

FACTORS AFFECTING SURVIVAL DYNAMICS IN BALSAM FIR IN NEW BRUNSWICK, CANADA

by

Christian K. Akpanya

BSc. Physics, University of Cape Coast, Cape Coast, Ghana, 2002

MSc. Atmospheric Science (Course work), Creighton University, Omaha NE, USA, 2011

Diploma in University Teaching, University of New Brunswick, 2013

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Supervisor: Charles P.-A. Bourque, Ph.D., Ecological Hydrometeorology

Examining Board: Emmanuel Stefanakis., Ph.D., Electrical and Computer
Engineering, Geodesy and Geomatics Engineering Department,
Jasen Golding, M.F.E., R.P.F., Forest Operations Planning, Faculty
of Forestry and Environmental Management

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ABSTRACT

Interaction of factors influencing individual-tree survival remains one of the least understood elements of forest growth and yield. An approach to the environment that addresses a combination of environmental variables is indispensable to the study of tree mortality. This thesis is based on an evaluation of mortality caused by unknown factors as well as eight documented factors, including insect damage, tree suppression, broken top, stem breakage, windthrow, over mature, stem wound, and cut. Data from 939 permanent sample plots (PSP's) in New Brunswick containing balsam fir are sampled to determine mortality over consecutive measurement periods. Tree data in PSP's are analyzed with environmental surface data accounting for water, energy, and light requirements of the trees. Spruce budworm [SBW; *Choristoneura fumiferana* (Clem.)] is the most important of all insects causing mortality in balsam fir. The impact of SBW during and after infestation is evaluated. Mortality as a "legacy effect" of the latest SBW infestation (1972-1993) is manifested in the form of windthrow (33.3%), stem breakage (33.3%), and broken tops (16.7%), mainly in the Highland ecoregion of the province where winds are frequently strong. Anthropogenic causes of mortality account for another 12.4% of observed mortality, i.e., 6.7% and 5.7% from likely cut and stem wound damage, respectively. Hot spot analysis of unexplained mortality suggests that greatest mortality occurs in the Grand Lake ecoregion, mostly in high soil water content and high growing degree-day areas of the province. Unexplained mortality may be largely ascribed to the process of self-thinning, while documented causes are more catastrophic in nature. This study fosters an improved understanding of regional survival dynamics in balsam fir.

Keywords: balsam fir, catastrophic, hot spot analysis, self-thinning, spruce budworm, water, energy, and light requirements

DEDICATION

This thesis is dedicated to the blessed memory of my beloved parents, Peter Kwami Akpanya, August 29, 1936 to April 11, 1996 and Victoria Esi Kporku-Akpanya, November 24, 1943 to July 20, 2015.

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1 LITERATURE REVIEW AND BACKGROUND

1.1 Introduction

Mortality of balsam fir [*Abies balsamea* (L.)] is a natural, but complex process that can be affected by many inter-related factors, such as competition, self-thinning, insect damage, disease, or extreme climate. In eastern Canada, spruce budworm [SBW, *Choristoneura fumiferana* (Clem.)] defoliation can produce varying levels of mortality in balsam fir stands (Pothier & Mailly, 2006). In their studies, Pothier & Mailly (2006) indicated that tree defoliation by SBW may account for between 6 and 100% of merchantable volume loss, depending on outbreak severity.

Interaction of factors influencing individual-tree survival remains one of the least understood elements of forest growth and yield (Teck & Hilt, 1990). Knowing a species' likelihood of surviving is essential in charting a forest's progression and development over time. The most commonly used measure of tree growth is diameter growth, an indicator of a tree's potential within the context of its environment (Buchman et al., 1983). Survival, in turn, can be characterized by tree growth and mortality.

One essential feature of a tree model is an accurate prediction of mortality (Monserud, 1976). This requirement is evident in the screening of sites and tree characteristics by Monserud (1976) and settling on predicted diameter, diameter growth, and competition level as key predictors of mortality. Buchman (1979); Landford & Cunia (1977) used diameter growth rate (DGR) and diameter at breast height (DBH) to predict tree mortality. Modeling tree species distribution can define potential habitats that fulfill species' requirements for survival (Fischer & Fisher, 1990). However, attempts to forecast

habitat suitability for tree species have often relied on their density or occurrence in landscapes (van Horne, 1983). The validity of this approach has been questioned because individual tree species can meet their environmental requirements beyond their limits of current occurrence (van Horne, 1983). Consequently, tree density and occurrence may be misleading indicators of habitat preference (Yost, 2008).

To consider a more reliable estimate, all environmental variables within which individual tree species can exist are adequately delineated. This consideration is the aim of potential species distribution models (PSD) as developed by Bourque et al. (2000) and Chuine & Beaubien (2001). In the study of PSD, quantifying the relations between species response and environmental conditions is based on a set of environmental variables selected from a possible range of variables because of their importance in influencing tree species habitat quality (e.g. Bourque et al., 2000; Gullison, 2002; Bourque & Hassan, 2009). The selected variables regularly include (i) photosynthetically active radiation (PAR), (ii) growing degree-days (GDD), and (iii) soil water content (SWC). These three biophysical variables reflect two primary qualities of the environment, i.e., energy and water, which, based on prior knowledge, have known roles in imposing a restriction on tree distribution because of widely shared physiological limitations (Prentice et al., 1992).

Understanding species' presence as a function of biophysical variables can be improved by accounting for species survival for current microclimatic conditions. As population viability depends strongly on survival rate, a species-specific understanding of balsam fir stand dynamics with and without insect disturbances is needed to determine impacts and potential benefits of individual species management. Only then can forests be managed in a way that preserves niches for sustainability of wildlife populations, while

protecting softwood timber supplies from widespread losses due to SBW outbreaks (Colford-Gilks et al., 2012).

Two main hypotheses are tested in this study:

- I. SBW defoliation impacts on the identified causes of mortality; and
- II. Balsam fir survival depends on environmental variables that contribute to their water, energy, and light requirements.

1.2 Climate

Geographically, New Brunswick (NB) is located at 46° N and 66° W with a land area of 72,908 km². Because of the distribution of land and waterbodies, the climate in the Maritime Provinces is usually quite variable. The climate in NB may be described as continental, with great fluctuations in daily and seasonal temperatures, but with relatively uniform precipitation.

The seven ecoregions of NB are the Highland, Northern Upland, Central Upland, Fundy Coastal, Valley Lowland, Eastern Lowland, and Grand Lake ecoregions. (Government of New Brunswick, 2011). Ecoregions are defined primarily by their climatic differences as shaped by major landforms, elevation, latitude, and marine influences. Ecoregions are distinguished based on tree species distribution patterns influenced by the various climate-related factors (Figure 1.1). The ecoregions are comparable in terms of their climatic, distribution of forest vegetation species, distribution of wetlands, and distribution of animal species. The Valley Lowland and Grand Lake ecoregions share the dramatic influence of major watercourses and large lakes, which create the required conditions for an impressive diversity of wetland types.

