ocean, despite the relatively high latitude of 49°N.
Climate Data

Agassiz Temperature and Precipitation Records

The Climate Monitoring and Data Interpretation Division of the Climate Research Branch of the Meteorological Service of Canada developed an Adjusted Historical Canadian Climate Data (AHCCD) record for 210 stations throughout Canada with long-term climate records (Environment Canada 2005). Sudden steps and longer-term trends have been removed to create homogenized data sets. Steps in climate data can be due to station relocation or instrument changes whereas longer-term trends can be due to nearby urbanization or changes in vegetation surrounding the station. The AHCCD was specifically developed for research of climate variation and change.

Climate-outbreak relations were examined using the AHCCD from Agassiz, BC. It is the longest climate record in the south coast region, with nearly continuous monthly temperature and precipitation records from 1895-2005. In the Agassiz record, mean monthly data were missing from less than 1% of the total record and these missing values were scattered through the time series, except 1928 that had missing precipitation values for 10 of 12 months. Missing values were estimated using homogenized temperature and/or rehabilitated precipitation data from stations at Abbotsford, Hope, Squamish and Vancouver located within 100 km of Agassiz (Figure 2.1). These neighbouring climate records were highly correlated with the Agassiz record and regression models were developed to estimate the missing values.
Only the Abbotsford station had a relatively complete homogenized temperature record, yet it was shorter than the overall Agassiz record (Table 2.1). However, missing temperature values in the Agassiz record were confined to the latter part of the 20th century in the time period for which the two records were coincident. Correlation between the two records for 1944 to 2003 was very strong ($R^2=0.95$, $p<0.05$). Missing precipitation data were more prevalent in the Agassiz record. The Hope, Vancouver and Squamish precipitation records were strongly correlated with the Agassiz precipitation record ($R^2 > 0.62$ for all stations, Table 2.2). A regression model for each of the three stations was developed and these were averaged to estimate the missing Agassiz precipitation values.

**Table 2.1** Climate stations with homogenized temperature and/or precipitation data in the south coastal (Lower Mainland) region of British Columbia.

<table>
<thead>
<tr>
<th>Station</th>
<th>Latitude / Longitude</th>
<th>Elevation (m)</th>
<th>Recorded Variable</th>
<th>Time Span</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abbotsford A</td>
<td>49.03 N 122.37 W</td>
<td>58</td>
<td>Temperature</td>
<td>1944-2005</td>
</tr>
<tr>
<td>Agassiz CDA</td>
<td>49.25 N 121.77 W</td>
<td>15</td>
<td>Temperature/Precipitation</td>
<td>1895-2004</td>
</tr>
<tr>
<td>Hope A</td>
<td>49.37 N 121.48 W</td>
<td>39</td>
<td>Precipitation</td>
<td>1910-1995</td>
</tr>
<tr>
<td>Squamish</td>
<td>49.70 N 123.13 W</td>
<td>31</td>
<td>Precipitation</td>
<td>1914-2004</td>
</tr>
<tr>
<td>Vancouver</td>
<td>49.18 N 123.17 W</td>
<td>3</td>
<td>Precipitation</td>
<td>1896-1995</td>
</tr>
<tr>
<td>INT'L A</td>
<td>123.17 W</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2: Correlation matrix of stations used in estimation of missing monthly precipitation data for the Agassiz record. Values indicate correlation ($R^2$) over the longest coincident time period (1929-1980) shared by all four stations for total annual precipitation.

<table>
<thead>
<tr>
<th></th>
<th>Hope</th>
<th>Squamish</th>
<th>Vancouver</th>
<th>Agassiz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hope</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Squamish</td>
<td>0.62</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vancouver</td>
<td>0.69</td>
<td>0.85</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Agassiz</td>
<td>0.70</td>
<td>0.72</td>
<td>0.80</td>
<td>1</td>
</tr>
</tbody>
</table>

Moisture Stress Index

Mean monthly temperatures represent the average of mean daily temperatures ($°C$) for each calendar month. Monthly precipitation is the cumulative amount of precipitation (mm) for each calendar month. To assess the combined effect of temperature and precipitation, deviations of both variables from their 1895-2005 means were calculated and converted to unitless Z-scores (standard deviations from a mean of zero) then combined in a “moisture stress index” so that positive deviations in temperature and negative deviations in precipitation would result in a higher degree of “moisture stress” (White 1969). The moisture stress index was calculated as:

$$\text{Moisture Stress Index} = \left(\frac{T_a - \bar{T}}{\sigma_T}\right) - \left(\frac{P_a - \bar{P}}{\sigma_P}\right)$$  \hspace{1cm} (Equation 2.1)

where, $T_a$ is recorded temperature,

$\bar{T}$ is the average temperature from 1895-2004,

$\sigma_T$ is the standard deviation for temperature from 1895-2004,

$P_a$ is recorded precipitation,

$\bar{P}$ is the average precipitation from 1895-2004, and

$\sigma_P$ is the standard deviation for precipitation from 1895-2004.
Higher than normal temperature and lower than normal precipitation combine to yield high moisture stress index values. Conversely, cool, wet weather yields low moisture stress index values.

Seasonal Data
To test for seasonal and annual effects of climate on outbreaks, Z-scores of monthly temperature, precipitation and the moisture stress index were used to represent several different time periods. These time periods included: annual records compiled for each calendar year; a five-month period from May to September representing the growing season, and the month of June which coincides with the most vulnerable larval stage of the western hemlock looper (Mason and Torgersen 1987).

Test for Climate Influence on Outbreaks
Superposed epoch analysis (SEA, Grissino-Mayer 2001) was used to test the null hypothesis that there was no relationship between climate (temperature, precipitation and moisture stress) and the onset of western hemlock looper outbreaks in coastal BC from 1911 to 2003. There have been seven outbreaks recorded in the south coast and lower mainland of BC during this time period, varying in size, severity and duration. Outbreaks of western hemlock looper have occurred along the south coast of BC in 1911-1914, 1927-1929, 1944-1947, 1958-1959, 1969-1973, 1987 and 2000-2003. The first recorded year of each outbreak was termed the ‘event’ year; outbreaks were not differentiated based on duration or severity. SEA tests for differences between event and non-event years by calculating mean climate conditions for a 6-year window including the event
year of each outbreak and five years preceding each outbreak. A 5-year window of antecedent climatic conditions was tested to quantify potential lags between climatic conditions and a biological response. SEA uses 1000 Monte Carlo simulations to calculate 95% confidence intervals and evaluate the significance of climate during events (Mooney and Duval 1993). Tests were conducted using temperature, precipitation and the moisture stress index at the annual, growing season and monthly time scales. For all statistical tests, significance was at the 0.05 level.

2.3 RESULTS

Climate Variation at Agassiz, BC

Climatic conditions recorded by the Agassiz meteorological station have displayed a marked change over the 1895 to 2004 study period that has resulted in an increasing moisture stress index over time. The average annual temperature was 10.0 ± 0.8 °C, ranging from 8.2 °C in 1909 to 11.8 °C in 1958, the coolest and warmest years in the record (Figure 2.3). Consistent with many meteorological stations in British Columbia (BC Ministry of Water, Land and Air Protection 2000), the average annual temperatures show a significantly increasing trend through time (R²=0.28, p<0.001). Average annual temperature at Agassiz has increased 1.4°C from 1895 to 2004. Similarly, the average temperature during the growing season has increased by 1.4°C during this time period (R²=0.29, p<0.01). The average temperature during the month of June has also increased by 1.4°C, yet not significantly so (R²=0.11, p=0.16). Average annual precipitation at Agassiz was 1727 ± 303 mm and ranged from a low of 827 mm in 1929, to a high of 2425 mm in 1932 (Figure 2.3). There was no directional trend in precipitation during the
recorded period. The annual moisture stress index ranged from a high of 2.70 in 1942 to a low of −3.22 in 1921 (Figure 2.3). By definition, the mean moisture stress index over the entire time period is zero. Owing to the increasing trend in temperature, the annual moisture stress index also increased significantly during the recorded time period, albeit modestly (R²=0.06, p<0.01) During the growing season (May to September inclusive), the calculated stress index ranged from a high of 4.15 in 1958 (an outbreak year) to a low of −3.60 in 1921. The June moisture stress index also peaked in 1958 at 3.83 (Figure 2.3).

**Climate Influence on Outbreaks.**

Historical outbreaks of western hemlock looper were associated with significant moisture stress occurring at annual, seasonal and monthly temporal scales.

**Annual**

At the annual scale, outbreaks occurred during years of significant moisture stress (Figure 2.3). Of the 10 years with the highest annual moisture stress indices (2.10 to 2.70), four years coincided with the onset of western hemlock looper outbreaks in 1944, 1958, 1987 and 2000 (stress indices = 2.16, 2.36, 2.63 and 2.10, respectively; Figure 2.3). Annual temperature was above-average and annual precipitation was below-average, although only precipitation was statistically significant (Figure 2.4).
Figure 2.3 Annual, growing season (May to September) and June temperature, precipitation and moisture stress index at Agassiz, BC from 1895-2004. Dots mark significant climate conditions corresponding to the onset of outbreaks of western hemlock looper. X’s mark significant climate conditions corresponding to two years prior to the onset of outbreaks.

Figure 2.4 Superposed Epoch Analysis (SEA) for annual, growing season (May to September) and June temperature, precipitation and moisture stress index at Agassiz, BC from 1895-2004 for the onset of western hemlock looper outbreaks (year ‘0’) and five years antecedent. Dots mark significant climate conditions corresponding to the onset of outbreak years of western hemlock looper, or years antecedent to outbreak years.
Departure from Stress Index

Departure from Precipitation

Departure from Mean Temperature

Annual

Growing Season

June
Growing Season - May to September

There were statistically significant high moisture stress indices two years prior to the onset of western hemlock looper outbreaks (Figure 2.3 and 2.4). In fact, three of the 10 warmest and driest growing seasons occurred two years prior to western hemlock looper outbreaks (Figure 2.3). The moisture stress index calculated for the five-month growing season (May to September) was above average for actual outbreak years, although it was not statistically significant.

June

At the monthly scale, June climate had the strongest association with the onset of western hemlock looper outbreaks. Significant below-average precipitation and above-average temperature contributed to significant moisture stress at the onset of outbreaks (Figures 2.3 and 2.4). June temperature was 16.8 ± 1.3°C (n = 7) during the first year of western hemlock looper outbreaks compared to 15.6 ± 1.2 °C (n = 110) for the entire record from 1895 to 2004. June precipitation averaged 55.3 ± 35.1 mm (n = 7) during the first year of recorded western hemlock looper outbreaks compared to 95.4 ± 53.9 mm (n = 110) for the entire record. Four of the seven recorded outbreaks of western hemlock looper occurred in years with extremely high June moisture stress: 1927 (June moisture stress index of 2.32), 1958 (3.84 – the highest on record), 1969 (2.86), and 1987 (1.98). June climate prior to the outbreaks was not significantly different from average conditions (Figure 2.4).
2.4 DISCUSSION

Combined, above-average temperature and below-average precipitation facilitate outbreaks of western hemlock looper. Western hemlock looper outbreaks were initiated during four of the warmest and driest years between 1895 and 2004. June conditions were particularly important at the onset of outbreaks as were climate conditions two years prior to the visual detection of severely defoliated patches of forest.

Drought can have both direct and indirect positive impacts on western hemlock looper population increases. The effects of warm dry weather on western hemlock looper larval growth and survival are strongest during the most vulnerable life stage, the early instar larvae (Mason and Torgersen 1987). The larvae of western hemlock looper emerge from their eggs in late May. Thus, warm, dry conditions during June increase the larvae’s chance of survival by increasing their metabolic rate and allowing larvae to reach pupation relatively quickly. This allows more larvae to reach reproductive capability as adult moths in late August and populations increase rapidly. Indirectly, western hemlock trees may become more vulnerable to defoliators during drought (Waring and Pitman 1985). The host trees may have weakened defensive systems, since the production of tree defensive compounds decreases when the tree is under stress due to the reallocation of resources to the re-growth of lost foliage (Waring and Pitman 1985). Furthermore, needles produced in warm, dry years are smaller and contain more stored carbohydrates. Therefore, during warm, dry years, larvae are more plentiful and have a more nutritious food source.
During several of the recorded outbreaks however, population abundance likely began to increase as early as two years before the effects of defoliation were observed and noted in the historical records. Most insects with cyclic populations can increase in abundance quickly during favourable conditions. However *Lambdina* species have a lower average fecundity than most species with cyclic populations and may require multiple generations to produce dramatic population growth (Nothnagle and Schultz 1987). Therefore, as noted above, under the influence of extremely favourable climatic conditions during their most vulnerable life stage, populations of western hemlock looper can increase rapidly; yet, it appears that another mechanism by which population growth may occur is when climatic conditions are favourable over the *entire* growing season, but are not exceptionally warm and dry in June. Under these conditions, larval survivorship may be high enough to allow populations to continue to grow in following generations yet at rates lower than in years with exceptionally warm and dry June’s. Within two years, or two generations of western hemlock looper, populations will have steadily grown from their endemic abundance to outbreak abundance. It is probable that several recorded outbreaks of western hemlock looper on the coast were driven by climate conditions that allowed populations to grow exponentially for a couple of generations before notable tree defoliation was observed. The western hemlock looper outbreaks that were first observed in 2000 and 1944 are most likely examples; in both cases, an extremely warm and dry growing season was recorded two years prior to the outbreak (growing season moisture stress index of 3.47 in 1998 – the second highest on record, and 2.43 in 1942).
Pheromone trap data from the Coquitlam River watershed, the site of the 2000-2003 outbreak, corroborate that the climatic trigger for this outbreak may have been the warm and dry growing season of 1998 (Table 2.3). Abundance of western hemlock looper was low during the late 1990s and reached outbreak abundance during 2000. By August 2000, the outbreak had resulted in defoliation of 448 ha of western hemlock-dominated forest (Burleigh and Gustafsson 2003). During this particular outbreak, climate was warm and dry during the growing season of 1998, but not particularly warm and dry the year the outbreak was recorded. The ten-fold increase in the number of moths per trap between 1998 and 2000 was most likely driven by the warm dry growing season in 1998.

Table 2.3 Average number of western hemlock looper moths caught in pheromone baited traps within the Coquitlam River watershed from 1997-2003 (Burleigh and Gustafsson 2003). June and Growing Season Stress Indices are given for the same time period.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of traps</th>
<th>Number of moths per trap (mean±sd)</th>
<th>June Stress Index</th>
<th>Growing Season Stress Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>41</td>
<td>120 ± 155</td>
<td>-1.012</td>
<td>0.433</td>
</tr>
<tr>
<td>1998</td>
<td>50</td>
<td>284 ± 211</td>
<td>1.312</td>
<td>3.119</td>
</tr>
<tr>
<td>1999</td>
<td>44</td>
<td>380 ± 377</td>
<td>-1.255</td>
<td>-0.593</td>
</tr>
<tr>
<td>2000</td>
<td>45</td>
<td>3054± 3912</td>
<td>0.574</td>
<td>-0.601</td>
</tr>
<tr>
<td>2001</td>
<td>45</td>
<td>2801 ± 3167</td>
<td>-0.937</td>
<td>0.483</td>
</tr>
<tr>
<td>2002</td>
<td>45</td>
<td>1512 ± 1900</td>
<td>0.778</td>
<td>1.089</td>
</tr>
</tbody>
</table>

Therefore, outbreaks of the western hemlock looper are at least partially driven by density-independent factors, specifically low rainfall and high temperatures during the growing season. These drought conditions favour faster development of the poikilothermic western hemlock looper larvae and improve the nutritional quality of their food source. If conditions are favourable during the most vulnerable life-stage of the larval looper (i.e. June), then populations may increase dramatically in one year.
However, if the warm and dry conditions are distributed over the entire larval, pupal and moth stages, then a two-year lag occurs between the drought year and the observed defoliation caused by the western hemlock looper outbreaks. This reflects the time necessary for western hemlock looper populations to reach abundances that cause visible defoliation of canopy trees.

Most western hemlock looper outbreaks last only two to four years and collapse due to density-dependent factors such as parasitism, predation or disease (Koot 1994). Climate conditions following outbreaks likely have little influence on populations of western hemlock looper as the density of parasites, predators and diseases lag behind those of looper populations and will remain high several years following each outbreak (Burleigh and Gustafsson 2003). Thus, while warm and dry conditions occur at variable intervals in coastal British Columbia, not every year of above-average moisture stress initiates a new western hemlock looper outbreak, particularly when drought recurs soon after an outbreak. For example, the highest moisture-stress value for June was in 1958, which initiated the 1958-9 outbreak. The second highest moisture stress value was for June was 1961, only 3 years after the 1958-9 outbreak and no new outbreak was observed. Another high moisture stress index that did not result in increased looper populations was seen in 2005, 2 years after the 2000-2003 Coquitlam outbreak (Figure 2.3).