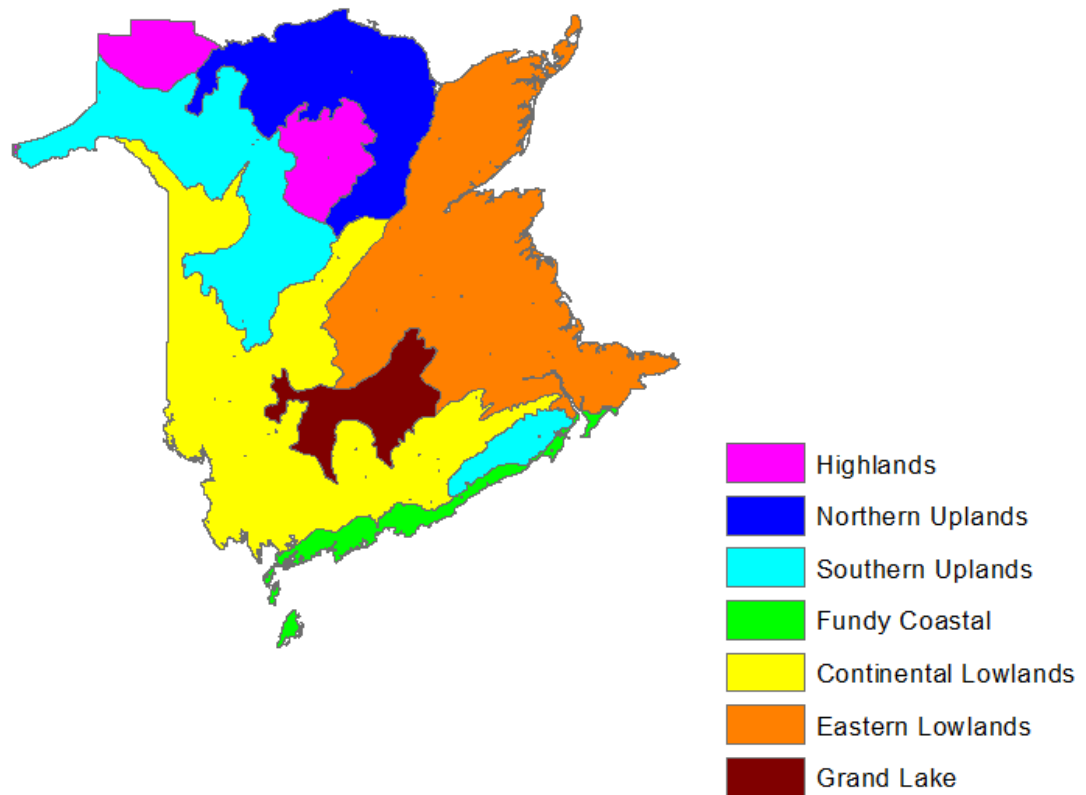


Figure 1.1 Ecoregions of New Brunswick primarily defining climatic differences as shaped by landforms, elevation, and marine influences.

Each of these ecoregion supports its own mixture of plant and animal life. The Highlands are mountainous with characteristics of boreal forest. A typical topographic feature in the area is Mount Carleton, the tallest peak in the Maritimes with an elevation of 834 m above mean sea level (AMSL). Winters are longer in this region with shorter and cooler growing seasons. This area is dominated by balsam fir, black spruce [*Picea mariana* (Mill.) B.S.P.], white spruce [*Picea glauca* (Moench) Voss], white birch (*Betula papyrifera* Marsh.), and intolerant hardwood and softwood species. The Grand Lake area has the warmest climate in NB. This area is elevated 150 m AMSL and has the longest growing

season and highest temperatures. The area is suitable for heat-loving trees, such as ash, oak, and silver maple (Government of New Brunswick, 2011).

1.3 Balsam fir

1.3.1 Response to microclimate

Balsam fir grows best in the eastern part of its range in southern Canada and the northeastern United States (USA). Cool temperatures and abundant moisture characterize these areas. Growth is optimum in areas with a mean annual temperature of 2 to 4°C, a January mean temperature of -18 to -12°C, a July mean temperature of 16 to 18°C, and mean annual precipitation of 760 to 1100 mm (Bakuvic & Hansen, 1965). Soil nutrient status has a reduced importance to the species (Page, 1976).

The range of balsam fir stretches from southern Maine, as far north as 55° latitude in Québec and west-central Canada; it is correspondingly more prevalent in the higher elevation, cooler areas of the province.

1.3.2 Growth and yield

Mature balsam fir diameters range from 30 to 46 cm at breast height (Frank, 1990). Where growth is optimum, as in the Green River watershed in northern NB, some trees can reach 75 cm in diameter at breast height (DBH) and 27 m in height. The greatest recorded DBH for balsam fir is 86 cm. Life expectancy of balsam fir in natural settings is about 70 years (Seymour & Hunter, 1992). Maximum age recorded from historical records is about 200 years (Bakuzis & Hansen, 1965). A more recent inventory by Porter et al. (2001) for this area revealed no trees of this age. How large or how fast balsam fir grows or how much a stand of balsam fir will yield is related to site factors, such as climate and soil conditions,

and tree age. Condition of tree stands, composition, and structure also influence growth. Balsam fir is a strong contender for space in stands in which it grows.

1.3.3 Reaction to competition

Balsam fir has a strong propensity to become established and grow under the shade of larger trees (Blum et al., 1981; Frank & Bjorkbom, 1973); balsam fir is classified as very tolerant to shading. Because relative tolerance of species may vary with soil fertility, climate, and age, balsam fir is rated as less shade tolerant than red spruce and more tolerant than either black or white spruce (Frank, 1990). Among the major competitors to balsam fir are shade-tolerant hardwoods.

1.3.4 Causes of mortality

Balsam fir has several insect enemies, the most important by far being the SBW. Despite its name, the SBW prefers fir to spruce; it is most likely to cause heavy damage and mortality to stands that contain mature fir, or that have a dense stocking of fir or a high proportion of fir in relation to other species (Bashir & MacLean, 2015).