Given that climate is one factor contributing to outbreaks, it is important to understand how the western hemlock looper disturbance regime differs between climate regions. There have been a number of recent studies that have noted how other insect populations,
and the resulting defoliation patterns, vary based on differences regional climate \textit{(i.e. Volney and Fleming 2000)}, however none have involved the western hemlock-looper. Outbreak patterns are thought to differ between the dry, inland forests \textit{(i.e. the Interior Cedar Hemlock biogeoclimatic zone)} and the wet coastal forests of British Columbia \textit{(i.e. the Coastal Western Hemlock biogeoclimatic zone)}, owing to differences in regional climate and the tree species composition of the forest. Regionally-specific information is becoming essential to ecologists as insect population dynamics are influenced by climate and could be altered by future climate changes linked to global warming and its associated large-scale climate change (Williams and Liebhold 2000).

There have been at least 15 recorded outbreaks during the past ninety years in BC, with the largest and most severe outbreaks located in the warmer and drier interior forests, south of 56°N latitude. On a regional scale, outbreaks in interior forests have been historically more frequent than outbreaks in coastal forests. Harris et al. (1982) estimated a mean periodicity of 8.8 years for outbreaks in the interior from five outbreaks at three sites, while Furniss and Carolin (1977) calculated a range of six to 11 years from data from six outbreaks in western North America. Borecky and Otvos (2001) suggest that interior western hemlock looper outbreaks are increasing in both size and intensity. For coastal forests, outbreaks have occurred somewhere in the region every 11 to 18 years. Coquitlam watershed has been the site of four of these outbreaks, 1927, 1944, 1969 and 2000 suggesting a watershed-level return interval of 17 to 31 years.
Edmonds et al. (1999) suggest that western hemlock looper outbreaks may be increasing in frequency and becoming more widespread than historically recorded outbreaks. The cutting of large-scale contiguous western hemlock-dominated forests during the 20th century reduced the area of late-successional forests that are considered most susceptible to western hemlock looper (Koot 1994). However, as second-growth stands develop, the area of mature hemlock forests is increasing and large-scale western hemlock looper outbreaks are predicted to become more frequent.

Most climate change models predict a warmer drier climate for coastal BC - for example, the Canadian Regional Climate Model (CRCM) from the Canadian Centre for Climate Modelling and Analysis (Plummer et al. 2006). Since these are the very conditions that have historically triggered outbreaks of western hemlock looper, it is possible that future outbreaks will increase in frequency on the coast. Therefore, with both the amount of vulnerable forest on the rise, and an increase in warm dry conditions, western hemlock looper outbreaks may become more frequent, and potentially more widespread, in coastal BC.
2.5 Literature Cited


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3.1 INTRODUCTION

In the contemporary view of vegetation dynamics, there is no assumption of long-term structural stability within ecosystems or a singular compositional endpoint to succession (Drury and Nesbit 1971). Instead, disturbances are assumed to continually act upon forest ecosystems, altering their structure and composition at a range of spatial and temporal scales. Therefore, a major objective of current research in forest ecology is to quantify natural disturbances and their effects on vegetation dynamics. Disturbance can be broadly described as a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985). Disturbances modify the physical environment by reducing live plant biomass (Reader et al. 1991) thereby increasing the level of resources to surviving plants (Canham and Marks 1985). Disturbances alter vegetation dynamics by influencing site availability, differential species availability or differential species performance (Glenn-Lewin and van der Maarel 1992).

The effect of a disturbance depends on its spatial extent, return time and magnitude (intensity or severity) (Glenn-Lewin and van der Maarel 1992). For example, at the landscape level, large, infrequent disturbances are important because they often become the dominant factor structuring an ecosystem and may create long-lasting ecological

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1 A version of this chapter will be submitted for publication.
legacies (Turner and Dale 1998, Franklin et al. 2002). Most disturbances do not affect the entire landscape equally, instead their patchy spatial distribution and varying severities create diverse landscapes wherein patches of recently disturbed vegetation are nested within a larger, less disturbed matrix (Allen 1987). At the patch-scale, the forest undergoes changes in species composition and structural development as they age. The resulting pattern of patches in various successional stages has been termed a "shifting mosaic" (Bormann and Likens 1979). Within a patch, fine-scale disturbances by wind, insects and pathogens drive gap-phase processes (Franklin et al. 2002). These disturbances influence stand structure, promoting many attributes of old-growth stands, such as a broad range in trees sizes and ages, horizontal and vertical diversity of the canopy, presence of snags and coarse woody debris, and a well-developed understory plant community (Parker and Peet 1984, Franklin et al. 1981, Franklin et al. 2002). Therefore, disturbances increase heterogeneity at a range of spatial scales from gaps, to patches, to landscapes (Romme 1982, Turner 1987, Turner and Romme 1994).

The effects that natural disturbances have on communities depend on the disturbance type and regime (White and Pickett 1985, Veblen et al. 1994). Native insects are an important agent of disturbance and an integral component of the disturbance regime of many forest ecosystems. Insects do not act as a uniform disturbance agent and the severity of disturbance often varies among forest stands (Stone and Wolfe 1996). Insects can influence composition and structure of forest stands by inducing species-specific mortality (Eveden 1940, Romme et al. 1986, Knight 1987, Alfaro et al. 1982, Alfaro et al. 1999). Often, this has the effect of decreasing the dominance of the host species and
increasing species diversity (Wohlgemuth et al. 2001). Disturbance by insects can increase the likelihood of other types of disturbance to occur, such as secondary insect attacks or fire (Rykiel et al. 1988, Stocks 1987). Thus, interacting and combined effects of different disturbance agents contribute to forest complexity at a range of scales, including stands that increasingly vary in structure and composition over time (Veblen et al. 1994, Peet 2000, Bebi et al. 2001).

This study quantifies the impacts of a western hemlock looper defoliation on the structure and composition of the coastal forests of British Columbia. My objective was to compare the effects of three different levels of disturbance severity on stands with comparable tree composition, density, age and stand structure. I hypothesized that defoliation from western hemlock looper would slow the growth of canopy western hemlocks at sites with low levels of defoliation and lead to the death of canopy western hemlocks at sites with more severe defoliation, as documented in the interior forests of British Columbia (Alfaro et al. 1999). I also hypothesized that the degree of canopy openness would increase with disturbance severity resulting in increased plant cover and species diversity.

3.2 METHODS

Study Area

An outbreak of western hemlock looper (Lambdina fiscellaria lugubrosa Hulst), occurred from 2000 to 2003 in several spatially discreet locations along the south coast of mainland British Columbia. The largest contiguous patch of defoliated forest (1 500 ha) was located within the Coquitlam River watershed, 40 km northeast of the city of
Vancouver (Burleigh and Gustafsson 2003). The affected forest is classified as the submontane (elevation < 900 metres above sea level) variant of the Very Wet to Moist Maritime Coastal Western Hemlock biogeoclimatic subzones (Parfett 1995). In these forests, western hemlock (*Tsuga heterophylla* (Raf.) Sarg) is the most common tree species but other frequently occurring species are western redcedar (*Thuja plicata* Donn ex D. Don), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) and amabilis fir (*Abies amabilis* Dougla. ex Forbs) (Klinka et al. 1991). The understory of these stands typically is characterized by a well-developed shrub layer of ericaceous species such as Alaskan blueberry (*Vaccinium alaskaense* Howell) red huckleberry (*V. parvifolium* Smith) and salal (*Gaultheria shallon* Pursh), ferns, and a well-developed moss layer (Acres et al. 1999). There is also a pervasive layer of advance regeneration of western hemlock and, to a lesser extent, amabilis fir.

**Research Design**

In June 2003, I established plots at 15 study sites in the Coquitlam River watershed in areas that were severely (>65% visible defoliation, n=5), moderately (26-65%, n=5), or lightly (5-25%, n=5) defoliated during 2000-2003 by an outbreak of western hemlock looper. Severity of the outbreaks was classified based on annual aerial defoliation surveys of the watersheds conducted in August 2002 and verified by field observations (Figure 3.1) (Burleigh and Gustafsson 2003). The plots were arranged in a nested design to be able to measure various forest attributes at appropriate spatial scales. Each site contained three canopy tree plots located 50 m apart in an equilateral triangle design. Depending on the size of the defoliated patch, the circular ‘canopy tree’ subplots were of either 100 m²
(four sites), or 200 m² (eleven sites) in size, resulting in total canopy tree sample areas of 300 or 600 m² per site. Each canopy plot contained three 2 m² understory vegetation plots located 120° from each other at randomly selected distances from the canopy plot centre (Figure 3.2). The azimuth for the first vegetation plot was randomly located.

Figure 3.1 Fifteen study sites in the Coquitlam River watershed located in five lightly (light grey), five moderately (grey) and five severely (dark grey) defoliated sites.
Figure 3.2 Layout of nested plots for measuring canopy trees understory vegetation, and understory light environment showing the radii of three two m² vegetation plots within each 200 m² canopy plots placed 50 m apart. Hemispherical photographs were taken at the centre of each canopy plot (*).

Within the canopy tree plots, the species of all trees and snags were recorded. Each tree and snag was assigned a canopy position class of either: dominant, co-dominant, intermediate or suppressed (Smith 1986). Each snag was assigned a decay class based on a modified version of the classification system developed by Thomas et al. (1979) that took into account a lack of foliage due to defoliation (Table 3.1).

Table 3.1 Snag decay classes based on Thomas et al. (1979).

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Tree is recently dead. Most fine branches and some needles still present. Top is intact. Bark is intact.</td>
</tr>
<tr>
<td>II</td>
<td>Most of the fine branches have dropped. More than 50% of the coarse branches are left. Top is intact. Bark may begin to loosen.</td>
</tr>
<tr>
<td>III</td>
<td>Fewer than 50% of the coarse branches are left. Top is intact. Bark may or may not have sloughed off.</td>
</tr>
<tr>
<td>IV</td>
<td>No coarse branches remain. Top is broken. Bark may or may not have sloughed off. Height at least 6 m.</td>
</tr>
<tr>
<td>V</td>
<td>No coarse branches remain. Top repeatedly broken. Bark may or may not have sloughed off. Height less than 6 m.</td>
</tr>
</tbody>
</table>
Radial Growth

Dendrochronological techniques were used to quantify radial growth suppression owing to western hemlock looper defoliation, determine year of death of snags, and reconstruct the pre-outbreak canopy (dominant or co-dominant) composition of living trees. All live hemlock trees or recently killed hemlock snags in decay class I in the dominant and co-dominant height classes were cored with an increment borer in the summer of 2003. If there were fewer than 20 live hemlock canopy trees or recently killed canopy hemlock snags within a site, then individuals immediately surrounding the canopy tree plots were also cored until a minimum of 20 individuals were sampled. Multiple cores per tree were taken to intercept the pith. Tree cores were taken approximately 30 cm from the ground to estimate tree ages and quantify defoliation impacts on growth. Cores from higher on the trunk would not provide reliable estimates of total radial growth loss due to the compensating effect of faster recovery from insect defoliation and smaller volume of wood in the upper stem (Swetnam et al. 1985). Diameter at core height, diameter at breast height, height of the core, proximity to pith and tree health measured as percentage of live crown were recorded for each cored tree.

Cores were air-dried and mounted in wooden supports (Stokes and Smiley 1968). They were sanded using a belt sander using successively finer grits (100, 220, 320 and 400) until the surface was smooth enough to display ring boundaries, micro-rings and other diagnostic characteristics. Tree-ring series were visually crossdated to identify unusually narrow “marker” rings (Yamaguchi 1991). Crossdating is the comparison of ring-width patterns of different trees to ensure that accurate calendar years are assigned to each ring (Douglas 1941). Because the width of any ring is partly controlled by regional growth-
limiting environmental factors that affect trees from the same area in the same way, synchronous variations in ring width occur within and between sites (Fritts 1976). Trees with large yearly fluctuations in ring-width are termed “sensitive”, whereas trees that do not show annual fluctuations related to a limiting factor are termed “complacent” (Swetnam et al. 1985).

Ring widths were measured to the nearest 0.001 mm using a sliding-stage Velmex micrometer interfaced with a computer. I used the program COFECHA to statistically crossdate each ring-width series to verify the visual crossdating of the cores (Holmes 1986). Statistical crossdating concurrently compares the ring-width patterns among many tree ring series so that missing rings or false rings can be identified. This is especially important in studies measuring the effect of defoliation on radial growth because of the above-average likelihood of missing rings due to the low growth rate of defoliated trees (Swetnam et al. 1985). Crossdating also allowed for the year of death for each snag to be determined. This is because the outermost ring in each series either represented the last year of radial growth for living trees (i.e. 2003) or the last year of radial growth before death for snags. Only recently dead snags were cored so that all cored snags had their bark attached and their outer rings were intact.

To represent annual growth rates, I used basal area increments (BAI) as it has been shown to be a better indicator of tree vigour than ring width (LeBlanc 1996). For each tree, basal area was calculated from measured ring-width series using the formula:

$$BA_t = \pi r_t^2$$  \hspace{1cm} (Equation 3.1)
where, \( r \) = the radius of the tree measured from the pith toward the bark and included the tree-ring of the year (t) being studied. This approach assumed symmetrical growth around the tree stem. Annual growth was measured as annual basal area increments (BAI\(_t\)) by subtracting the basal area of the previous year (t-1) from the basal area of the year being studied (t). I calculated annual BAI for five years preceding the outbreak (1995 to 1999) and the first three years of the outbreak (2000 to 2002) for each crossdated tree and snag within each site (total cored trees \( n=217 \)).

It was hypothesized that there would be no differences in BAI among sites in pre-outbreak years, as all sites were similar in age and structure and subjected to similar climatic conditions. Thus, differences among BAI of the five lightly-, the five moderately- and the five severely-defoliated sites during the western hemlock looper outbreak were assumed to represent differing levels of ‘lost’ growth due to varying levels of defoliation by western hemlock looper. Annual BAI for each cored tree were grouped by site to represent an average tree response per site and sites were grouped according to defoliation severity (\( n=5 \) severe, \( n=5 \) moderate, \( n=5 \) light) to allow comparison of growth responses to disturbances. I used a non-parametric, repeated-measures ANOVA to compare the annual growth during a three-year period prior to the outbreak (1995-1997) to the first three years of the outbreak (2000-2002). I used Tukey’s post-hoc test to test for pairwise multiple comparisons among sites and among years. For all statistical tests, \( \alpha = 0.05 \).
**Canopy Openness**

As a surrogate for determining light levels reaching the forest floor, I used hemispherical photography to quantify canopy openness for each site. Photos were taken 1 m above the ground at the centre of each canopy plot (n=3 per site, Figure 3.2). They were taken in August 2003, after the end of the hemlock looper pupal stage, when defoliation had achieved its maximum extent. Photographs were taken on an evenly overcast day with diffuse light, as direct sunlight is detrimental to canopy photographs due to the high intensity of sunlight which produces scattering effects through the canopy. Photographs of the canopy were formatted and analyzed using Gap Light Analyzer version 2.0 (Frazer et al. 1999).

I calculated the average canopy openness for each site by averaging the canopy openness of the three corner photos per site. I tested for differences among defoliation classes (light, moderate, severe) using a non-parametric one-way ANOVA. To determine significant pairwise multiple comparisons, I employed Tukey’s post-hoc test. For all statistical tests, $\alpha = 0.05$.

**Understory Vegetation and Ground Cover**

In the understory subplots, I visually estimated the cover (%) of all herbaceous, fern, shrub and tree species less than 1 m in height during July of 2003. Percent cover was estimated for all non-vascular plants and club mosses, grouped by life form (i.e. fungus, lichen, club moss and moss) as well as non-vegetated ground cover, including bare rock and duff. Total plant cover exceeded 100% in some plots due to overlapping layers of
vegetation. Vascular plant species richness was calculated for each vegetation plot as the number of tree, shrub, fern and herbaceous species in the plot. Vascular plant species diversity was calculated using the Shannon-Weiner Index of Diversity ($H^1$, Shannon and Weaver 1949):

$$H^1 = - \sum (p_i)(\ln p_i)$$

(Equation 3.2)

where, $p_i =$ relative cover of species $i$, expressed as a proportion. $H^1$ ranges from 0 in mono-specific communities to >7 in species-rich communities (DeJong 1975)

Each of the 15 sites contained nine vegetation plots for a total of 135 vegetation plots: three vegetation plots per canopy plot, and three canopy plots per site. Therefore, a nested ANOVA was used in all vegetation analyses to adjust for potential differences in variation between understory vegetation plots located within different canopy plots at the same site. Thus, differences in total cover, vascular plant species richness and vascular species diversity were tested among the three levels of defoliation severity using nested ANOVA. Tukey’s method for post-hoc assessments of significant variables was used.