The interaction of factors influencing individual-tree survival remains one of the least understood elements of forest growth and yield (Teck & Hilt, 1990). According to Waring (1987), “trees die when they cannot acquire or mobilize sufficient resources to heal injuries or otherwise sustain life”. Most of the trees die as a direct or indirect consequence of failing to compete successfully for sunlight, water, or soil nutrients (Peet & Christensen, 1987). This type of mortality, commonly referred to as self-thinning (Lee, 1971), can occur at any stage of stand development and is discussed in full in Kramer & Kozlowski (1979). By contrast, catastrophic mortality is caused by major disturbances, such as fire,

windstorms, epidemic insect attacks, and other external agents. It is irregular in occurrence and difficult to predict (Lee, 1971).

1.3.5 Spruce budworm

According to Blais (1983) and Krause (1997), SBW epidemics are major recurrent forest disturbance in northeastern North America. The SBW are driving forces in host stand dynamics (Baskerville, 1975). In NB, SBW outbreaks have resulted in substantial mortality of balsam fir, on the average is about 85% in mature stands (MacLean, 1980).

A review of the historical outbreak of SBW indicates a recurrence almost periodically at an average interval of 35 years (Royama et al., 2005). One of the most recent outbreaks, 1970-1986, affected an area across eastern Canada of about 60 million ha (Kettela, 1983; Blais, 1983). From 1977-1981, SBW accounted for 41% of timber loss as a result of pests each year in Canada (Sterner & Davidson, 1982). Studies conducted on the effects of SBW defoliation on growth rates and survivorship indicated that the impact of defoliation can potentially last up to 10 years after an outbreak (Maclean, 1980; Erdle & McLean, 1999). In spite of the severity, only a few studies have examined the “legacy effect” of SBW defoliation beyond 10 years. Studies have shown that already weakened trees are predisposed to the effects of secondary stressors, including from strong winds promoting extensive windthrow and top and stem breakage.

Given the extent of past SBW outbreaks in eastern Canada (Blais, 1983; Kettela, 1983), it is possible that past cumulative defoliation may affect timing, quantity of trees, and severity of stand decline. In NB, the most recent SBW outbreak occurred over a 21-year period (circa 1972-1993). Governing the timing controlled by SWB are factors

influenced by climate, such as sunlight, temperature, and dryness, SBW spring-emergence (Figure 1.2) and feeding are climatically-timed processes.

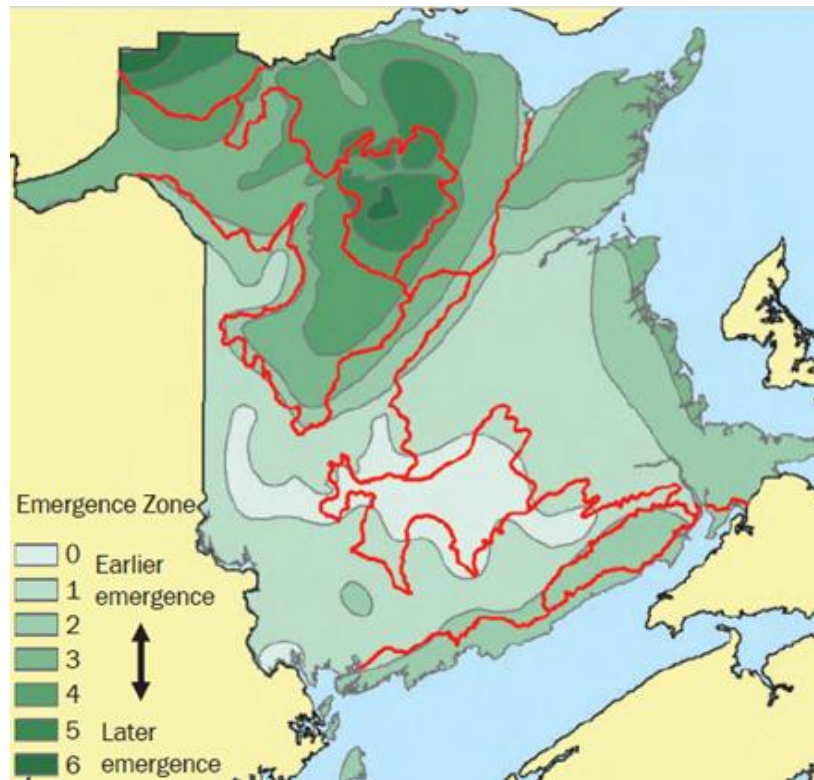


Figure 1.2 Spruce budworm spring emergence zones (green shading in the background) and ecoregion boundaries (red lines; after NB DNR, 2007).

1.4 Survival and growth

Key indicators of a tree species probability of surviving are its genetic makeup and its environment (Spurr & Barnes, 1973). The environmental components affecting tree growth and survival, includes competition from other trees, and external factors, such as insects, disease, and wind. Variables commonly used to estimate an individual tree's survival probability, include (i) local competition, (ii) growth rate, and (iii) size.

To survive, a tree must grow. The most commonly used measure of tree growth is diameter growth, an indicator of a tree's potential within its environment (Buchman, et. al., 1983). Growth reflects a tree's vigor and indicates its likelihood of surviving (Buchman, 1979; Landford & Cunia, 1977; Monserud, 1976). However, a given level of cambial growth does not reflect the same probability of survival for all trees. As trees become larger, an ever-increasing fraction of total dry weight exists as wood that is photosynthetically non-productive (Kramer & Kozlowski, 1979) and the relative growth rate decreases with increasing size. Diameter growth patterns in suppressed trees and young trees differ from those in mature trees (Oliver & Larson, 1996).

Quantifying the relations between species growth and survival under the influence of climatic variables is considered based on the set of three environmental variables selected from a broader range of possible variables, because of their importance in influencing tree species-habitat quality (e.g., Bourque et al., 2000; Hassan & Bourque., 2009), particularly (i) PAR (Xing et al., 2007), (ii) GDD (Bourque et al., 2000), and (iii) SWC (Prentice et al., 1992; Bourque et al., 2000).

1.5 Survival analysis

Survival analysis is generally defined as a set of methods in analyzing data, where the outcome variable is the amount of time that it takes before a particular event of interest occurs. The time to an event or “survival time” can be measured in days, weeks, years, and so on. According to Buchman et al., (1983), trees surviving at the “*t*-year” interval repeat the survival process annually until each has succumbed to competition, senescence, or external factors.

1.6 Hot spot analysis

Finding “hot and cold spots” in a dataset is useful in identifying causes and prediction of future trends. A feature with a high value (a hot spot) is interesting, but may not be statistically significant. Hot spot analysis is a statistical technique that calculates the G_i^* -statistic for each feature (attribute) in a dataset. The resultant Z-score, due to the mathematical definition of the Getis-Ord G_i^* -statistic (ESRI, 2015), tells where features with either high or low values cluster spatially. The mathematical expression for hot spot analysis is given by

$$[1.1] \quad G_i^* = \frac{\sum_{j=1}^n w_{i,j} x_j - \bar{X} \sum_{j=1}^n w_{i,j}}{\sqrt{\frac{n \sum_{j=1}^n w_{i,j}^2 x_j^2 - (\sum_{j=1}^n w_{i,j} x_j)^2}{n-1}}},$$

and

$$[1.2] \quad \bar{X} = \frac{\sum_{j=1}^n x_j}{n},$$

where x_j is the attribute value for feature j , $w_{i,j}$ is the spatial weight between features “ i, j ”, n is the total number of features, and

$$[1.3] \quad s = \sqrt{\frac{\sum_{j=1}^n x_j^2}{n} - (\bar{X})^2}.$$

A group of features around a given feature, and the feature itself, is called the feature’s neighborhood. Collection of all neighborhoods of a particular feature defines the study area. Hot spot analysis answers the question whether the feature in question is statistically significant from other features, including single PSP’s to entire neighborhoods

of PSP's. To be statistically significant, a feature (in this case a hot spot) will have a high value and be surrounded by other features with high values as well. The local sum for a feature and its neighbors is compared proportionally to the sum of all features; when the local sum is significantly different than the expected local sum and that difference is too large to be the result of random chance alone, a statistically-significant Z-score results. This is done by comparing neighborhoods in the study area to determine if they are significantly different.

A hot spot can be assigned one of three levels of confidence, i.e., 90, 95, and 99%, indicating the strength of statistical inference. If the occurrence in the neighborhood is significantly lower than in the study area (within a level of confidence of 90, 95, or 99%), this is an indication of the presence of a cold spot. If the neighborhood is not significantly different from the study area as a whole, the neighborhood is randomly clustered and is statistically not significant.

1.7 Problem statement and thesis objectives

One criticism of predicting species distribution by simply relating biophysical variables to species habitat preferences is that past studies fail to select areas where species have higher probabilities of persistence (Araujo & Williams., 2000). The research questions of this study are:

- I. What are the major factors causing major and severe mortality in balsam fir in New Brunswick, and what is the quantity (number of trees) and spatial distribution (number of plots) of the interaction of these factors?

II. How is tree survival affected by site conditions, including SWC, GDD, and PAR?

To answer these questions, the objectives of this research are to:

1. Calculate and characterize plot-level tree mortality of balsam fir based on each of eight known causes;
2. Determine the predominant cause of mortality, both temporally and spatially;
3. Identify SBW “legacy effects” on balsam fir mortality;
4. Generate survival maps for NB with application to balsam fir tree-status based on diameter distribution over a growing period of 27 years;
5. Re-map the environmental variables (i.e., SWC, GDD, and PAR) at 30-m resolution so that PSP’s (permanent sample plots) site variables can be based on existing biophysical conditions; and
6. Account for tree mortality under variable environmental conditions of SWC, GDD, and PAR.

1.8 Thesis structure

This thesis consists of four chapters. Chapter 1 provides an overview of the study and issues relating to balsam fir mortality and its survival across NB in terms of species requirements, capabilities, and shortcomings. Background to survival analysis is discussed, highlighting requirements and expected outputs from the literature. An overview of the concept of hot spot analysis is also provided. The chapter continues with the general and specific objectives of this study, and a summary description of the climate of the study

area, as well as a brief overview of the species chosen for the study and its requirements for survival.

Chapter 2 presents the components of recorded causes of balsam fir mortality both in space and time. The chapter further describes methods used in extracting balsam fir-relevant data with their respective attributes based on eligible inventory plots selected for analysis. I describe methods of characterizing DBH classes and criteria used in calculating mortality from one measurement period to the next, across a 27-year time span. I also present the processes involved in calculating and accounting for the spatial and temporal attributes of maximum percentage (%; as an indicator of severity of mortality) and spatial distribution of balsam fir mortality based on each of eight known causes and a descriptive account of the latest SBW outbreak.

Chapter 3 describes the PSP data representing the components of balsam fir mortality whose causes were not identified. Methods of conducting survival and growth analysis of trees that survived in the same regions where mortality occurred without any identified causes and methods of calculating the survival estimates along with their DBH class and DGR distributions are presented with results. The chapter presents mortality information, leading to derivatives of survival rate extraction with GIS-mapping procedures. Diameter at breast height and DGR classifications associated with survival calculations are explained along with their spatial variation. A description of derivations of environmental surface data from the Landscape Distribution of Soil Moisture Energy and Temperature model (LanDSET; Bourque et al., 2000) to generate landscape-level descriptions of PAR and SWC is presented. Further description of how GDD surfaces in this study were generated from thermal data using the Moderate Resolution Imaging

Spectroradiometer (MODIS) sensor on the Terra satellite (Hassan et al., 2007) is presented. How the environmental variables explain the unknown component of balsam fir mortality in the data is presented and results of relative importance of the three environmental variables to balsam fir mortality is examined.

Chapter 4 presents an account of summary results and general and specific conclusions. This includes discussion of methods and results obtained with limitations and recommendations.

2 SPATIOTEMPORAL VARIATION OF BALSAM FIR MORTALITY IN NEW BRUNSWICK AS A FUNCTION OF RECORDED CAUSES

2.1 Introduction

In investigating the causes and rates of mortality in balsam fir, this chapter takes into consideration the effect of previous SBW defoliation and known natural external disturbances of the forested environment.

This Chapter investigates the effect of SBW outbreak on balsam fir mortality in terms of timing, spatial distribution (impact on plot area), severity of impact (maximum % trees that died) and its adverse effects on each of eight known causes of mortality. Using the NB Department of Natural Resources (DNR) permanent sample plot (PSP) database, I can better understand future mortality patterns associated with stand decline in both space and time.

2.2 Methods

The PSP database from NB DNR (Porter et al., 2001) provides a unique opportunity to assess the status of balsam fir in NB during the 1987-2014 measurement period. The PSP's generally consist of 400-m² circular plots. The PSP's are distributed across the entire province with the exception of some large freehold blocks. Balsam fir plots are selected from 3,596 PSP's (Figure 2.1). The sampling is based on a minimum of five percent (5%) mix of balsam fir in capturing the most possible spatial variation across the province (Figure 2.1b).