3.3 RESULTS

Forest Structure and Composition

In 2003, the density of live trees and snags was relatively consistent among sites. The five lightly-defoliated sites had a mean live tree density of $520 \pm 88$ trees/ha and a mean snag density of $153 \pm 87$ snags/ha. Of the 242 sampled trees and snags, 173 (71.5%) were living. At moderately-defoliated sites, mean densities were $473 \pm 116$ trees/ha and $180 \pm 165$ snags/ha. The proportion of live trees was 62.4% (123 of 197 sample trees).
Severely-defoliated sites had the lowest mean living tree density of 407±310 trees/ha and the highest average snag density of 400±244 snags/ha. Only 22.4% (39 of 174 sample trees) were alive (Figure 3.3). Basal area did not differ significantly between sites (F=0.865, p=0.45). Lightly-defoliated sites had a mean basal area of 87.7±9.6 m²/ha, moderately-defoliated sites had a mean basal area of 81.3±26.8 m²/ha, and severely-defoliated sites had a mean basal area of 100.5±29.2 m²/ha.

Recent snags, belonging to decay class I, represented 72.2% of all snags (n=122) in severely-defoliated sites, 55.4% of all snags (n=74) in moderately-defoliated sites and 37.7% of all snags (n=69) in lightly-defoliated sites (Figure 3.4). Most Class I snags were western hemlock (94.5%, 100.0% and 61.1% in severely-, moderately- and lightly-defoliated sites, respectively).

In terms of species composition, all sites were dominated by western hemlock, although lightly-defoliated sites had the lowest proportion of live western hemlock (67.4%, 120 of 178 trees) compared to moderately defoliated sites (86.2%, 106 of 123 trees) and severely-defoliated sites (90.6%, 48 of 53 trees). Western redcedar was present at seven of the 15 sites. Together, the lightly-defoliated sites had highest proportion of living western redcedar (21.9%, 39 live trees) compared to only five western redcedar at moderately defoliated sites (4.7%) and three at severely-defoliated sites (5.7%). Amabilis fir was present at 5 of 15 sites, Douglas-fir at 3 of 15, and bigleaf maple at 2 of 15.
Figure 3.3 Diameter distribution of all trees (light) and snags (dark) within all lightly, moderately and severely defoliated sites. Note that the actual area of sampled plots differed among defoliation severity classes (light: 3 000 m$^2$, moderate: 2 700 m$^2$, severe: 2100 m$^2$) making direct comparison of the raw number of trees per diameter class difficult.
Figure 3.4 Snag distribution by decay class within all lightly, moderately and severely defoliated sites. Decay classes are described in Table 3.1.

Stand age was not significantly different among defoliation classes (F=0.786, p=0.459).

Canopy trees in the lightly-defoliated stands had a mean age at core height (30 cm above ground) of 70.9±10.0 years (range = 57-90, n = 25), moderately-defoliated stands averaged 78.9±24.7 years (range= 46-136, n=28), and severely-defoliated stands 79.4±29.0 years (range= 59-171, n=26).

**Basal Area Increments and Tree Mortality**

A total of 271 trees were cored and crossdated using COFECHA to build plot-level chronologies (Table 3.2). Defoliation had a significant negative impact on tree growth
rates (Table 3.3, Figure 3.5, Figure 3.6). Prior to the defoliation, average annual BAI per tree did not differ significantly among the three defoliation levels, except during 1997 and 1998. During these two years, basal area increment was significantly greater at the moderately-defoliated sites relative to those that became lightly and severely defoliated (Figure 3.5, Figure 3.6). In 2000, the first year of visible defoliation at the site level, average BAI per tree did not differ significantly among the three defoliation levels. In 2001 and 2002 average BAI per tree differed significantly among defoliation levels. Severely-defoliated sites had significantly smaller average annual BAI and lightly-defoliated sites had significantly greater average annual BAI relative to moderately-defoliated sites (Table 3.3, Figure 3.5, Figure 3.6).

Table 3.2 COFECHA output for chronologies of canopy western hemlock trees for five lightly (L1-5), five moderately (M1-5) and five severely defoliated (S1-5) sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Crossdated (N)</th>
<th>Series Length (years)</th>
<th>Correlation</th>
<th>Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>L1</td>
<td>17</td>
<td>65</td>
<td>0.412</td>
<td>0.231</td>
</tr>
<tr>
<td>L2</td>
<td>16</td>
<td>74</td>
<td>0.428</td>
<td>0.266</td>
</tr>
<tr>
<td>L3</td>
<td>12</td>
<td>96</td>
<td>0.324</td>
<td>0.263</td>
</tr>
<tr>
<td>L4</td>
<td>14</td>
<td>82</td>
<td>0.342</td>
<td>0.242</td>
</tr>
<tr>
<td>L5</td>
<td>15</td>
<td>84</td>
<td>0.404</td>
<td>0.282</td>
</tr>
<tr>
<td>M1</td>
<td>28</td>
<td>74</td>
<td>0.475</td>
<td>0.263</td>
</tr>
<tr>
<td>M2</td>
<td>23</td>
<td>73</td>
<td>0.506</td>
<td>0.255</td>
</tr>
<tr>
<td>M3</td>
<td>23</td>
<td>283</td>
<td>0.427</td>
<td>0.296</td>
</tr>
<tr>
<td>M4</td>
<td>22</td>
<td>192</td>
<td>0.319</td>
<td>0.305</td>
</tr>
<tr>
<td>M5</td>
<td>21</td>
<td>140</td>
<td>0.387</td>
<td>0.290</td>
</tr>
<tr>
<td>S1</td>
<td>17</td>
<td>77</td>
<td>0.428</td>
<td>0.263</td>
</tr>
<tr>
<td>S2</td>
<td>15</td>
<td>88</td>
<td>0.387</td>
<td>0.283</td>
</tr>
<tr>
<td>S3</td>
<td>16</td>
<td>72</td>
<td>0.421</td>
<td>0.260</td>
</tr>
<tr>
<td>S4</td>
<td>17</td>
<td>115</td>
<td>0.428</td>
<td>0.296</td>
</tr>
<tr>
<td>S5</td>
<td>15</td>
<td>71</td>
<td>0.344</td>
<td>0.281</td>
</tr>
</tbody>
</table>
Table 3.3 Results of repeated measures ANOVA describing effects on average basal area increment growth of western hemlock canopy trees in Coquitlam River watershed. Main effect terms include the level of defoliation (lightly, moderately or severely) and the years prior to and during defoliation by western hemlock looper. The contrast variable was the first year of defoliation (2000).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defoliation class</td>
<td>2</td>
<td>175511478</td>
<td>3.43</td>
<td>0.0339</td>
</tr>
<tr>
<td>Year</td>
<td>7</td>
<td>556598746</td>
<td>51.18</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Defoliation class x Year</td>
<td>14</td>
<td>191807975</td>
<td>8.99</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Year - Contrast variable: 2000

<table>
<thead>
<tr>
<th>Year</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>1</td>
<td>71146482</td>
<td>11.33</td>
<td>0.0009</td>
</tr>
<tr>
<td>1996</td>
<td>1</td>
<td>218147</td>
<td>0.86</td>
<td>0.3357</td>
</tr>
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<td>1997</td>
<td>1</td>
<td>1150313</td>
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<td>0.5210</td>
</tr>
<tr>
<td>1998</td>
<td>1</td>
<td>12919437</td>
<td>6.67</td>
<td>0.0104</td>
</tr>
<tr>
<td>1999</td>
<td>1</td>
<td>100550135</td>
<td>14.71</td>
<td>0.0002</td>
</tr>
<tr>
<td>2001</td>
<td>1</td>
<td>140499585</td>
<td>105.49</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>2002</td>
<td>1</td>
<td>466605228</td>
<td>125.79</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Defoliation class - Contrast variable 2000

<table>
<thead>
<tr>
<th>Year</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>2</td>
<td>4745604</td>
<td>0.38</td>
<td>0.6856</td>
</tr>
<tr>
<td>1996</td>
<td>2</td>
<td>3419025</td>
<td>0.61</td>
<td>0.5467</td>
</tr>
<tr>
<td>1997</td>
<td>2</td>
<td>17331182</td>
<td>3.11</td>
<td>0.0461</td>
</tr>
<tr>
<td>1998</td>
<td>2</td>
<td>14518184</td>
<td>3.75</td>
<td>0.0249</td>
</tr>
<tr>
<td>1999</td>
<td>2</td>
<td>11966872</td>
<td>8.34</td>
<td>0.0003</td>
</tr>
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<td>2001</td>
<td>2</td>
<td>12280440</td>
<td>4.61</td>
<td>0.0108</td>
</tr>
<tr>
<td>2002</td>
<td>2</td>
<td>127629035</td>
<td>17.20</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
**Figure 3.5** Average annual basal area increment (BAI) for trees in lightly-, moderately- and severely-defoliated sites before and during the 2000-2003 western hemlock looper outbreak in the Coquitlam River watershed. Bars show standard error.

(Figure 3.6 on page 57)

**Figure 3.6** Comparison of annual basal area increment (BAI) for trees in lightly- (L1 to L5), moderately- (M1 to M5) and severely- (S1 to S5) defoliated sites during the 2000-2003 western hemlock looper outbreak in the Coquitlam River watershed. Median site mortality is shown by a bar, box limits = 25th and 75th percentiles, the whiskers indicate 10th and 90th percentiles, and dots represent outliers. The median values for treatments labeled with the same letter were not significantly different at the 0.05 level.
Plots by Defoliation Severity
In the year 2000, the first year of defoliation, mean BAI was 2450±726 mm$^2$. This value was used as the reference level when comparing annual BAI for all sites through time. Between 1995 and 2002, average annual BAI differed significantly relative to growth in 2000 during five years. BAI was higher during 1995 (2977±982 mm$^2$) and lower during 1998 (2225±647 mm$^2$), 1999 (2248±654 mm$^2$), 2001 (1708±719 mm$^2$) and 2002 (1094±1060 mm$^2$) (Table 3.3).

There was little mortality of canopy hemlock trees at any of the sites prior to the year 2000 (Figure 3.7). Canopy tree mortality in the severely-defoliated sites began in 2000, the first year of the outbreak, with 17 out of 89 trees dying that year, and increased substantially in 2001 when 50 trees died. By 2002, only 14 trees remained alive from the original population. Mortality rates were lower in the moderately- and lightly-defoliated sites. At the moderately-defoliated sites, 46 of 117 trees died and at the lightly-defoliated sites, 6 of 91 trees died between 2000 and 2002 (Figure 3.7).
Figure 3.7 Change in abundance of living western hemlock canopy trees for a) lightly, b) moderately and c) severely defoliated sites during the 2000-2003 western hemlock looper outbreak in the Coquitlam River watershed. Trees and recent snags were cored in 2003 and years of last radial growth were reconstructed using cross-dated site specific chronologies.
Canopy Openness

Canopy openness increased significantly with increasing severity of defoliation ($F=53.78$, $p<0.001$; Table 3.4). Canopy openness in severely-defoliated sites ranged from 17.1-31.1%, with a mean and standard deviation of 23.7±5.8%. Moderately-defoliated sites ranged in canopy openness from 8.5-17.2% (12.6±5.8%) and lightly-defoliated sites ranged in canopy openness from 2.7-8.5% (5.2±2.3%).

Table 3.4 Percent canopy openness determined by hemispherical photography for five lightly, five moderately and five severely defoliated sites. Percent openness is the average canopy openness of three photographs taken 50 m apart at each plot.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Defoliation Category</th>
<th>Mean Canopy Openness (standard deviation)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Light</td>
<td>5.6 (0.6)</td>
</tr>
<tr>
<td>2</td>
<td>Light</td>
<td>6.2 (0.7)</td>
</tr>
<tr>
<td>3</td>
<td>Light</td>
<td>8.5 (1.2)</td>
</tr>
<tr>
<td>4</td>
<td>Light</td>
<td>3.0 (0.5)</td>
</tr>
<tr>
<td>5</td>
<td>Light</td>
<td>2.7 (0.4)</td>
</tr>
<tr>
<td>6</td>
<td>Moderate</td>
<td>15.3 (6.7)</td>
</tr>
<tr>
<td>7</td>
<td>Moderate</td>
<td>8.9 (2.1)</td>
</tr>
<tr>
<td>8</td>
<td>Moderate</td>
<td>12.2 (6.0)</td>
</tr>
<tr>
<td>9</td>
<td>Moderate</td>
<td>17.2 (8.5)</td>
</tr>
<tr>
<td>10</td>
<td>Moderate</td>
<td>9.6 (0.7)</td>
</tr>
<tr>
<td>11</td>
<td>Severe</td>
<td>17.1 (2.7)</td>
</tr>
<tr>
<td>12</td>
<td>Severe</td>
<td>31.1 (2.5)</td>
</tr>
<tr>
<td>13</td>
<td>Severe</td>
<td>22.2 (3.7)</td>
</tr>
<tr>
<td>14</td>
<td>Severe</td>
<td>26.0 (6.8)</td>
</tr>
<tr>
<td>15</td>
<td>Severe</td>
<td>22.4 (1.1)</td>
</tr>
</tbody>
</table>

Understory Vegetation

A total of 42 species of vascular plants were identified in this study, including seven trees, 13 shrubs, seven ferns and 15 herbaceous plants. In terms of frequency, the most common tree species was western hemlock (*Tsuga heterophylla* Hulst), with seedlings growing in 86 of 135 vegetation plots. No other tree species was present in more than
four vegetation plots. *Vaccinium* species were the most common shrubs, with red huckleberry (*V. parvifolium* Sm.) (96 plots), oval-leafed blueberry (*V. ovalifolium* Sm.) (83 plots), and Alaska blueberry (*V. alaskaense* T.J. Howell) (29 plots) being the most frequent. Other common shrubs included salmonberry (*Rubus spectabilis* Pursh) (60 plots), red elderberry (*Sambucus racemosa* L. var. *pubens* (Michx.) Koehne) (25 plots), dwarf dogwood (*Cornus canadensis* L.) (14 plots), and salal (*Gaultheria shallon* Pursh) (13 plots). Common ferns were spiny wood fern (*Dryopteris expansa* (K. Presl) Fraser-Jenkins & Jermy) (96 plots), deer fern (*Blechnum spicant* (L.) Sm.) (72 plots), sword fern (*Polystichum munitum* (Kaulfuss) K. Presl) (35 plots), and lady fern (*Athyrium filix-femina* (L.) Roth) (28 plots). The only herbaceous plant growing in more than four plots was foamflower (*Tiarella trifoliata* L. var. *trifoliata*), which occurred in 49 plots. By comparison, moss was in all 135 plots, lichen was in 18 plots, fungus was in six plots and club moss was in five plots.

The severely-defoliated sites were significantly richer (7.60±1.75 species plot⁻¹, N=45) than either lightly-defoliated (4.82±2.60 species plot⁻¹, N=45) or moderately-defoliated sites 4.91±2.05, N=45) (F<sub>richness</sub>=23.92, p<sub>richness</sub><0.0001, Figure 3.8). Severely-defoliated plots had significantly more shrub species (3.53±0.61), fern species (2.42±1.47) and herbaceous species (1.00±0.95) than either moderately- (2.00±1.00, 1.56±1.20 and 0.42±0.66, respectively) or lightly- defoliated plots (2.22±1.29, 1.60±1.31, and 0.29±0.51, respectively) (F<sub>shrub</sub>=19.15, p<sub>shrub</sub><0.0001; F<sub>fern</sub>=7.26, p<sub>fern</sub>=0.001; F<sub>herb</sub>=12.09, p<sub>herb</sub><0.0001). Moderately-defoliated plots had significantly more tree species (0.93±0.50) than either severely- (0.64±0.61) or lightly-defoliated plots (0.71±0.54)
(F<sub>tree</sub>=3.37, p<sub>tree</sub>=0.038; Figure 3.8). There were no significant differences among any of the plots nested within the treatments.