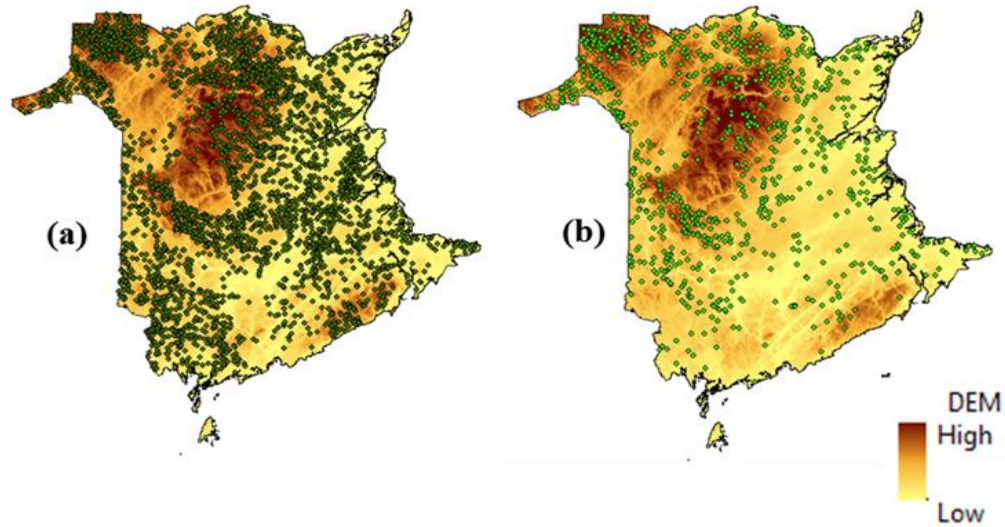


Figure 2.1 Location of permanent sample plots in New Brunswick; (a) 3596 plots of mixed species, and (b) 939 plots with a mix of balsam fir ($\geq 5\%$ of trees present) sampled from 1987 to 2014.

2.2.1 Calculation of mortality

Balsam fir trees are grouped by measurement year. All measurement years are subgrouped into DBH classes at the plot level. Each DBH class is tracked between measurement periods using tree identification numbers (ID). The intersection between consecutive measurement years defines a set of trees that survived or lived since the previous measurement period. The annual % mortality (MT) is based on the number of trees that died in a measurement year divided by the total number of trees (living and dead) in the same measurement year, normalized to the number of years within a particular measurement interval (MI, with MI varying from 3 to 5 years), i.e.,

$$[2.1] \quad MT = \frac{\frac{T}{T_{total}} \times 100\%}{MI},$$

where T and T_{total} are the number of dead trees and the total number of trees in a given plot, respectively.

In this study, cause of mortality is assigned a mortality code. This code is intended to identify individual tree mortality per measurement period according to cause. The codes listed in Table 2.1 differentiate the various causes of mortality. The known and unknown causes are grouped according to codes -1 through 9 (Table 2.1).

Table 2.1 Codes associated with various causes of tree mortality.

Mortality Code	Cause	Dead or Alive
-1	Status unknown	Unknown
0	Alive, not dead	Alive
1	Insect damage	Dead
2	Windthrow	Dead
3	Stem wounds	Dead
4	Broken top	Dead
5	Stem breakage	Dead
6	Suppression	Dead
7	Over mature	Dead
8	Other (likely cut)	Dead
9	Unknown cause of death	Dead

In quantifying tree attributes, timing, quantity, and causes of mortality, the difference in mean DBH of each class between measurement periods were calculated to determine the diameter growth rate (or vigor). This is used to assess the effect of tree attributes (i.e., size, vigor, and SBW defoliation) on mortality of balsam fir and how these relate to declining and eventual breakup of stands. Mortality and growth of trees in the 939 PSP's (Figure 2.2) selected to represent balsam fir located throughout NB were compared with those in the SBW zones to determine the quantity and spatial distribution of mortality. The temporal components of mortality were calculated across the measurement periods and compared with the SBW outbreak periods to determine the SBW defoliation effect and subsequent "legacy effect" with respect to each of eight known causes.

This study is based on the 1972-1993 SBW outbreak period. PSP-data analysis was based on six measurement periods from 1987, when the plots were first established, to 2014. A measurement period of PSP's from 1987-1993 corresponds to the SBW-outbreak period (six years), whereas measurement periods 1994-2014 corresponds to the post-outbreak period (20 years).

Measurement-period M1 refers to the first measurement year (1987) and re-measured every 3-5 years by NB DNR and industrial cooperators. Subsequent measurement periods are represented by M2, M3, and so on, up to the last measurement period (2014) when tree measurements were recorded. Measurement periods M1, M2, and M3 correspond to the SBW-outbreak period in NB (1972-1993, due to timing variation across NB), whereas measurement periods M4, M5, and M6 correspond to the post-outbreak period (1994-2014). The SBW-defoliation impact on balsam fir mortality, in terms of severity and timing, is explained by comparing the temporal patterns of mortality of each of the eight known causes with the timing of the SBW outbreak.

2.3 Results and discussion

2.3.1 Temporal component of balsam fir mortality as a function of known causes: Timing rates of decline

Table 2.2 is a summary account of the number of balsam fir trees recorded in each measurement year. This result only considers the cohort of trees at the start of M1. In general, plots did not undergo cutting. Balsam fir stand decline has increased in agreement with other studies, i.e., Taylor (2007). As evident in Table 2.2, from measurement periods M1 (1987) to M6 (2014), 82% decline in balsam fir was recorded. This result is consistent with findings by MacLean (1980); i.e., the most recent SBW outbreak resulted in 85%

mortality of balsam fir in mature stands in NB. This represents a 27-year interval, leaving 18% of balsam fir trees at the end of the measurement period (M6).

Table 2.2 Number of balsam fir trees recorded in all sampled plots (939, in total) across measurement periods.

Measurement Period	Total Number of Trees	Number of trees per ha
M1 (1987)	27,412	730
M2	25,269	673
M3	19,771	526
M4	16,451	438
M5	8,252	220
M6 (2014)	4,955	132

2.3.2 Spatial distribution and quantity of decline

Each of the eight known causes of mortality is characterized as natural and anthropogenic in nature. The maximum % mortality per measurement period is given in Table 2.3.

Table 2.3 Maximum % mortality per measurement period for all plots as a function of known causes.

Measurement Year	Insect damage	Broken top	Suppression	Stem wound	Stem breakage	Wind throw	Over mature	Other likely cut
M2	22.81	16.67	11.11	3.33	33.33	33.33	16.67	6.4
M3	12.5	6.67	15.09	5.13	20	16.67	12.5	6.67
M4	6.67	7.83	10	5.71	16.67	25	10	3.64
M5	1.67	3.85	3.64	1.74	11.43	6	10	7.5
M6	0	0.36	6.67	0	1.33	1.09	1.09	0

Table 2.3 records the highest % mortality during M2 and M3 corresponding to the SBW-outbreak period, with the exception of mortality as a result of stem wound, which occurred during M3 and M4. This result reflects the fact that the most severe levels of mortality for the eight known causes occurred during the SBW outbreak

Percentage of plots affected per measurement period is presented in Table 2.4. With the exception of maximum % plots corresponding to stem-wound-caused mortality, all anthropogenic causes of mortality occurred during the SBW-outbreak period. In general, anthropogenic causes of mortality were low compared to the natural causes. Some of the anthropogenic damage may have occurred after the trees were already affected by insect defoliation.