Overall, total ground and vegetation cover was significantly lower at lightly-defoliated sites (106.4% mean ± 10.4 standard deviations, N=45 plots), than at either moderately- (114.4±20.1%, N=45) or severely- (114.9±43.2%, N=45) defoliated sites (F<sub>cover</sub>=3.96, p<sub>cover</sub>=0.021). There were also differences in the contribution of the various components of ground and vegetation cover. The percentage of non-vegetated ground cover (rock and duff) was significantly lower at severely-defoliated sites (mean: 11.1±16.7%) than at lightly- (43.9±26.0%) or moderately- (37.3±27.9%) defoliated sites (F<sub>non-vegetated</sub>=26.49, p<sub>non-vegetated</sub><0.0001; Figure 3.9). The percentage of shrub (24.9±19.6%), fern (27.6±27.6%) and herbaceous species cover (8.7±23.5%) at severely-defoliated sites was significantly higher than at lightly- (16.7±17.5%, 13.3±16.3% and 1.0±4.6%, respectively) or moderately- (15.8±18.0%, 15.8±22.2% and 2.8±6.8%, respectively) defoliated sites (F<sub>shrub</sub>=3.38, p<sub>shrub</sub>=0.037; F<sub>fern</sub>=5.50, p<sub>fern</sub>=0.005; F<sub>herb</sub>=9.21, p<sub>herb</sub>=0.0002; Figure 3.7). The percentage of moss cover was significantly higher at moderately- (40.8±26.1%) and severely- (41.9±24.2%) defoliated sites compared to lightly-defoliated sites (27.1±19.6%) (F<sub>moss</sub>=5.86, p<sub>moss</sub>=0.0037). Conversely, tree (seedling) cover decreased significantly with increasing severity of defoliation, ranging from 4.0±9.1% at lightly-defoliated sites to 1.7±4.1% at moderately- and 0.5±0.9% at severely-defoliated sites (F<sub>tree</sub>=4.19, p<sub>tree</sub>=0.017; Figure 3.9). There were no significant differences among any of the plots nested within the treatments.
Figure 3.8 Comparison of species richness (mean and standard error) among defoliation categories for total plant species, trees, shrubs, ferns and herbs. The mean values labeled with the same letter were not significantly different at the 0.05 level based on the results of a nested ANOVA.
Figure 3.9 Comparison of percent cover (mean and standard error) among defoliation categories for non-living ground cover, moss, tree, shrub, fern and herb. The mean values labeled with the same letter were not significantly different at the 0.05 level based on the results of a nested ANOVA.
The Shannon-Weiner index of diversity for vascular plants was significantly higher at severely-defoliated sites (0.404 mean ± 0.185 standard deviation, N=45) than at lightly- (0.291±0.237, N=45) or moderately- (0.288±0.221, N=45) defoliated sites based on a results of a nested ANOVA using least square means (F=3.73, p=0.025). There were no significant differences among plots nested within treatments.
3.4 DISCUSSION

Tree Growth and Mortality
Analyses of ring-width series from individual hemlock trees demonstrated that growth and mortality of these trees were impacted by the severity of defoliation. Prior to defoliation, all study sites generally displayed the same annual trends in radial growth. For instance, trees in 1995 had consistently wide rings, most likely in response to beneficial climatic conditions during the summer months (Chapter 2). In contrast, 1998 was an exceptionally dry year (170 mm of summer precipitation compared to an average summer precipitation of 277 mm), which resulted in reduced radial growth of all trees, equally at all sites, and most likely reduced growth rates the following year as well.

Although defoliation of the sites by western hemlock looper began in 2000, reductions in basal growth were not apparent until 2001 at any of the sites. This delayed response was despite the fact that some trees within the severely defoliated sites could have lost >65% of their photosynthetic tissue in 2000. Other studies of the impacts of defoliators also note that reduced tree-ring growth may be delayed until two years after the onset of major defoliation (Blais 1983, Filion et al. 1998). The lagged response between defoliation and decreased basal area increments results when mature trees sustain growth by drawing on a cache of carbohydrates and nutrients in their roots or trunk. Earlywood is usually formed using a tree’s carbohydrate and nutrient reserves rather than photosynthates created that year; therefore, the earlywood of the annual tree ring generally is not affected in the first year of a defoliation event (Huber 1982). In the case of western hemlock looper, the effects of defoliation in spring and early summer in the first year of an event
are also limited since the larvae are small and have affected few needles (Hébert 2001). Following multiple years of defoliation, however, a tree’s reserves are depleted and growth is increasingly sensitive to environmental conditions (Haak and Benjamin 1982, Straw 1996). In fact, tree response to defoliation is cumulative, meaning the effects of defoliation are additive during successive years of the outbreak (MacLean and Ebert 1999).

In 2001 many trees in this study ceased radial growth and died, especially at the severely-defoliated sites. Mortality continued in 2002. The significant mortality rates of canopy (dominant and co-dominant) and understory (intermediate and suppressed) trees in the most severely defoliated sites left only about one-fifth of all trees living. Moreover, I expect tree mortality to continue for several more years (see Chapter 4). Little is known about the ecological effects of the observed changes in structure and composition of these forests due to the traditional practice of immediately salvage logging stands that have undergone severe defoliation by western hemlock looper (Johnson et al. 1970, Alfaro et al. 1999).

**Canopy Openness**

The loss of needles through defoliation and the death of large numbers of canopy trees directly altered the physical structure of the forest stands by increasing the openness of the forest canopy. Although I did not measure incoming radiation levels, hemispheric photos provide a surrogate for quantitatively estimating light levels in the understory by directly measuring canopy openness (Chazdon and Field 1987). Based on my results, I surmise that increasing canopy openness increases the amount of photosynthetically
active radiation reaching the forest floor. Even with severe defoliation, tree stems, lateral branches, dead needles and other structures maintained canopy openness within the range of 17 to 31%. In comparison, canopy openness measured using the same hemisphere photographic techniques in forests in the same biogeoclimatic subzone of coastal British Columbia were 3-7% for immature stands, 3-9% percent for mature stands and 6-15% percent for old growth stands (Frazer et al. 2001). My study sites were located within mature stands, thus the lightly- (5.2±2.3%), and moderately-defoliated sites (12.6±5.8%) were within the range of natural variation for canopy openness in non-defoliated forests in the region while the 23.7±5.8% canopy openness of severely defoliated sites was well above the range of canopy openness commonly observed in coastal forests.

**Understory Composition**

After disturbance, a more open canopy can result in profound impacts on the microenvironment of the understory, such as a rise in temperature, increase in evapotranspiration and a decrease in soil and litter moisture content (Matlack 1994). In the most severely defoliated sites, these environmental conditions undoubtedly would have changed and had an effect on the understory flora. Following three years of continuously severe defoliation by western hemlock looper, the five sites that recorded the highest levels of canopy openness also showed the greatest cover of vascular plants in the understory. These results are consistent with Bailey et al. (1998) who showed that the abundance of understory vegetation usually increases with a reduction in overstory density. Yet, perhaps more importantly in terms of species diversity and stand development, the higher levels of species richness and cover within the more open
severely-defoliated sites was due to higher levels of shrub, fern and herbaceous species, and not tree species that could potentially recruit to the canopy. Severely-defoliated sites had the lowest levels of tree richness and cover. Thus, following severe defoliation, few tree seedlings or saplings survive (see Chapter 4) yet robust fern and shrub re-growth is observed. This increase in shrub, fern and herbaceous species cover and richness point to the establishment of a more diverse understory, although it is unknown whether these increases in species richness were due to immigration of propagules or a seedbank already present in the forest soil. Repeated vegetation surveys would determine which species most benefited from the increased openess of the canopy. In this study, the more intact canopy at less severely-defoliated sites left much of the understory without herbaceous vegetation, and with a significant portion of living tree seedlings.

**Impacts on Succession and Stand Development**

Prior to 1999, the low-elevation forests of the Coquitlam River watershed were dominated by even-aged forests that originated after clear-cut logging in the early 1900s (Acres et al. 1999). At the landscape and stand scales, these forests were homogenous in structure and composition. The closed-canopy of the stands resulted in low understory plant cover and species diversity. The canopy and subcanopy strata were dominated by western hemlock, with lesser amounts of western redcedar and Douglas-fir (Acres et al. 1999). In coastal British Columbia, these tree species often dominate late-successional stands, as western hemlock and western redcedar are shade-tolerant and regenerate beneath existing canopies and all three species are long-lived (Packee 1990, Wang et al. 1994). Thus, the composition of the canopy of these forests would be unlikely to change for decades to centuries in the absence of stand-level disturbance. Defoliation by western
hemlock looper has increased the structural and compositional diversity among the study stands by increasing snag density, thinning the canopy, shifting the relative composition of the canopy and altering the biomass and composition of the understory plant community. The resultant increase in spatial heterogeneity of these low-elevation forests may in fact be essential for the long-term coexistence of the canopy tree species (Getzin et al. 2006).

The development of a variety of forest patches in the landscape has created a more complex forest with a greater array of possible future structural development and successional pathways. At the lightly-defoliated sites, the western hemlock looper outbreak appeared to have little impact on stand development and successional trajectories. In coastal forests of western North America, understory vegetation is generally lacking following crown closure due to low light levels (Oliver and Larson 1990, Franklin et al. 2002). These conditions persist through the biomass accumulation / competitive exclusion stage of development, which commonly extend until stands are 80 to 100 years old. Understory vegetation begins to re-establish during the forest maturation stage, when disturbances cause patchy mortality of canopy trees giving rise to gaps that allow more light to reach the forest floor (Bailey et al. 1998, Franklin et al. 2002). At lightly-defoliated sites, canopy tree mortality was low and the understory plant cover and species richness remained low. Thus, in term of forest structure and species composition, the lightly-defoliated sites do not differ substantively from the surrounding non-disturbed stands of the landscape mosaic. Future development of these stands will
likely be a slow transition from even-aged, closed-canopy stands to mature stands with multiple age cohorts and increasingly diverse stand structure (Franklin et al. 2002).

In contrast, in severely-defoliated areas, forest composition and structure have been altered in ways that will substantively affect future forest development. In coastal forests, the major developmental changes in forests are structural rather than compositional due to low tree species diversity and the high number of shared species among age-classes (Arsenault and Bradfield 1995). And, while some compositional changes in understory vegetation associations have been noted as stands age (e.g. Klinka et al. 1985, Blackwell et al. 2002), it is problematic in these species-poor forests to use composition alone as a predictor of successional development. The increased snag density and canopy openness at severely-defoliated sites resulted in significant changes to canopy structure, and facilitated a shift in understory composition.

I propose that the high level of canopy tree mortality and changes in understory plant composition at severely-defoliated sites will increase the variety of potential stand-level successional pathways. For instance, severe defoliation in my study stands altered canopy structure and understory composition in ways that may retard the re-development of a closed canopy through 1) the death of existing saplings and seedlings, and 2) by development of a dense understory plant community that includes little or no tree regeneration. As observed in many study stands, the death of advanced tree regeneration means a loss of opportunity for trees to recruit from subcanopy to overstory strata and replace the canopy trees killed by defoliation. Thus, there will most likely be a prolonged
period of open canopy and a lag in canopy closure as new seedlings require time to establish in the understory and recruit to the canopy. Exactly how long the lag in regeneration may persist is unknown. It may be exacerbated at severely-defoliated sites, where the understory plant community is now well-developed, with significant increases in ferns and shrubs which may exclude new tree seedling regeneration through competition (Riege and del Moral 2004). Conversely, fern and shrub cover may facilitate tree regeneration by shading seedlings and increasing survival during drought conditions (Berkowitz et al. 1995). Another factor that may influence the regeneration dynamics of disturbed stands is the increase in snags and downed woody debris associated with western hemlock looper defoliations (Chapter 4). Downed woody debris provides an opportunity for the successful establishment of species such as western hemlock and western redcedar that use nurse logs as a means of reducing competition from ground cover on the forest floor (Harmon and Franklin 1989, Daniels and Gray 2004). There is also evidence that the changes in the light environment and understory plant composition and cover may benefit broad-leaved trees, such as vine maple, that regenerate in medium sized canopy gaps and/or vegetatively. Moreover, a cover of tall shrubs or broad-leaved trees can significantly increase the resistance of coastal forests to conifer seedling establishment (Shatford et al. 2003). Therefore, the decision by managers not to log the defoliated stands in the Coquitlam River watershed, has provided a unique research opportunity to monitor the mechanisms and processes of stand development and succession following defoliation of different severities.
Conclusions
I conclude that defoliation by western hemlock looper and the resultant death of canopy trees had varying, but statistically and ecologically significant, impacts on canopy openness and understory composition within the study stands. Due to variation in the severity of defoliation, the 2000-2003 western hemlock looper outbreak produced distinct forest patches within a landscape that had been relatively homogenous prior to disturbance. These patch-specific structural and compositional changes and the resulting variability in successional pathways greatly contribute to the landscape heterogeneity of the Coquitlam River watershed and, more generally, the coastal forests of British Columbia.
3.5 LITERATURE CITED


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CHAPTER 4: TREE MORTALITY CAUSED BY WESTERN HEMLOCK LOOPER DEFOLIATION IN COASTAL BC FORESTS

4.1 INTRODUCTION

In coastal forests of western North America, insects, diseases and wind are important causes of tree mortality as forests mature (Franklin et al. 2002). Native insects are natural agents of disturbance and integral components of forest ecosystems. Insect folivory regulates primary productivity of photosynthetic tissue (Mattson and Addy 1975) and increases nutrient cycling and availability (Scholwalter 1981). Through defoliation and tree mortality, insects increase snag frequency and canopy openness (Chapter 3). The elevated snag density results in increases to the fuel load that may lead to an increased probability of subsequent forest fires (McCullough et al. 1998). Insects also alter forest succession and forest structure by causing species-specific tree mortality through host tree preference (Alfaro et al. 1999). Consequently, the effects of these outbreaks are important in the decision-making process for many resource managers because of the impacts to nutrient cycling, wildlife habitat, timber supply, fire hazard and forest development.

In British Columbia, there are approximately 140 species of defoliating insects known to feed on native conifers with the western hemlock looper (Lambdina fiscellaria lugubrosa Hulst) being one of the most prolific defoliators in British Columbia (Ministry of Forests and Range 1995). Noncontiguous and spatially independent outbreaks of western

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1 A version of this chapter will be submitted for publication.
hemlock looper tend to occur in the interior, south of 56° latitude, within the Interior Cedar Hemlock (ICH) biogeoclimatic zone, and in coastal forests within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Turnquist 1991). Defoliation reduces growth and increases mortality of host trees, altering forest composition and structure (Chapter 3) often with significant impacts on timber volumes and wildlife habitat. Research on the impacts of western hemlock looper defoliations in ICH forests indicate tree mortality of >65% (Alfaro et al. 1999, Hoggett and Negrave 2001, 2002).

Since 1911, approximately 1 000 000 ha of forest has been defoliated by western hemlock looper in British Columbia, with about 15 000 ha of this occurring during seven separate outbreaks in coastal forests (Parfett et al. 1995, Burleigh and Gustafsson 2003). In coastal BC, mature and old-growth western hemlock-dominated forests containing a complex canopy structure consisting of a layered canopy of dominants and co-dominants and a subcanopy with numerous suppressed and intermediate individuals are considered most susceptible to western hemlock looper defoliation (Koot 1994, Ministry of Forests and Range 1995, Acres et al. 1999). However, during the 2000-2003 outbreak in the Coquitlam River watershed, second growth stands that were 80 to 100 years old were impacted most severely (Burleigh and Gustafsson 2003, Chapter 3). Forests with a history of defoliation by western hemlock looper are considered a high risk for future defoliation (Borecky and Otvos 2001). Given the prevalence of hemlock-dominated second growth forests in coastal BC, and a history of severe outbreaks of western hemlock looper, knowledge of forest stands defoliated by western hemlock looper is essential for forest management in this region.
Although the qualitative impacts of western hemlock looper defoliation of coastal forests, such as large-scale tree mortality are well known, a quantitative understanding of the pattern and timing of mortality remains elusive. This limits our ability to predict with certainty the specific effects of outbreaks. Traditionally, all defoliated stands were salvage-logged within two to three years of defoliation in an attempt to eradicate the insects and reduce timber losses (Johnson et al. 1970). As a result, few sites in coastal BC that were defoliated during the past 100 years remain intact today and little is known about the effects of defoliation and recovery of stands after defoliation. Currently, we can make only general statements about when, where, and how much timber may be damaged or lost as a result of defoliation.

This study analyzes the temporal pattern of tree death and resulting rates of mortality after a western hemlock looper outbreak that defoliated c.1500 ha of ecologically managed coastal forest in 2000-2003. I hypothesized that mortality of trees in defoliated areas would be influenced by tree diameter, with smaller trees more susceptible to defoliation and dying at a greater rate than larger trees. I also expected to show species-specific responses with the preferred host, western hemlock, having the greatest mortality and other canopy species such as Douglas-fir, western redcedar and amabilis fir having lesser amounts of mortality (Ministry of Forests and Range 1995).
4.2 METHODS

Study Area
The study area is located in the Coquitlam River watershed, located 40 km northeast of the city of Vancouver, British Columbia (Figure 4.1) and is located in the submontane (elevation < 900 metres above sea level) variant of the Very Wet to Moist Maritime Coastal Western Hemlock biogeoclimatic subzone. In these forests, western hemlock (*Tsuga heterophylla* (Raf.) Sarg) is the most common tree species but other frequently occurring species are western redcedar (*Thuja plicata* Donn ex D. Don), Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in drier subzones and sites, amabilis fir (*Abies amabilis* Dougl. ex Forbs) in the wetter parts of the zone and at higher elevations (Klinka et al. 1991).

Research Design
Twenty-eight study sites were established in summer 2002 at areas that were defoliated by an outbreak of western hemlock looper during 2000-2003 (Figure 4.1, Table 4.1). Sites were chosen to include stands of varying degrees of defoliation based on aerial surveys flown in the summer of 2002: light (5-25% visible defoliation), moderate (26-60%), and severe (>60%) (Burleigh and Gustafsson 2003). All sites were located at elevations between 165 and 390 meters above sea level (masl). Slope angle and aspect were recorded at the centre of all sites (Table 4.1). At each site, three circular ‘canopy plots’ were established. Depending on the size of the disturbed areas, canopy plots measured 200 m$^2$ (12 sites), 100 m$^2$ (12 sites) or 50 m$^2$ (4 sites). Thus, there were 28 sites and three plots per site, for a total of 84 plots. Because of variation in plot size, relative
abundances, proportions or percentages were used instead of absolute values when data were analyzed at the site level.