Table 2.4 Maximum % of plots affected by different mortality causes per measurement period.

Measurement Period	Insect damage	Wind throw	Broken top	Suppression	Stem wound	Stem Breakage	Over mature	Other, Likely cut
M2	18.6	11	7.5	27.8	1.6	19.7	5.9	3.9
M3	6.1	14.8	17.7	21	0.7	16.2	4.6	2.9
M4	1.7	14.2	14.8	13.6	2	15.1	6.2	1.6
M5	0.3	3.7	1.8	3.6	0.5	5.9	2.8	0.5
M6	0	0.2	0.1	8.9	0	0.1	0.1	0

Percentage of plots affected by mortality caused by insect damage decreased from 18 to 0% between measurement periods M2 and M6 (Table 2.5). This temporal decline is also reflected in the maximum % mortality recorded from 22.8 to 0%. An observation consistent with this trend is wind-related outcomes in the form of broken tops, windthrow, and stem breakage.

Table 2.5 Summary of mortality caused by insect damage; for other summaries of mortality related to the other causes, consult Appendix A.

Measurement Period	Maximum Percentage	Minimum Percentage > Zero	Number of Plots with Zero Mortality	Percentage of Plots with Some Level of Mortality
M2	22.81	0.13	616	18.6
M3	12.5	0.22	620	6.1
M4	6.67	0.36	579	1.7
M5	1.67	1.11	343	0.3
M6	0	0	203	0

2.3.3 Spatial component of balsam fir mortality as a function of known causes:

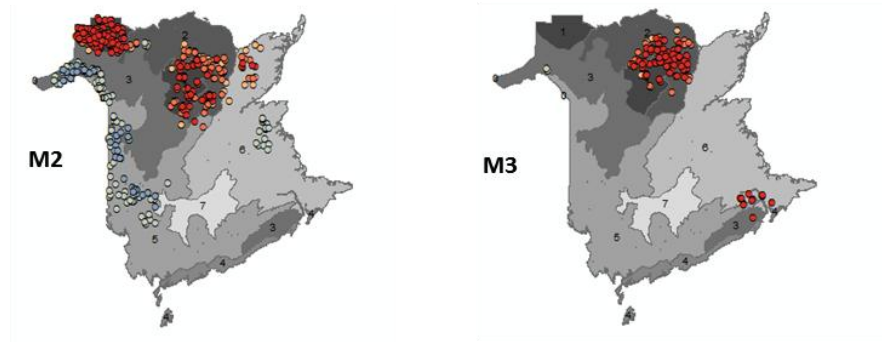
Mortality distribution during and after the SBW outbreak

Offering analytical and data summary possibilities in both Python-programming language and ESRI ArcGIS™ (Appendix B), mortality of balsam fir trees whose causes are known have been extracted. Spatial variation of known natural causes across measurement periods are given in Figures 2.3 through 2.7.

Non-fatal insect damage during the outbreak period can lead to tree mortality later on in the form of windthrow, stem breakage, and broken top as a result of a “legacy effect” (Figures 2.3-2.7). This SBW “legacy effect” extends well beyond the outbreak period. This

is evident in the coincidence of the hot spots of mortality causes expressed in Figures 2.3-2.7. All factors affecting mortality, including temperature, topography, aspect, light and moisture availability, as well as SBW emergence interact with each other.

Insect damage (During SBW outbreak)



Insect damage (After SBW outbreak)

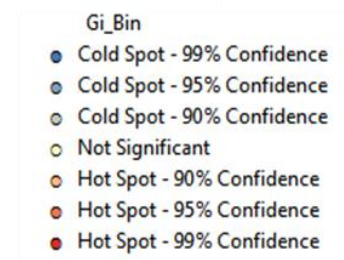
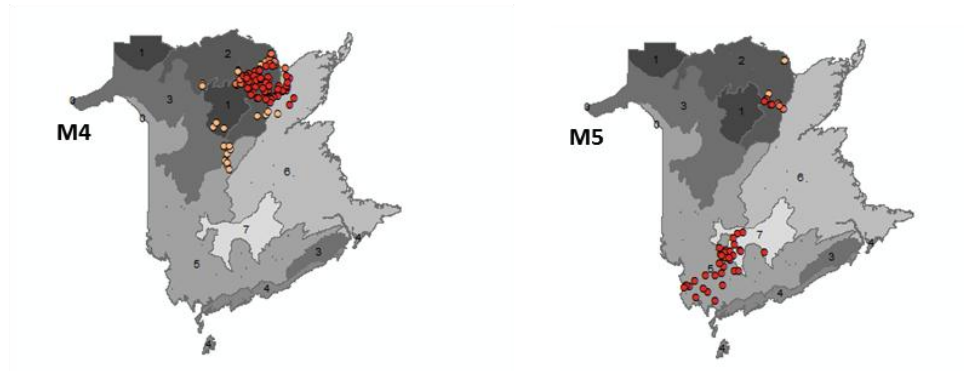
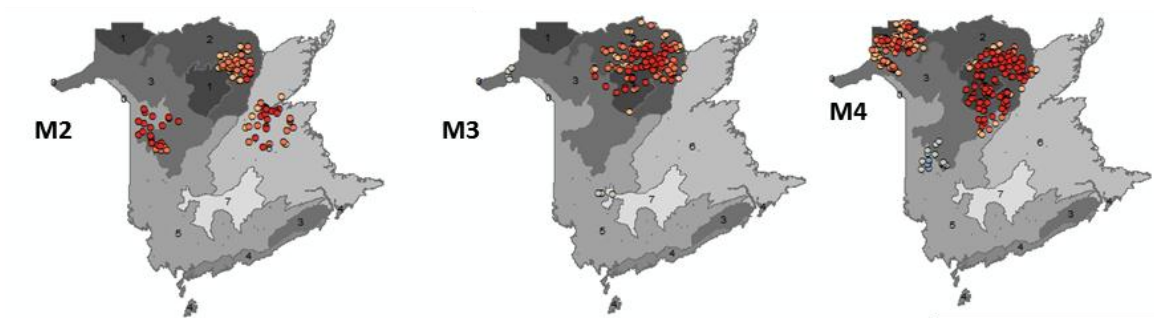


Figure 2.2 Spatiotemporal distribution of mortality caused by insect damage; M2 and M3 corresponds to second and third measurement periods, respectively (the SBW-outbreak period); M4 and M5 are the fourth and fifth measurement periods corresponding to the post-outbreak period. Absence of M6 indicates that there was no significant mortality due to insect defoliation.