Figure 4.1 Map of study area showing location of the 28 plots in the Coquitlam River watershed.
Table 4.1 Biophysical attributes for 28 study sites in the Coquitlam River watershed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation (masl)</th>
<th>Slope (%)</th>
<th>Aspect (°)</th>
<th>Tree density (number/ha)</th>
<th>DBH (mean ± SD)</th>
<th>Hemlock stems (%)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>205</td>
<td>14</td>
<td>335</td>
<td>1000</td>
<td>31.2 ± 10.4</td>
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<td>2266.7</td>
<td>28.7 ± 26.7</td>
<td>54.0</td>
</tr>
<tr>
<td>15</td>
<td>360</td>
<td>35</td>
<td>314</td>
<td>733.3</td>
<td>42.2 ± 37.0</td>
<td>63.6</td>
</tr>
<tr>
<td>16</td>
<td>232</td>
<td>60</td>
<td>255</td>
<td>733.3</td>
<td>39.6 ± 26.8</td>
<td>31.8</td>
</tr>
<tr>
<td>17</td>
<td>180</td>
<td>10</td>
<td>90</td>
<td>816.7</td>
<td>21.5 ± 31.7</td>
<td>94.0</td>
</tr>
<tr>
<td>18</td>
<td>154</td>
<td>30</td>
<td>100</td>
<td>383.3</td>
<td>33.7 ± 29.1</td>
<td>53.5</td>
</tr>
<tr>
<td>19</td>
<td>194</td>
<td>5</td>
<td>0</td>
<td>633.3</td>
<td>32.9 ± 17.6</td>
<td>61.9</td>
</tr>
<tr>
<td>20</td>
<td>329</td>
<td>60</td>
<td>40</td>
<td>866.7</td>
<td>19.4 ± 17.6</td>
<td>96.0</td>
</tr>
<tr>
<td>21</td>
<td>715</td>
<td>55</td>
<td>70</td>
<td>1100</td>
<td>13.4 ± 20.6</td>
<td>90.9</td>
</tr>
<tr>
<td>22</td>
<td>225</td>
<td>0</td>
<td>0</td>
<td>633.3</td>
<td>29.2 ± 23.2</td>
<td>70.5</td>
</tr>
<tr>
<td>23</td>
<td>260</td>
<td>15</td>
<td>32</td>
<td>400</td>
<td>43.5 ± 10.2</td>
<td>81.5</td>
</tr>
<tr>
<td>24</td>
<td>165</td>
<td>15</td>
<td>36</td>
<td>866.7</td>
<td>24.6 ± 23.0</td>
<td>84.0</td>
</tr>
<tr>
<td>25</td>
<td>210</td>
<td>40</td>
<td>190</td>
<td>566.7</td>
<td>25.6 ± 20.8</td>
<td>18.5</td>
</tr>
<tr>
<td>26</td>
<td>260</td>
<td>5</td>
<td>100</td>
<td>533.3</td>
<td>24.2 ± 21.8</td>
<td>90.0</td>
</tr>
<tr>
<td>27</td>
<td>265</td>
<td>5</td>
<td>40</td>
<td>766.7</td>
<td>14.5 ± 15.0</td>
<td>81.5</td>
</tr>
<tr>
<td>28</td>
<td>238</td>
<td>5</td>
<td>40</td>
<td>1133.3</td>
<td>18.4 ± 11.2</td>
<td>97.2</td>
</tr>
</tbody>
</table>
Repeated Census

All live and standing dead trees with diameter at breast height (dbh) greater than 1.0 cm were censused in each of the 84 plots during the summers of 2002, 2003, 2004 and 2005. Species, diameter at breast height, and canopy class (dominant, co-dominant, intermediate or suppressed) were recorded for all trees. By visual estimation, each live tree was assigned to one of five ‘health’ classes based on the percentage of the live crown canopy that was not defoliated – I: 0-19%, II: 20-39%, III: 40-59%, IV: 60-79%, V: 80-100%. Similarly, each snag was assigned to one of five decay classes (Table 4.2). Dead trees with intact bark, fine branches and some needles were categorized as class I snags and assumed to have died as a result of the western hemlock looper outbreak.

Dendrochronological analysis of a sub-sample of these snags concluded that 97.8% (220 of 225) of class I snags died within the first three years of the western hemlock looper outbreak that occurred from 2000-2003 (Chapter 3).

<table>
<thead>
<tr>
<th>Class</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Tree is recently dead. Most fine branches and some needles still present. Top is intact. Bark is intact.</td>
</tr>
<tr>
<td>II</td>
<td>Most of the fine branches have dropped. More than 50% of the coarse branches are left. Top is intact. Bark may begin to loosen</td>
</tr>
<tr>
<td>III</td>
<td>Fewer than 50% of the coarse branches are left. Top is intact. Bark may or may not have sloughed off</td>
</tr>
<tr>
<td>IV</td>
<td>No coarse branches remain. Top is broken. Bark may or may not have sloughed off. Height at least 6 m.</td>
</tr>
<tr>
<td>V</td>
<td>No coarse branches remain. Top repeatedly broken. Bark may or may not have sloughed off. Height less than 6 m.</td>
</tr>
</tbody>
</table>
Statistical Analysis

The repeated census data for all sites were combined and differences among the diameter of trees and snags were tested by using one-way ANOVA after a logarithmic transformation of tree diameters to achieve a normal distribution. Mortality rates among species were examined using contingency table analysis that described differences in the distribution of live and recently-dead snags by species. Mantel-Haenzsel chi-squared tests were used to test the statistical significance of the contingency table results. In instances when the contingency table produced at least 20% expected cell values below five, Monte Carlo estimates of a Fisher's Exact Test were used to test for statistical significance (Quinn and Keough 2002).

Multiple regression analysis was used to determine if physical, forest structural or compositional characteristics influenced cumulative tree mortality among sites. Elevation, slope, aspect, average diameter at breast height, tree density, and percent hemlock were entered into the regression, yet I found no significant relationships between these variables and cumulative tree mortality (results not shown).

In an alternate approach, I used logistic regression (SAS proc LOGISTIC) to determine how time since outbreak, tree diameter and tree species affects the probability of mortality and took the general form:

\[ M = \alpha + \beta_1 t + \beta_2 \text{dbh} \]  

(Equation 4.1)

where, the probability of mortality was a function of the linear model M in which \( \alpha \) was the intercept; \( \beta_1 \) was the estimated coefficient for the number of years since outbreak.
began in 2000, \( \beta_2 \) was the estimated coefficient for diameter at breast height (dbh). A forward stepwise procedure was used to evaluate the significance of each term in the model where terms were added and retained in the model if they were statistically significant and improved the fit of the model. In total, five models were developed – one for all trees combined and one each for the four most abundant tree species: western hemlock, western redcedar, Douglas-fir and amabilis fir. Model fit was evaluated using Wald \( \chi^2 \) and improvements in stepwise additions to the models were noted using Akaike’s Information Criterion (AIC) (Akaike 1974). To illustrate the effect of tree diameter on the probability of mortality, the species-specific models were compared after inputting four distinct tree diameters typical of the four canopy positions used in this study: 1 cm dbh (suppressed subcanopy), 20 cm dbh (intermediate subcanopy), 40 cm dbh (co-dominant canopy) and 80 cm dbh (dominant canopy).

4.3 RESULTS

Repeated Census
From 2002 to 2005, a total of 931 trees and snags were censused within the 84 plots at 28 sites. The absolute number of trees varied slightly among years as 37 individuals (4 trees and 33 snags) fell during the 4-year period, while 36 new trees were added to the database as saplings grew larger than the minimum dbh criterion of 1.0 cm. In 2002 there were 563 live trees and 332 snags, including 168 class I or recently-dead snags (Figure 4.2). Tree death occurred between each census, raising the number of class I snags each year. Class I snags represented 18.8% of all trees (168 individuals) in 2002, 33.4% (303)
in 2003, 40.2% (361) in 2004 and 42.2% (377) in 2005. In total, only 321 trees remained alive throughout the 4-year period (Figure 4.2).

As a percentage of all trees per site, cumulative mortality of trees averaged 37.1% (±21.0%, standard deviation) in 2002 and varied among sites ranging from 3.0% to 94.4%. Mortality continued each year, yet the annual rate of mortality slowed. Plot level cumulative mortality increased to an average of 59.4±22.7% by 2005, ranging from 19.1% to 100% among sites (Figure 4.3).
Figure 4.2 The number of living trees by health class (above line) and the number of snags by decay class (below line) for western hemlock, western redcedar, amabilis fir, Douglas-fir, and vine and bigleaf maples, censused from 2002 to 2005. Note that a different scale was used for the number of western hemlock trees and snags due to large numbers of this species relative to the others. Health classes are based on the percentage of living crown (i.e. the percentage of full crown not defoliated) (by quintile: $1=0.1-19\%$, $2=20-39\%$, $3=40-59\%$, $4=60-79\%$, $5=80-100\%$). Snag decay classes are modified from Thompson et al. (1979) and are defined in Table 4.2.
Figure 4.3 Box plots showing the cumulative percent mortality for all trees greater than 1.0 cm dbh at 28 sites by year. Median site mortality is shown by a bar, box limits = 25th and 75th percentiles, the whiskers indicate 10th and 90th percentiles, and dots represent outliers.

Tree Diameter
The diameter distribution of all trees within all plots followed a reverse-J distribution (Figure 4.4). In 2002, there was no difference among the mean diameters of living trees (29.56±23.49 cm, n=563), recently-dead (class I) snags (26.18±18.18 cm, n=178), or more decayed snags (classes II-V) (24.81±28.21 cm, n=164) (F=0.934, p=0.39). A large number of relatively small trees died over the census period and entered snag class I. By 2005, the mean diameter of surviving trees (31.21±23.65 cm, n=353) was significantly larger than the mean of class I snags (24.99±21.70 cm, n=377) and class II-V snags (25.20±29.00 cm, n=151) (F=20.47, p<0.0001).
Figure 4.4. Histogram of living trees, recently-dead snags (class I) and older snags (classes II through V) by diameter class censused from 2002 to 2005.
**Tree Species and Canopy Position**

In 2002 there were 364 canopy (82 dominant, 282 co-dominant) and 567 subcanopy (146 intermediate, 421 suppressed) trees. Of the canopy trees, 279 were living in 2002, 73 were class I snags and 12 were class II-V snags. Western hemlocks represented 83.8% (305 trees) of all canopy trees and snags, 97.3% (71) of all class I snags and 91.7% (11) of class II-V snags. Western redcedar represented 7.4% (27) of all canopy trees and snags, amabilis fir 4.7% (17), Douglas-fir 3.0% (11) and deciduous species 1.1% (4).

Between 2002 and 2005, 74 canopy hemlocks died. Thus, the number of class I canopy hemlock snags increased from 71 to 145 and the number of live hemlocks decreased from 223 to 149 trees, significantly altering the ratio of living to dead hemlocks ($\chi^2=214.39, p<0.0001$). Five canopy Douglas-fir also died, significantly altering the ratio of living to dead Douglas-fir (Fisher's Exact Test=0.000026, p=0.0105). No canopy western redcedar, amabilis fir, or deciduous trees died during the census period. By 2005, 200 canopy trees remained alive (Figure 4.5a).

In 2002, only 285 of the 567 subcanopy trees were living and dead trees included 95 class I snags and 187 snags in classes II-V. Western hemlock represented 79.6% of the live subcanopy (227 intermediate or suppressed trees) in 2002, but this proportion decreased significantly to 68.1% (111 trees) ($\chi^2=354.17, p<0.0001$) as 116 trees died in the four-year census period. The number of living western redcedar significantly decreased from 19 to 10 subcanopy trees ($\chi^2=19.93, p<0.0001$), as did amabilis fir, which decreased from 19 to 13 subcanopy trees ($\chi^2=17.91, p<0.0001$). The only other coniferous species in the
subcanopy, Douglas-fir and yellow cedar, were represented by single individuals that both died during the census period. No broad-leaved, deciduous subcanopy trees died from 2002 to 2005. In fact, the number of living broad-leaved trees increased from 18 to 29 individuals, mostly through the recruitment of 10 new vine maple saplings by vegetative propagation of adventitious roots (Figure 4.5b).

**Figure 4.5** The total number of live trees by species over the four-year census period (2002-2005) for a) canopy and b) subcanopy position classes.
**Tree Mortality**

Time, in years since the beginning of visible western hemlock looper defoliation in 2000, was the dominant, significant factor affecting tree mortality for all species combined (Table 4.3) and the four main canopy trees – western hemlock, western redcedar, amabilis fir and Douglas-fir (Table 4.4). Similarly, tree diameter significantly influenced tree mortality, with small trees more susceptible than large trees in all models (Tables 4.3 and 4.4).

**Table 4.3.** Stepwise development of a logistic regression model for the probability of tree mortality in the years following a western hemlock looper outbreak.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>Wald $\chi^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M_1=-1.9583$</td>
<td>4714.4</td>
<td>745.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_2=-1.9583 + 0.6422t$</td>
<td>4040.5</td>
<td>510.1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_3=-1.9583 + 0.6422t - 0.0183dbh$</td>
<td>3930.2</td>
<td>573.7</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Overall, the probability of mortality for all species increased with the time since the onset of defoliation; yet, the rate of mortality slowed after three or four years for smaller trees (Figure 4.6). For all species, the probability of mortality decreased with increasing tree diameter and the probability of mortality approached zero for western redcedar and amabilis fir with dbh greater than 20cm. Tree diameter accounted for a significant amount of variation in tree mortality rates for all species, but the coefficients for dbh and contributions to the logistic models (Table 4.4) for Douglas-fir and western hemlock models were lower than those of western redcedar and amabilis fir. In comparison to the model for western hemlock, the probabilities of death for western redcedar and amabilis
fir were significantly less indicating a decreased probability of tree death for western redcedar and amabilis fir over the 2000-5 time period (western redcedar: $\chi^2 = 25.63$, $p<0.0001$; amabilis fir: $\chi^2 = 36.65$, $p<0.0001$). The probability of mortality for Douglas-fir did not differ significantly from that of western hemlock ($\chi^2=1.93$, $p=0.16$) (Table 4.4) (Figure 4.6).

**Figure 4.6** Probability of tree mortality during the 2000-2003 western hemlock looper outbreak in Coquitlam River watershed. Four representative tree diameters have been plotted for western hemlock (closed circles), western redcedar (open circles), amabilis fir (closed triangles) and Douglas-fir (open triangles).
Table 4.4 Comparison of logistic regression models for the probability of mortality in the years following a western hemlock looper outbreak for western hemlock, western redcedar, amabilis fir and Douglas-fir.

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>Wald $\chi^2$</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Western hemlock</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{H1} = -2.1061$</td>
<td>4114.3</td>
<td>610.63</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{H2} = -2.1061 + 0.6484t$</td>
<td>3476.3</td>
<td>477.13</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{H3} = -2.1061 + 0.6484t - 0.0135dbh$</td>
<td>3430.6</td>
<td>503.07</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Western redcedar</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{C1} = -0.6987$</td>
<td>215.7</td>
<td>44.68</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{C2} = -0.6987 + 0.6606t$</td>
<td>165.5</td>
<td>27.82</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{C3} = -0.6987 + 0.6606t - 0.1059dbh$</td>
<td>144.6</td>
<td>36.49</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Amabilis fir</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{F1} = 0.3955$</td>
<td>230.3</td>
<td>67.87</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{F2} = 0.3955 + 0.6655t$</td>
<td>149.1</td>
<td>31.80</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{F3} = 0.3955 + 0.6655t - 0.2136dbh$</td>
<td>127.9</td>
<td>35.24</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td><strong>Douglas-fir</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_{D1} = -1.0928$</td>
<td>86.5</td>
<td>22.52</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$M_{D2} = -1.0928 + 0.9715t$</td>
<td>71.1</td>
<td>11.62</td>
<td>0.0007</td>
</tr>
<tr>
<td>$M_{D3} = -1.0928 + 0.9715t - 0.0467dbh$</td>
<td>61.1</td>
<td>14.90</td>
<td>0.0006</td>
</tr>
</tbody>
</table>
4.4 DISCUSSION

Tree Mortality
During the 2000-2003 outbreak of western hemlock looper in the Coquitlam River watershed, the rate of mortality varied with tree diameter and canopy position for all species. Overall, trees with small diameters showed significantly higher levels of mortality than larger trees. Similarly, subcanopy trees had higher mortality than canopy trees. Although the high levels of mortality in the smaller diameter classes were most likely due to western hemlock looper defoliation, I cannot discount the effects of other naturally-occurring factors which may have contributed to tree mortality. In fact, tree death is often the consequence of multiple factors or events and determining the exact cause of death can be difficult (Franklin et al. 1987). At 80 to 100 years after a severe stand-replacing disturbance, closed-canopy stands in the Pacific Northwest typically are near the end of the “biomass accumulation/competitive exclusion” stage of forest development, which is characterized by a high rate of self-thinning (Franklin et al. 2002). During this time, density-dependent mortality is especially high among smaller diameter-class trees, although absolute rates of mortality are typically lower than in the earlier stages of stand development (Lutz and Halpern 2006). Smaller trees are also susceptible to drought and other environmental stresses and a significant drought in the summer of 1998 may have caused or contributed to mortality of smaller trees in the study area (Chapter 2). Thus, although I assume western hemlock looper defoliation is the ultimate cause of subcanopy tree mortality in my study, I recognize that other factors may have contributed to their mortality.
Tree mortality caused by western hemlock looper defoliation varied by species and the differing rates of mortality altered the composition of the surviving forest. In 2002, western hemlock was the dominant canopy and subcanopy species throughout the study area, accounting for approximately four-fifths of living trees. However, 97% of class I snags were western hemlock. In a companion study (Chapter 3), I found that mortality of almost all recently-dead western hemlock snags in defoliated areas of the Coquitlam River watershed coincided with the western hemlock looper outbreak in 2000-2003. Thus, I suggest that the number of living trees combined with the number of recently-dead (class I) snags provides a legitimate estimate of the number of living western hemlocks prior to the outbreak in this study. Therefore, 611 living western hemlock were likely present in the study stands prior to the outbreak, accounting for 80.8% of living trees. The proportion of living western hemlock decreased steadily to 72.5% by 2002 to only 43.2% by 2005. Conversely, cumulative western hemlock mortality was 56.8% of all individuals by 2005. Similarly, western redcedar had a cumulative mortality of 20% (9 of 45 individuals), amabilis fir 30% (12 of 40) and Douglas-fir 61.5% (8 of 13). Thus, species-specific mortality associated with western hemlock looper defoliation altered composition of the living forest by significantly reducing the absolute and relative abundance of western hemlock and increasing the relative abundance of other species.

In some instances, the biophysical attributes of the forest at stand to landscape scales are reported to strongly influence the spatial extent and severity of a disturbance (Turner et al. 1998). For example, in areas defoliated by western hemlock looper in the interior forests of British Columbia, the highest levels of tree mortality were observed in stands at
high elevations (up to 940 m) and with a large proportion of subalpine fir, which is an alternate host for western hemlock looper and showed even greater levels of mortality than western hemlock (Alfaro et al. 1999). In contrast to the interior forests, I found no significant relationships between biophysical attributes and cumulative tree mortality in my sample plots. Specifically, tree mortality at the plot level was not related to elevation, slope angle or aspect of the site or the average dbh, tree density, and percentage of western hemlock in the canopy. In part, these negative results reflect the population of sites included in my analysis. In this study, I selected stands to represent varying severities of defoliation and they represent only a subset of forest types in the Coquitlam River watershed; therefore, the sample population was relatively homogenous in location and forest structure and composition. Hoggett and Negrave (2002) reported high variability in mortality among stands defoliated by western hemlock looper in the interior forests of British Columbia. Similar to my study, they did not find that stands with a high basal area composition of host hemlock and subalpine fir experienced commensurately high mortality. Rather, they found that among all levels of defoliation, the same species-specific trends in mortality held true.

**Stand Dynamics**

No canopy western redcedar or amabilis fir died during the census period of this study. These two species increased their proportion in the surviving canopy as defoliation by the western hemlock looper killed many western hemlock and Douglas-fir canopy trees. The effects of the disturbance were more severe for subcanopy than canopy trees, and all four coniferous species had significant mortality within this stratum. The composition of the subcanopy was further altered by the recruitment of vine maple saplings through...
adventitious sprouting of existing trees. Therefore, after defoliation by western hemlock looper, the composition of the surviving canopy changed from dominance by western hemlock towards a greater relative abundance of western redcedar and amabilis fir, while the subcanopy showed large-scale mortality of conifers yet increases in vine maple. These results are consistent with the natural shift in relative composition of canopy trees observed in the CWHvm biogeoclimatic subzone as forests transition from mature to old-growth stages of development, in which western hemlock dominance decreases and the proportion of western redcedar increases (Blackwell et al. 2002).

The determination of which species will dominate following a disturbance depends on the type, timing and impact of the event. Oliver et al. (1980) found that severe disturbance to the canopy in the stem exclusion stage of a western hemlock and amabilis fir-dominated forest facilitated the regeneration of species with light, easily dispersed seeds (e.g. red alder), while severe disturbance in the understory re-initiation or old-growth stages favoured advanced regeneration of shade-tolerant species (e.g. western hemlock and amabilis fir), or sprouting species (e.g., Vaccinium spp.). Normally, as forests enter the maturation stage of development, the understory community is re-established as more light reaches the forest floor due to thinning of the canopy. Both the herbaceous and shrub components of the understory increase (Bailey et al. 1998) and shade-tolerant tree species establish advanced regeneration, from which individuals can be recruited as canopy gaps form (Franklin et al. 2002). Similarly, following defoliation by western hemlock looper, I would expect advanced regeneration of shade-tolerant western hemlock, western redcedar and amabilis fir to recruit to fill canopy gaps. However, at the
most severely-defoliated study sites, the near-complete mortality of shade-tolerant seedlings and saplings may contribute to a prolonged period of canopy openness during which the understory will be dominated by ferns and shrubs (Chapter 3).

**Management Implications: Predicting Tree Mortality**
The species-specific logistic regression models formulated in this study provide forest managers with empirically-based guidelines for anticipating mortality and survivorship of the dominant tree species during outbreaks of western hemlock looper in coastal forests. These models quantify mortality based on the time since the onset of the outbreak and tree diameter. They predict high rates of mortality for western hemlock and Douglas-fir in all diameter classes, but mortality of western redcedar and amabilis fir is restricted to smaller diameter classes. The dominant factor in the model is time since the outbreak began, meaning, levels of mortality and survivorship are primarily controlled by the duration of the defoliation. Thus, during short-term outbreaks of less than 2 years, survivorship for all species would most likely be quite high, especially for trees >20 cm dbh. In contrast, during outbreaks that last four or more years, such as the 2000-2003 outbreak in Coquitlam watershed, mortality of canopy trees can exceed >50% for species such as western hemlock and Douglas-fir, yet almost all large canopy western redcedar and amabilis fir would survive.

Given relatively high survivorship after outbreaks of short duration, most large trees would most likely recover which would not justify immediate salvaging logging. Alternatively, after two years, forests with high proportion of hemlock will have high degrees of mortality that would justify salvage logging in areas managed for timber.
production. Therefore, I would recommend that forest managers not salvage log affected stands at the end of the first year of defoliation since outbreaks of western hemlock looper may last anywhere from one to five years, and if the outbreak ends after one year there will be little permanent damage, especially to the canopy. Even if defoliation ends after two years, more than half of western hemlock will survive and non-host species such as western redcedar and amabilis fir will be hardly affected. However, in defoliations lasting longer than 2 years, mortality of more than half of all host species can be expected and salvage logging may be justified in these instances.

**Conclusions**

Folivory by western hemlock looper causes varying degrees of mortality in both canopy and subcanopy trees within coastal BC forests leading to a marked increase in snag density. Herbivore preference for western hemlock caused a decrease in the dominance of western hemlock and an increase in less frequent species within the surviving canopy and subcanopy trees of the affected stands. Thus, western hemlock looper defoliations have an important role in altering the composition and successional pathways of coastal forests. The logistic regression models created in this study serve as a guide for predicting mortality of western hemlock, Douglas-fir, western redcedar and amabilis fir due to western hemlock looper defoliation in coastal BC forests. In particular, they suggest that the length of a western hemlock looper outbreak determines overall mortality rates, yet mortality will also be significantly influenced by tree diameter. Thus, I suggest that salvage logging may not be justified for outbreaks of short duration since there will be little lasting damage to the canopy. In longer outbreaks however, overall canopy tree mortality will be high, but strongly species-specific. For instance, canopy western
hemlock and Douglas-fir will have mortality rates greater than 50%, yet almost all canopy western redcedar and amabilis fir would survive.
4.5 LITERATURE CITED


CHAPTER 5: HISTORICAL RECONSTRUCTION OF WESTERN HEMLOCK LOOPER OUTBREAKS IN COASTAL BRITISH COLUMBIA

5.1 INTRODUCTION

Western hemlock looper (*Lambdina fiscellaria lugubrosa* Hulst) is one of the most destructive defoliating insects in British Columbia (Ministry of Forests and Range 1995). Outbreaks of western hemlock looper have occurred in the province every 10 to 15 years during the 20th century, defoliating approximately 1,000,000 hectares of forest (Koot 1994, Parfett et al. 1995). Historical surveys of insect outbreaks have been conducted by the Pacific Forestry Centre of the Canadian Forest Service’s Forest Insect and Disease Survey (FIDS) and its predecessor agencies since 1909, and since 1911, there have been seven recorded outbreaks of western hemlock looper along the south coast of British Columbia (Parfett et al. 1995, Burleigh and Gustafsson 2003). Outbreaks usually last 2 to 4 years before populations collapse to endemic levels due to high levels of larval parasitism or an epizootic of a nucleopolyhedrosis virus (Turnquist 1991). In coastal British Columbia, the preferred host for western hemlock looper is western hemlock (*Tsuga heterophylla* (Raf.) Sarg) and extensive mortality of western hemlock canopy and subcanopy trees can occur following severe defoliation (Chapter 4). During moderate and severe outbreaks, western hemlock looper will feed on almost any foliage, including other conifers, broad-leaved deciduous trees and shrubs (Jardine 1969). Douglas-fir, amabilis fir and western redcedar are commonly defoliated during outbreaks in coastal BC, but amabilis fir and western redcedar have higher levels of survivorship than western

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1 A version of this chapter will be submitted for publication.
hemlock (Duncan 2006, Chapter 4). Outbreaks lead to increased forest heterogeneity at stand to landscape spatial scales because of the patchy nature of tree death due to defoliation and species-specific mortality rates (Chapter 3). These effects on the forest are particularly important since fire and other large-scale stand-replacing disturbances are rare in coastal British Columbia (Gavin et al. 1996, Wong et al. 2003, Daniels and Gray 2006). Since western hemlock looper outbreaks are a natural and important part of the disturbance regime of forests in coastal BC, knowledge of their historical occurrence is essential for ecosystem management based on the principles of natural range of variation.

Dendrochronological methods have been used extensively in North America to reconstruct the historical occurrence of insect outbreaks (i.e. Veblen et al. 1991, Filion et al. 1998, Girardin et al. 2001, Speer et al. 2001, Simard and Payette 2001, Parish and Antos 2002, Boulanger and Arseneault 2004). These studies typically use distinctive tree-ring patterns, or signatures, that occur when there is a reduction in photosynthetic output due to insect folivory (Kulman 1971). Different types of insect outbreaks can be distinguished based on their associated tree-ring patterns. For instance, the two-year cycle budworm (Choristoneura biennis Freeman) feeds in alternate years producing an alternate growth rhythm in ring widths described as a ‘saw tooth’ (Zhang and Alfaro 2002), while the western spruce budworm (Choristoneura occidentalis Freeman) feeds exclusively on new growth, producing a noticeable radial growth suppression that lasts for several years (Van Sickle et al. 1983, Swetnam et al. 1985).
In contrast to budworms, western hemlock looper consumes needles of all ages, often defoliating entire trees in a single season, resulting in severe and abrupt growth suppression of affected trees (Turnquist 1991, Chapter 3). As western hemlock looper outbreaks often last for several years, mortality of host western hemlock trees can range from 19 to 100% following outbreaks (Chapter 4). Therefore, many of the affected trees do not survive and the distinctive tree-ring signatures used in dendrochronological historical reconstructions are not preserved, since western hemlock snags decay quickly in the moist climate of the Pacific Northwest (Hennon and Loopstra 1991). Even in areas of less severe defoliation, where lightly defoliated western hemlock trees may have survived an outbreak, the trees are often salvage logged following defoliation (Johnson et al. 1970). Thus, few stands remain along the south coast of British Columbia with a preserved tree-ring pattern of western hemlock looper defoliation.

This study is the first attempt to use dendrochronological methods to reconstruct western hemlock looper outbreaks in coastal British Columbia. I have focused on isolated forest stands located on Coquitlam Island. The island is 75 ha and surrounded by the Coquitlam Reservoir which is 1 100 ha. The reservoir and island were formed in 1905 when the Coquitlam River was dammed to generate hydro-electric power and to provide drinking water to the regional municipality of Greater Vancouver (Koop 1994). Historical records show that the island has undergone at least three known defoliations in the past century but none of the affected trees were salvage logged since access to the island was limiting (Burleigh and Gustafsson 2003). The main goal of this study was to reconstruct occurrences of western hemlock looper outbreak in coastal British Columbia prior to the
first recorded outbreak in 1911 and assess the timing, frequency and periodicity of outbreaks. Specifically, these analyses will include: (1) a calibration and verification of reconstruction techniques at sites on Coquitlam Island using differential rates of tree-ring growth between ‘host’ western hemlock and ‘non-host’ western redcedar; and (2) reconstruction of recurring western hemlock looper outbreaks over a longer time period prior to the written record at a network of sites distributed throughout the island.

5.2 METHODS

Study Area
The Coquitlam River watershed lies within the Pacific Ranges of the Coast Mountains – an area of rugged landscape 40 km northeast of the city of Vancouver, BC with glacially-carved slopes typically steeper than 35°, which rise 900 to 1300 meters above sea level from valley floor to summit. Mid and upper elevations have an exposed intrusive igneous rock bedrock, while lower to mid slopes are mantled by glacial drift and post-glacial deposits (Acres et al. 1999). The soil is predominately a Humo-Ferric Podzol, consisting of a thin eluviated (Ae) horizon and deep dark reddish B horizons rich in iron, aluminum and organic matter (Jungen and Lewis 1986). Soils are medium to coarse textured as they developed on glacial till and colluvial parent material, and leaching is intense and subject to continuous seepage in many locations due to an abundant annual precipitation, exceeding 1700 mm.

The south coast and lower mainland of British Columbia are in the Marine West-Coast Climate (Csb) of the Köppen classification in the mid-latitude zone where upper air
westerlies predominate throughout the year (Geiger and Pohl 1953). Largely influenced by the positions of the Pacific anticyclone and the Aleutian low, the position of the jet stream shifts latitudinally so that high- and low-pressure synoptic weather patterns alternate between the seasons along the south coast of British Columbia. During the growing season (May-September), high pressure systems dominate resulting in a distinct summer drought when moisture deficits occur and many plants experience water deficiency (Bertrand et al. 1991).

The forests on Coquitlam Island are a mix of second-growth and old-growth stands and are classified as the submontane (elevation < 900 metres above sea level) variant of the Very Wet to Moist Maritime Coastal Western Hemlock biogeoclimatic subzones (Acres et al. 1999). In these forests, western hemlock (*Tsuga heterophylla* (Raf.) Sarg) is the most common tree species but other frequently occurring species are western redcedar (*Thuja plicata* Donn ex D. Don), Douglas-fir (*Pseudotsuga menziesii* var. *mensieisii* (Mirb.) Franco) and amabilis fir (*Abies amabilis* Doug. ex Forbs) (Klinka et al. 1991). Coquitlam Island was defoliated to varying degrees during western hemlock looper outbreaks in 1927-1929, 1969-1973 and 2000-2003, and no other insects have visibly defoliated forests on this island during the 20th century (Acres et al. 1999, Parfett 1995, Burleigh and Gustafsson 2003).

**Study Plots**
In 2003 and 2004, I established 10 circular 900 m² plots on Coquitlam Island (Figure 5.1). The plots were systematically dispersed over the entire island and were at least 100 m apart to increase the likelihood of detecting past western hemlock looper outbreaks,
which defoliate trees in spatially distinct patches (Chapter 3). Within each plot, I recorded the species of all trees and snags with dbh ≥ 1 cm and assigned a canopy position class of either dominant, co-dominant, intermediate or suppressed (Smith 1986). Each snag was assigned a decay class based on a modified version of the classification system developed by Thomas et al. (1979) that took into account a lack of foliage due to defoliation.

**Figure 5.1** Map showing the location of study plots on Coquitlam Island.
**Dendroentomology**

Dendroentomological techniques were used to quantify annual radial growth for both western hemlock and western redcedar trees. Western hemlock is the primary host for western hemlock looper in the Coastal Western Hemlock biogeoclimatic zone (Ministry of Forests and Range 1995). As the second most prevalent species on the island, I used western redcedar as a secondary-host “control” species for reconstruction of western hemlock looper outbreaks. Western redcedar is affected by western hemlock looper during moderate and severe outbreaks, however larger individuals are rarely killed (Chapter 4).

All western hemlock and western redcedar trees and snags in the dominant and co-dominant canopy classes in each of the 10 plots were cored with an increment borer in the summers of 2003 and 2004. Tree cores were taken approximately 30 cm from the ground to best quantify defoliation impacts on growth. Cores from higher on the trunk would not provide reliable estimates of total radial growth loss due to the compensating effect of faster recovery from insect defoliation and smaller volume of wood in the upper stem (Swetnam et al. 1985). Diameter at core height, diameter at breast height, height of the core and proximity to pith were recorded for each cored tree.