Windthrow (During SBW outbreak)

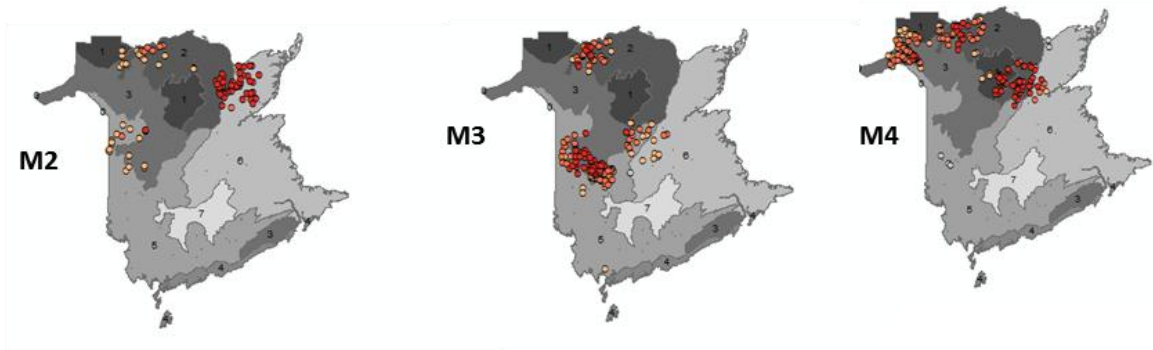


Windthrow (After SBW outbreak)



Figure 2.3 Spatiotemporal distribution of mortality caused by windthrow; M2 and M3 correspond to second and third measurement periods, respectively (the SBW-outbreak period); M4 and M5 are the fourth and fifth measurement periods corresponding to the post-outbreak period.

Stem Breakage (During SBW outbreak)



Stem Breakage (After SBW outbreak)

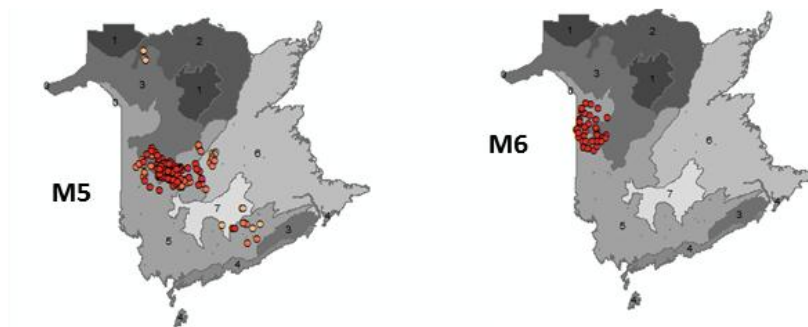
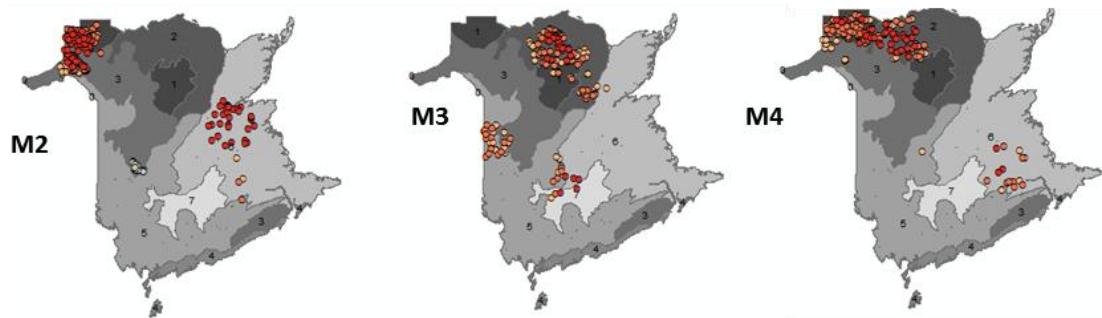


Figure 2.4 Spatiotemporal distribution of mortality caused by stem breakage; M2 and M3 correspond to second and third measurement periods, respectively (the SBW-outbreak period); M4 and M5 are the fourth and fifth measurement periods corresponding to the post-outbreak period.

Broken top (During SBW outbreak)



Broken top (After SBW outbreak)

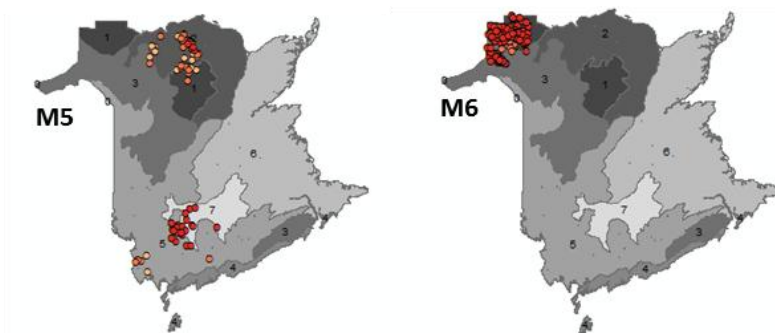
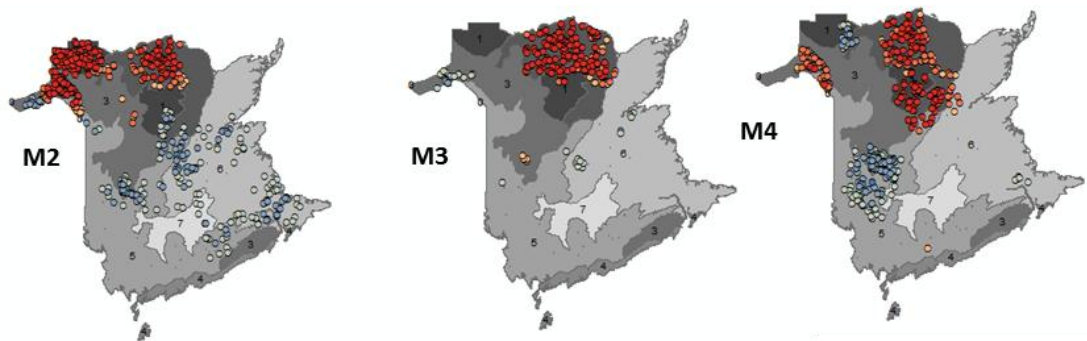


Figure 2.5 Spatiotemporal distribution of mortality caused by broken tops; M2 and M3 correspond to second and third measurement periods, respectively (the SBW-outbreak period); M4 and M5 are the fourth and fifth measurement periods corresponding to the post-outbreak period.