Cores were air-dried and mounted in wooden supports (Stokes and Smiley 1968). They were sanded using a belt sander using successively finer grits (100, 220, 320 and 400) until the surface was smooth enough to display ring boundaries, micro-rings and other diagnostic characteristics. Tree-ring series for both species were visually crossdated to identify unusually narrow “marker” rings (Yamaguchi 1991).
Ring widths were measured to the nearest 0.001 mm using a sliding-stage Velmex micrometer interfaced with a computer. I used the program COFECHA to statistically crossdate each ring-width series to verify the visual crossdating of the cores (Holmes 1986) (Table 3.2). Statistical crossdating concurrently compares the ring-width patterns among many tree ring series so that missing rings or false rings can be identified. This is especially important in studies measuring the effect of defoliation on radial growth because of the above-average likelihood of missing rings due to the low growth rate of defoliated trees (Swetnam et al. 1985). Crossdating also allowed for the year of death for each snag to be determined. This is because the outermost ring in each series either represented the last year of radial growth for living trees (i.e. 2003) or the last year of radial growth before death for snags. Crossdated tree-ring series for western hemlock were grouped by site to establish plot level chronologies. All crossdated tree-ring series for western redcedar were grouped into a single island-level, control chronology.

To remove age-related trends in growth, each dated ring-width series was standardized with the program ARSTAN (Cook and Holmes 1996, Grissino-Mayer and Fritts 1997). Each tree-ring series was fit with a flexible, 40 year, 50% frequency response cubic spline (Cook and Peters 1981). This meant that the computed tree-ring indices retained 90% of the variance in the original ring-width series with wavelengths of 20 yr. Thus, almost all of the tree-ring width changes occurring over time scales of less than two decades were preserved in the index series, so most of the relatively short-term effects of individual western hemlock looper outbreaks should have been retained in the index.
series. Autocorrelation was not removed from the standardized chronologies to preserve the outbreak signal. Individual ring-width values for each tree-ring series were then divided by the value of the fitted curves to produce unit-less tree-ring indices with a mean of 1.0.

Calibration of OUTBREAK
OUTBREAK is a computer program developed to identify periods of growth suppression in tree-ring indices (Holmes and Swetnam 1996). It compares the ring-width series of host and non-host, ‘control’ species to identify past insect outbreaks. If the host and control species respond similarly to climate, then comparing their chronologies accounts for periods of common growth variation, which is most often a response to climate conditions (Nash et al. 1975, Holmes and Swetnam 1996) and amplifies periods of differential growth (Swetnam et al. 1985). In this region, both western hemlock and western redcedar are known to react similarly to climate. For instance, ring-widths of both species are limited by high August temperatures of the previous growing season and high June temperatures of the current growing season (A. Stan, unpublished data). To further confirm that the site-specific western hemlock chronologies and the island-level western redcedar chronology from Coquitlam Island responded to climate similarly, I verified that all chronologies displayed common narrow marker rings during years of documented summer drought (i.e. 1897, 1959, 1969, 1989; Chapter 2).

OUTBREAK detects periods of insect defoliation by examining the duration and magnitude of tree-ring suppression of host trees relative to tree-ring growth of non-host, control trees. These parameters can be modified to account for the distinct pattern of
defoliation by different species of insect. As there have been no previous studies using OUTBREAK to detect western hemlock looper defoliations, I adapted the screening criteria used in studies of detecting spruce budworm (Veblen et al. 1991, Parish and Antos 2002, Boulanger and Arseneault 2004) and Pandora moth (Speer et al. 2001) to modify the program’s default settings. Based on preliminary analysis of western hemlock tree-ring series from areas known to have been defoliated during the 2000-2003 outbreak, there is a lagged response in tree-ring suppression after the onset of a western hemlock looper outbreak (Chapter 3). As well, mortality of defoliated trees continued for at least three years following the collapse of western hemlock looper populations (Chapter 4). Thus, I hypothesized that periods of below-average growth would last several years longer than actual western hemlock looper outbreaks and that a window of three to seven years of below-average growth would identify radial growth suppression of western hemlock trees that survived past western hemlock looper outbreaks.

The second parameter in OUTBREAK is a threshold of ring-width suppression that detects significant reductions in growth. As with other defoliation studies, a significant growth suppression occurred when the ring-width index was $\geq 1.28$ standard deviations below average for at least one year (Swetnam and Lynch 1989, Speer et al. 2001, Boulanger and Arseneault 2004). This level of suppression corresponds approximately to the smallest 10th percentile of values in any tree-ring series. I recorded the beginning and end of each suppression as the first and last years when the ring-width indices crossed the threshold of the below-average growth.
Verification of Known 20th Century Outbreaks

Using the program OUTBREAK, I compared the individual standardized western hemlock (host) tree-ring series to the western redcedar (control) master chronology. OUTBREAK identified periods of significant growth suppression and computed the duration, percentage maximum growth reduction, and percentage mean growth reduction for each suppression. Percentage maximum growth reduction for each outbreak is defined as the mean index value minus the smallest index value during outbreak, multiplied by 100. Percentage periodic growth reduction for each outbreak is defined as the mean series index value minus the mean index value during outbreaks, multiplied by 100. In both cases the ‘mean series index value’ was 1.0 as the chronologies had been standardized.

Western hemlock trees were grouped by plot and the frequency of suppressions was calculated. As all 10 plots displayed the same general timing in the frequency of identified periods of suppressed trees, I grouped all trees for an island-level analysis of outbreaks. The number of trees included in the chronologies decreased with increasing time before the present, thus I divided the absolute number of trees identifying periods of suppression by the total number of trees included in the chronologies for each year to calculate a relative frequency of trees with suppression per year. To verify the effectiveness of OUTBREAK to detect western hemlock looper outbreaks, I compared the relative frequency of identified suppressions in radial growth to known dates of outbreaks in the FIDS record (Parfett et al. 1995). I expected a high frequency of suppression and low growth to occur during the four known 20th century outbreaks.
Reconstruction of Outbreaks Prior to Known 20\textsuperscript{th} Century Outbreaks

Using the frequency distribution for known outbreaks the 20\textsuperscript{th} century, I noted that >35\% of western hemlocks showed suppression following outbreaks and <35\% of western hemlocks showed suppression during other periods. Thus, 35\% was defined the threshold percentage of trees that must show suppression in an outbreak and used to assess the relative frequency of releases in the 19\textsuperscript{th} century and infer past outbreaks.

Quantification of Temporal Aspects of Outbreaks

I used all inferred outbreaks during the 19th and 20th century to quantify the temporal aspects of the western hemlock looper disturbance regime. For each outbreak, I chose the calendar year with the highest number of trees recording their maximum radial growth suppression to assign a singular date for each outbreak to be used to: (a) calculate the interval between successive outbreaks, (b) calculate mean, standard deviation, and range of intervals for entire study period, and (c) calculate mean, standard deviation, and range of intervals for the 1911-2003 versus 1775-1910 time periods and test for differences using a t-test. To test for the effects of outbreaks on western hemlock growth, I calculated the mean, standard deviation, and range of the periodic growth reduction of western hemlock ring-widths for the entire study period and for the 1911-2003 versus 1775-1910 and tested for differences using a t-test.
5.3 RESULTS

Stand Structure and Composition

A total of 863 trees and snags with dbh > 1.0 cm were recorded within 10 plots (900 m²) on Coquitlam Island. These included 516 western hemlock (59.8% of total trees and snags), 313 western redcedar (36.3%), 13 amabilis fir (1.5%) and 10 Douglas-fir (1.2%). Eleven snags were too decayed to determine species (1.3%). Average tree density (dbh ≥1 cm) was 978±785 trees/ha and average basal area was 117±28 m²/ha (Table 5.1).

Many stands on Coquitlam Island were moderately to severely defoliated during a 2000-2003 western hemlock looper outbreak; thus, only 299 trees were living at the time of the study while 297 were classified as “recently-dead” snags (representing 34.4% of all trees). Recently-dead snags most likely died during the 2000-2003 western hemlock looper outbreak (Chapter 3).

Table 5.1. Structural and compositional attributes of the forest in 10 plots located on Coquitlam Island.

<table>
<thead>
<tr>
<th>Plot No.</th>
<th>Density (trees/ha)</th>
<th>Basal area (m²/ha)</th>
<th>Relative abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All trees</td>
<td>Live trees</td>
<td>Recent snags</td>
</tr>
<tr>
<td>1</td>
<td>1310</td>
<td>733</td>
<td>122</td>
</tr>
<tr>
<td>2</td>
<td>688</td>
<td>422</td>
<td>111</td>
</tr>
<tr>
<td>3</td>
<td>400</td>
<td>133</td>
<td>222</td>
</tr>
<tr>
<td>4</td>
<td>577</td>
<td>144</td>
<td>344</td>
</tr>
<tr>
<td>5</td>
<td>622</td>
<td>233</td>
<td>333</td>
</tr>
<tr>
<td>6</td>
<td>1020</td>
<td>422</td>
<td>356</td>
</tr>
<tr>
<td>7</td>
<td>389</td>
<td>22</td>
<td>300</td>
</tr>
<tr>
<td>8</td>
<td>611</td>
<td>178</td>
<td>244</td>
</tr>
<tr>
<td>9</td>
<td>866</td>
<td>422</td>
<td>111</td>
</tr>
<tr>
<td>10</td>
<td>3210</td>
<td>611</td>
<td>1256</td>
</tr>
</tbody>
</table>
Chronologies

A total of 165 western hemlock and 94 western redcedar trees and snags were cored and crossdated to construct 10 plot-level western hemlock chronologies and one island-level master western redcedar chronology (Table 5.2). The chronologies were truncated to include only years when both species were represented by at least 5 trees (i.e. 1775-2003). The western hemlock chronologies had low inter-series correlations (0.374±0.060, mean ± standard deviation) and mean sensitivity values (0.252±0.020). These values indicate relatively complacent ring-width patterns among western hemlock in the low-elevation coastal forest where climate and resource availability generally do not limit tree growth. The western redcedar chronology had an inter-series correlation of 0.500 and a mean sensitivity of 0.202, meaning the western redcedar in this study shared a stronger common signal among trees than western hemlock, but western redcedar is one of the most complacent species (Grissino-Mayer 2001).

Table 5.2. Summary of descriptive statistics for the 10 plot-level western hemlock chronologies and the island-level western redcedar chronology from Coquitlam Island.

<table>
<thead>
<tr>
<th>Plot no.</th>
<th>Species</th>
<th>No. of cores (n)</th>
<th>Time series</th>
<th>Mean inter-series correlation</th>
<th>Mean sensitivity</th>
<th>First order autocorrelation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Hemlock</td>
<td>30</td>
<td>1918-2002</td>
<td>0.438</td>
<td>0.245</td>
<td>0.44</td>
</tr>
<tr>
<td>2</td>
<td>Hemlock</td>
<td>10</td>
<td>1922-2002</td>
<td>0.312</td>
<td>0.225</td>
<td>0.68</td>
</tr>
<tr>
<td>3</td>
<td>Hemlock</td>
<td>9</td>
<td>1918-2002</td>
<td>0.435</td>
<td>0.239</td>
<td>0.65</td>
</tr>
<tr>
<td>4</td>
<td>Hemlock</td>
<td>13</td>
<td>1902-2000</td>
<td>0.401</td>
<td>0.266</td>
<td>0.56</td>
</tr>
<tr>
<td>5</td>
<td>Hemlock</td>
<td>18</td>
<td>1926-2001</td>
<td>0.384</td>
<td>0.287</td>
<td>0.56</td>
</tr>
<tr>
<td>6</td>
<td>Hemlock</td>
<td>14</td>
<td>1753-2003</td>
<td>0.270</td>
<td>0.229</td>
<td>0.68</td>
</tr>
<tr>
<td>7</td>
<td>Hemlock</td>
<td>12</td>
<td>1873-2001</td>
<td>0.449</td>
<td>0.238</td>
<td>0.70</td>
</tr>
<tr>
<td>8</td>
<td>Hemlock</td>
<td>14</td>
<td>1838-2002</td>
<td>0.366</td>
<td>0.264</td>
<td>0.60</td>
</tr>
<tr>
<td>9</td>
<td>Hemlock</td>
<td>20</td>
<td>1725-2004</td>
<td>0.321</td>
<td>0.274</td>
<td>0.60</td>
</tr>
<tr>
<td>10</td>
<td>Hemlock</td>
<td>25</td>
<td>1695-2004</td>
<td>0.363</td>
<td>0.251</td>
<td>0.62</td>
</tr>
<tr>
<td>Island</td>
<td>Redcedar</td>
<td>94</td>
<td>1469-2004</td>
<td>0.500</td>
<td>0.202</td>
<td>0.79</td>
</tr>
</tbody>
</table>
Verification of Known 20th Century Outbreaks

Western redcedar can be defoliated during severe western hemlock looper outbreaks. Evidence of western redcedar tree-ring suppression was seen in the master chronology (Figure 5.2). In fact, for western redcedar trees, the tree-ring pattern associated with the four outbreaks during the 20th century was consistent. During outbreaks, tree-ring growth was below average, with smallest values near or at the end of each outbreak (i.e. 1914, 1927, 1959 and 1972). Each outbreak was followed by a period of steady recovery and above-average growth lasting four to 10 years (i.e. peaks in 1919, 1935, 1964 and 1982). The relative differences in radial growth between western redcedar and western hemlock during the 20th century were clearly identified by the program OUTBREAK. Thus, in spite of these impacts of western hemlock looper on the absolute growth of western redcedar, the western redcedar chronology served as an effective control for reconstructing past outbreaks.

The four recorded outbreaks of western hemlock looper in the 20th century were clearly evident as ring-width suppressions in many of the 10 plot-level western hemlock chronologies (Figure 5.2) and were consistently detected by the program OUTBREAK (Figure 5.3). According to the FIDS records, severe defoliations by western hemlock looper were recorded on Coquitlam Island during 1927-1929 and 1969-1973. Seven of the 10 plot-level western hemlock looper chronologies had below-average ring-width indices during 1929-1932 and nine of 10 during 1969-1973. OUTBREAK detected island-wide suppressions following both of these defoliations. FIDS records also indicate
Figure 5.2 Standardized western hemlock chronologies for each of the 10 plots on Coquitlam Island and the master western redcedar chronology from the island. Shaded areas are years of known western hemlock looper outbreaks. The dotted lines indicate the sample depth or number of cores included in each chronology in each year.
Figure 5.3 Frequency of significant radial growth suppressions of western hemlock in each study plot. Radial growth suppressions were considered significant when the smallest ring-width index was ≥ 1.28 standard deviations below the average.
that severe defoliations were recorded in nearby (~30 km) forests during 1911-1914 and 1958-1959, and all sites had below-average ring-width growth during 1911-1914 while seven of 10 sites displayed below-average ring-widths during 1958-1959. Again, OUTBREAK detected island-wide defoliations during these periods.

Although OUTBREAK detected known western hemlock looper outbreaks during the 20th century, the timing of the reconstructed outbreaks consistently differed from the FIDS record. The periods of western hemlock growth suppression detected by OUTBREAK occurred two to six years (4.2±1.7) after recorded western hemlock looper outbreaks in the 20th century.

**Reconstruction of Outbreaks Prior to Known 20th Century Outbreaks**

Prior to the first recorded outbreak in 1911, I identified four periods of suppression in 1803-1809, 1829-1831, 1865-1869 and 1901-1906 (Figure 5.4, Table 5.3). Nine smaller peaks in which 13% to 22% of trees showed suppression were also detected.

For all eight periods in which OUTBREAK identified suppression in at least 35% of all trees, the duration varied between three and seven years (Table 5.3). The highest percentage of western hemlock trees showing suppression during each reconstructed outbreak occurred in 1980, 1964, 1943, 1919, 1904, 1868, 1829 and 1806 (Table 5.3, Table 5.4). Based on these peak years, the average return interval between successive outbreaks on Coquitlam Island was 24.9±9.3 years with a range of 15 to 39 years. Differences in the number of years between outbreaks after 1911 (20.3±4.0 years, n = 3)
and outbreaks before 1911 (32.7±8.5, n = 3) were not statistically different, although sample sizes were low.

The periodic growth reduction of western hemlock ring-widths during the eight reconstructed outbreaks was 43.5±15.2%. There was no significant difference in period growth reduction between outbreaks after 1911 (49.78±5.51 %) and outbreaks before 1911 (46.15±8.02 %) (Table 5.4).
Figure 5.4 The (a) absolute frequency and (b) relative frequency of western hemlock trees sampled on Coquitlam Island with significant radial growth suppression (grey bars). Radial growth suppressions were considered significant when the ring-width index was $\geq 1.28$ standard deviations below the average. (a) The sample depth line is the number of trees in the dataset in each year. (b) The dashed line at 35% indicates the threshold percentage of suppressed trees used to identify outbreaks of western hemlock looper.
Table 5.3 Summary of radial growth criteria used to infer western hemlock looper outbreaks. For outbreaks after 1911, the dates of the reconstructed outbreaks were compared with the Forest Insects and Disease (FIDS) records.

<table>
<thead>
<tr>
<th>Years</th>
<th>No. hemlock recording outbreak</th>
<th>% hemlock recording outbreak</th>
<th>No. trees with max. growth reduction</th>
<th>Known 20\textsuperscript{th} century outbreak (interval before detection)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1803</td>
<td>7</td>
<td>43</td>
<td>0</td>
<td></td>
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<td></td>
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<td>1829</td>
<td>6</td>
<td>50</td>
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<tr>
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<td>1</td>
<td></td>
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<td>67</td>
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<td>1958-1959 (4)</td>
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<td>1984</td>
<td>61</td>
<td>38</td>
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Table 5.4 Summary of radial growth response of western hemlock trees during eight reconstructed outbreaks of western hemlock looper on Coquitlam Island.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Trees with maximum radial growth suppression during period</th>
<th>Average duration of below-average radial growth (years±SD)</th>
<th>Periodic growth reduction (%±SD)</th>
<th>Most common year of maximum growth reduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1803-1809</td>
<td>5 (71)</td>
<td>5.80±1.64</td>
<td>47.74±0.16</td>
<td>1804</td>
</tr>
<tr>
<td>1829-1831</td>
<td>6 (50)</td>
<td>5.00±1.26</td>
<td>43.14±0.08</td>
<td>1829</td>
</tr>
<tr>
<td>1865-1869</td>
<td>10 (50)</td>
<td>5.20±1.55</td>
<td>52.54±0.12</td>
<td>1868</td>
</tr>
<tr>
<td>1901-1906</td>
<td>16 (48)</td>
<td>6.06±1.24</td>
<td>55.70±0.15</td>
<td>1904</td>
</tr>
<tr>
<td>1916-1920</td>
<td>30 (67)</td>
<td>4.93±1.31</td>
<td>57.83±0.14</td>
<td>1919</td>
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<tr>
<td>1935-1944</td>
<td>103 (74)</td>
<td>4.95±1.52</td>
<td>39.60±0.14</td>
<td>1943</td>
</tr>
<tr>
<td>1963-1965</td>
<td>62 (37)</td>
<td>4.60±1.31</td>
<td>43.95±0.16</td>
<td>1964</td>
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<tr>
<td>1978-1984</td>
<td>96 (59)</td>
<td>5.76±1.53</td>
<td>43.22±0.14</td>
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</table>

5.4 Discussion

This study represents the first reconstruction of western hemlock looper outbreaks using dendroentomological methods. I have successfully used periods of western hemlock suppression within the tree-ring record to confirm four previously documented, local western hemlock looper outbreaks in the Coquitlam River watershed, and to identify four additional outbreaks that occurred prior to the first recorded outbreak in 1911. Together, these eight outbreaks allowed me to calculate a stand-level return interval of 24.9±9.3 years for western hemlock looper outbreaks. This study demonstrates that outbreaks of western hemlock looper have been ongoing along the south coast of British Columbia for at least 200 years. This information allows for a greater understanding of the temporal aspects of western hemlock looper as a disturbance agent in coastal British Columbia.
**Temporal Aspects of Outbreaks**

Eight western hemlock looper outbreaks were inferred in this study by comparing the individual tree-ring series of western hemlock to a control western redcedar chronology using the program OUTBREAK. Although effective for detecting outbreaks, the tree-ring reconstructions consistently over-estimated the duration of the outbreaks and underestimated dates of the outbreaks by 2 to 6 years relative to the FIDS records. This discrepancy is explained by considering the approach and assumptions that underlie the dendroentomological method. Specifically, reconstructions using tree rings are based on the relative responses of host and non-host species and detect tree responses to the outbreak rather, which may be delayed up to 2 years after an outbreak begins.

The delay in ring-width suppression of western hemlock may reflect, in part, a lag period related to stored food reserves that support growth during the initial phases of defoliation (Fritts 1976). This lag has been well documented for many other defoliators, including Pandora moth (Speer et al. 2001) and two-year budworm (Parish and Antos 2002, Zhang and Alfaro 2002). In this study, a lag was also detected in the western redcedar chronology, reflecting the fact that western redcedar are also defoliated, albeit to a lesser degree than western hemlock, during western hemlock looper outbreaks.

Western redcedar was the best choice for a control species in this study given that it co-dominates the forests on Coquitlam Island and responds to climate similarly to western hemlock. However, it was not an ideal comparison because it was a secondary-host for western hemlock looper during severe outbreaks. Therefore, ring-widths of western...
redcedar showed suppression during known outbreaks. However, western redcedar recovers from defoliation faster than western hemlock so that relative growth rates, which were measured by OUTBREAK, only differed significantly between the two species after each outbreak. Furthermore, due to the death of severely defoliated trees, only lightly defoliated western hemlocks survived any given outbreak (Chapter 3). Therefore, this decreases the likelihood of detecting severe western hemlock looper suppression during actual outbreak years as the degree of suppression for surviving western hemlock and western redcedar may be too similar to be detected using host/non-host comparisons. This reasoning may explain why there was a moderate amount of western hemlock suppression detected during the 2000-2003 (a peak of 22% in 2000, Figure 5.4). A closer examination of the trees showing this suppression revealed that the majority of these trees were recorded as ‘recently-dead’ snags and had died prior to sampling. Mortality from this event will likely continue for several more years (Chapter 4). Therefore, a significant portion of the trees contributing to the 2000-2003 peak in suppression of western hemlock will be removed from the living tree-ring record and the remaining small peak may not be detected in future dendroentomological studies of this area.

Lastly, inter-annual climate variation may also contribute to the date of onset and duration of reconstructed outbreaks. Chapter 2 demonstrated a correlation between warm dry Junes, and the beginning of western hemlock looper outbreaks. These are also conditions that lead to the formation of narrow rings in both western hemlock and western redcedar (A. Stan unpublished data). Thus, western hemlock looper outbreaks tend to follow years of drought and the prolonged periods of below-average radial growth.
identified in this study were probably due to the combined effects of defoliation and drought.

**Reconstruction Threshold**

To infer outbreaks prior to 1911, a quantitative criterion was required for the percent of trees that were suppressed. In this study, a threshold of 35% was objectively chosen, based on observations from known outbreaks in the 20th century. The selection of any threshold however, inevitably involves a tradeoff between the risk of not detecting past outbreaks and falsely detecting outbreaks that did not occur (Parish and Antos 2002). My selection of 35% of western hemlock showing significant suppression may have established an overly conservative threshold for the detection of historical outbreaks since the chances of older western hemlock tree surviving multiple western hemlock looper outbreaks is relatively low (Chapter 4). A more liberal criterion would have been more inclusive for older outbreaks. For example, a threshold of 25% would have include the 1840s peak in Figure 5.4, which would have increased the number of outbreaks and intervals and deceased the mean return interval to 25.9±7.9 years for the pre-1911 period. However, this peak represents only 5 trees of 17 recorder trees (29%), which may been due to causes other than a western hemlock looper outbreak given the fact that western hemlock radial growth is very sensitive to fine-scale gap dynamics in coastal British Columbia and individual western hemlock trees have repeated suppressions and releases throughout their tree-ring record (A. Stan unpublished data). An even lower threshold would have included the smaller peaks in 1800s. Nonetheless, the selection of a conservative threshold was justified due to the low inter-series correlations for my western hemlock tree-ring chronologies, which demonstrate a high degree of variability in the radial growth patterns of western hemlock in this study.
Detection of Historical Outbreaks

Moderate- and low-severity outbreaks were successfully captured in the tree-ring record and identified by OUTBREAK. For instance, during both the 1958-1959 and 1911-1914 outbreaks, visible defoliation was not directly recorded on Coquitlam Island, yet these dates were established as western hemlock looper outbreaks based on visible defoliation in the neighbouring Capilano River watershed, ~30 km to the west. Therefore, it is probable that the detection of these outbreaks in the tree-ring record from Coquitlam Island represent legitimate suppression and release owing to higher than endemic levels of western hemlock looper during 1911-1914 and 1958-1959, even though these levels were not high enough to cause visible defoliation of large patches of forests on Coquitlam Island and be detected by FIDS. A similar situation existed during 2000-2003 when stands in the Capilano River watershed were not visibly defoliated, yet pheromone trap catches of western hemlock looper in the area were significantly higher than endemic levels and stands in the Coquiltam River watershed were severely defoliated (Burleigh and Gustafsson 2003).

Therefore, the tree-ring approach may have been more effective for detection of low- and moderate-severity outbreaks than the earlier (i.e. pre-1960) FIDS records. This may reflect the fact that regular aerial surveys by FIDS and its predecessor agencies began only in the 1960s and that the earlier FIDS record relied heavily on the detection of visible defoliation from ground surveys (Parfett et al. 1995). Therefore, like many historical records, the quality of the record is greatest in recent decades and decreases in the earlier part of the record.
Is Coquitlam Island Representative of the Coastal Forest?
This research was a case study, designed to determine if dendroentomological methods could be used to successfully reconstruct western hemlock looper outbreaks. I chose Coquitlam Island for my study area because of the prevalence of historical visible defoliations by western hemlock looper, and because the island had not been subjected to subsequent salvage logging. In contrast, the FIDS records indicate repeated outbreaks of western hemlock looper in only a few coastal forests since 1911 (see Figure 2.1 in Chapter 2). Using dendroentomological methods, I was able to identify eight outbreaks of western hemlock looper over a 225-year time span at the stand level, with a mean interval of 25 years and a range of 15-39 years. These numbers are higher than any stand-level return intervals that could have been estimated for coastal forests based on the FIDS records alone. This is most likely due to the fact that lower severity outbreaks may be more easily detected by tree-ring analysis than by earlier ground surveys conducted by FIDS and suggests a bias in the FIDS records towards severe outbreaks leading to large-scale visible defoliation. My results however, suggest that outbreaks of western hemlock looper may have been more widespread, but had lower impacts, than the discrete patches of visibly defoliated trees detected in historical records (Chapter 3).

To test the hypothesis that low- to moderate-severity outbreaks of western hemlock looper may be more common and widespread in coastal forests than previously believed would require a detailed understanding of the frequency, spatial distribution and severity of past outbreaks. A landscape-scaled dendroentomological study, including old-growth stands to potentially lengthen the reconstruction record, would help address questions surrounding the frequency of past outbreaks. This study could use the FIDS records as a
guide to site selection, yet choose to focus on nearby stands that may not have been recorded as visibly defoliated. Given the spatially noncontiguous nature of severe defoliation from outbreaks, I believe that many of these stands may have escaped salvaged logging following outbreaks. Therefore, a landscape-scaled study would help elucidate some of the details surrounding frequency and spatial distribution of historical western hemlock looper outbreaks, although assessing the severity of each outbreak may be more difficult to discern.

Understanding the historical frequency and severity of western hemlock looper outbreaks is important for anticipating future changes in forest dynamics. In coastal BC, climate is predicted to become warmer and drier during the growing season, which may facilitate more frequent outbreaks (Chapter 2) and potentially result in more severe outbreaks. This study clearly demonstrated that tree-ring methods are effective for identifying past outbreaks. Landscape-level analyses would quantify historic frequency and, potentially, severity of outbreaks and provide a baseline against which future outbreaks can be compared.
5.5 LITERATURE CITED


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MacLean, D.A. and Ebert, P. 1999. The impact of hemlock looper (Lambdina fiscellaria fiscellaria (Guen.)) on balsam fir and spruce in New Brunswick, Canada. Forest Ecology and Management 120: 77-87.


CHAPTER 6: SUMMARY

The main goal of my dissertation was to increase knowledge of the causes and effects of western hemlock looper outbreak activity in the coastal forests of British Columbia. My research was necessary because little was known about the role that this biological disturbance agent plays in the processes that have created and continue to maintain coastal forests. To this end, my dissertation has provided new information that is essential for effective ecosystem management based on natural range of variation in this region.

Ecosystem management involves ensuring the sustainability of the structure, function and processes of an ecosystem. To be successful, it must be firmly based upon sound models and scientific research that emphasize the interactions and processes that create and maintain ecosystems. The use of natural variability in ecosystem management requires that managers have sufficient knowledge of historical conditions, and the processes that created and maintained them. The studies I present in this dissertation were conducted at temporal and spatial scales that specifically correspond to these research objectives.

I have empirically established a link between inter-annual climate variation and western hemlock looper populations in coastal forests. Prior to this study, little was known about the factors that facilitate western hemlock looper population growth and ultimately drive populations to outbreak levels in coastal British Columbia. I demonstrated that climate has a significant influence on the timing of historic western hemlock looper outbreaks by developing a ‘moisture stress index’ to examine correlations between monthly, seasonal, and annual climate variation and western hemlock looper outbreaks that have occurred.
along the south coast and lower mainland of British Columbia during the 20th century. My results indicate that above-average temperature and below-average precipitation facilitate outbreaks of western hemlock looper.

The link between historical western hemlock looper outbreaks and antecedent climatic conditions allowed me to anticipate ecosystem responses to human-caused global climate change. I hypothesize that future outbreaks of western hemlock looper will increase in frequency and severity on the south coast given the large abundance of maturing second-growth forest combined with warmer and drier climate conditions along coastal British Columbia predicted by many models.

I examined the effects of varying severities of defoliation by western hemlock looper on tree mortality rates, canopy openness and understory composition in coastal forests. The decision by managers not to log defoliated stands in the Coquitlam River watershed provided a unique research opportunity to monitor the mechanisms and processes of stand development and succession following defoliation of different severities. As the severity of outbreaks increased, canopy tree mortality and canopy openness increased as well, resulting in changes to the composition of the forest understory and potentially altering the regeneration dynamics of disturbed stands. Therefore, due to variation in the severity of defoliation, the 2000-2003 western hemlock looper outbreak in the Coquitlam River watershed produced distinct forest patches within a part of the landscape that had been relatively homogenous prior to disturbance. I concluded that these patch-specific structural and compositional changes increase the variability in successional pathways of
affected forest stands and will increase the heterogeneity at the landscape scale. This knowledge is critical in understanding the ecological effects following disturbance by native insects in coastal forests.

In a second study of disturbance effects, I determined that the composition of the surviving forest was altered by species-specific mortality rates associated with western hemlock looper defoliation. High levels of mortality for western hemlock and Douglas-fir caused a decrease in the dominance of these species and an increase in the relative density of western redcedar, amabilis fir and deciduous species within the surviving canopy and subcanopy trees of affected stands. Using repeated census data of trees in defoliated areas, I developed logistic regression models to serve as a guide for predicting mortality of western hemlock, Douglas-fir, western redcedar and amabilis fir due to western hemlock looper defoliation in coastal forests of British Columbia. These models suggest that the length of a western hemlock looper outbreak determines overall mortality rates for different conifer trees, yet mortality will also be significantly influenced by tree diameter. Therefore, this study has provided new information on how western hemlock looper outbreaks can alter forest structure by causing species-specific tree mortality. Knowledge of the effects of that these outbreaks have on tree mortality and survival is essential for resource managers to make ecologically-based decisions about if and when salvage logging of forests defoliated by western hemlock looper is justified.

Finally, I have been the first to reconstruct outbreaks of western hemlock looper in coastal forests using dendroentomological techniques. I found that periods of western
hemlock suppression relative to western redcedar growth were successfully detected by the program OUTBREAK. I verified the effectiveness of this approach by comparing the dates of outbreaks determine by the program OUTBREAK with known western hemlock looper outbreaks in the 20th century Forest Insects and Disease Survey (FIDS) records for British Columbia. I determined the growth responses of western hemlock detected by OUTBREAK occurred 2 to 6 years following recorded outbreaks of western hemlock looper. After identifying periods of known western hemlock looper outbreaks in the 20th century, I was able to reconstruct four outbreaks between 1775 and 1910 and determine that the frequency of outbreaks at the stand-level has not significantly changed over the past 200 years. At the stand level, I detected more outbreaks during the 20th century using dendroentomological methods than were recorded in the FIDS records. Therefore, the return interval for stand-level outbreaks determined dendroentomologically was less than the intervals calculated using the FIDS records. I concluded that dendroentomological studies have the capacity to detect outbreaks of low, moderate, and high severity while the FIDS records include only moderate to high severity outbreaks, explaining these discrepancies.

Based on my historical reconstruction of outbreaks, I established that defoliation by western hemlock looper has been an ongoing disturbance agent that has influenced forest dynamics along the south coast of British Columbia for over 200 years. Understanding the historical frequency of western hemlock looper outbreaks is essential for understanding its role in the disturbance regime of coastal forests. This information is required for detecting and anticipating possible future changes in forest dynamics.
Overall, my dissertation has provided a fundamental contribution to the understanding of disturbance in coastal forest ecosystems. Knowledge of the role that climate plays in driving historical outbreaks and the natural variation in the historical frequency of outbreaks is crucial for predicting future occurrence of western hemlock looper outbreaks. Furthermore, knowledge of the impacts that outbreaks of western hemlock looper have had on coastal forests is essential in predicting forest response to defoliation by western hemlock looper and is necessary for sustainable, ecologically-based management.