Suppression (During SBW outbreak)



Suppression (After SBW outbreak)

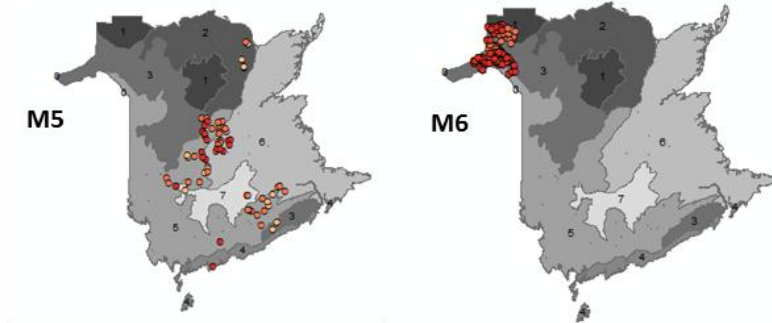


Figure 2.6 Spatiotemporal distribution of mortality caused by suppression; M2 and M3 correspond to second and third measurement periods, respectively (the SBW-outbreak period); M4 and M5 are the fourth and fifth measurement periods corresponding to the post-outbreak period.

Insect damage-related mortality statistically predominate in the Northern Upland and Highland regions of the province (Figure 2.3). Characterized by warmer climate than the Highlands, due to its lower elevation, the Northern Uplands is the driest ecoregion characterized by balsam fir as its main forest cover. The Highlands are characterized by high elevations over 500 m AMSL, with highest reaching up to 800 m AMSL, generally, have the coldest temperatures.

The northern affinity of balsam fir is due to their prominence in colder and drier ecoregions. These regions have also become statistically-significant mortality hot spots caused by insect damage. Anthropogenic causes, i.e., stem wound and other (likely cut), as well as mortality due to trees being over mature, were all relatively low (< 10%) and as a result were excluded in this summary. Following the 1972-1993 outbreak, trees were subjected to aggressive insecticide spraying (Colford-Gilks et al., 2012). Shade-tolerant mixedwood stands tend to contain balsam fir stands in the Highlands and Northern Uplands ecoregions (Figure 1.1). Spruce budworm development is mainly driven by temperature (Colford-Gilks et al., 2012) and, as a result, correlates fairly well to ecoregion (NB DNR, 2003). Defoliation is earlier in the warmer Continental Lowland, Eastern Lowland, and Grand Lake Lowland ecoregions.

Spatial records of % mortality caused by insect damage affected a maximum of 175 plots during the SBW outbreak (Table 2.6) occurring mostly in the Highland, Southern Upland, Northern Upland, and Eastern Lowland ecoregions (Figure 2.2). Declining numbers between the second and third measurement periods may have resulted in a shift in mortality to wind-related causes, especially broken tops (Figure 2.5) and windthrow (Figure 2.3). Post-SBW outbreak, maximum mortality due to insect damage recorded is 15

plots in M4 and 3 in M5, reducing to zero in M6 (Table 2.6). This is an indication of a steady decline in mortality caused by insects. Assessing areas prone to insect defoliation, Figure 2.2 shows mortality in the Northern Uplands and Highlands in M2, which reduced in the Southern Uplands in M3. During the post-outbreak period, the Highlands and Southern Uplands were affected the most by mortality compared to the Eastern Lowlands. Spruce budworm prosper in regions of cooler temperatures, where balsam fir is abundant.

Windthrow caused mortality affected a maximum of 140 plots during the SBW outbreak (Table 2.6) occurring in the middle and upper SBW-outbreak zones, respectively. The Southern Uplands, Eastern Lowlands, Southern Lowlands, and Northern Uplands are consistent with insect damage caused during the same measurement period with the exception of the Highland ecoregion. This is likely due to the interaction of SBW with temperature, topography, aspect, and source of balsam fir that are common to the ecoregions.

Post-SBW outbreak records of mortality affected a maximum of 133 plots. Measurement period M6 recorded low mortality as a reduction from M4 and M5, respectively. This also represents a shift to and from other wind and insect causes. The ecoregions prone to tree mortality during this period are the Highlands and Southern Uplands, all of which have cooler, windy climates.

In broken top, 245 plots experienced highest mortality during the SBW outbreak. Not surprisingly, SBW impact on mortality manifested mostly as broken tops before the end of the outbreak. An indication of severity of mortality increase from measurement period M2 to M3 reflects the effect of the initial predisposition to SBW in M2, leading to

mortality in M3, with the Eastern Lowlands, Northern Uplands, and Continental Lowlands facing the greatest impact. The highest post-outbreak records of 50 plots show delayed effect in successive measurement periods. High mortality was recorded in one plot in both M5 and M6. Affected regions were predominantly in the Highlands. These regions are generally cooler and have a high balsam fir presence.

Stem breakage caused mortality occurred in a maximum of 185 plots during the SBW-outbreak. These numbers were prominent in the Southern and Northern Uplands and Eastern Lowlands; post-outbreak records affected a maximum of 143 plots. The predominant ecoregions, where a high-level of mortality occurred are the Highlands, Northern Uplands, Continental Lowlands, and Grand Lake ecoregion.

Suppression causing mortality of balsam fir trees occurred in a maximum of 260 plots during the SBW outbreak. Ecoregions prone to this mortality cause were mainly in the Highlands and Southern Uplands. This significant number reduced to 198 plots during M3, however, maintaining the Highlands as the most important region facing decline in balsam fir.

Post-outbreak records of suppressed trees that died occurred in a maximum of 125 plots occurring during (M4). The Eastern Lowland, Fundy Coastal, Continental Lowland, and Highland ecoregions were the most prone to balsam fir mortality during and after the SBW outbreak. Consistent with the spatial distribution of tree mortality caused by insect damage, broken top, windthrow, and stem breakage during and post-SBW-outbreak, respectively, the Highland ecoregion remains the most important among all ecoregions affected by high-levels of balsam fir mortality.

Predisposition of suppressed trees coupled with increasing competition during earlier and recent outbreaks account for the escalating numbers in mortality compared to other causes. This effect is further confirmed by the sharp decrease in mortality during the fifth measurement period. These results illustrate the effect of SBW outbreak well beyond the period of defoliation (Colford-Gilks et al, 2012). Mortality due to insect damage, suppression, and wind-related causes, i.e., broken top, stem breakage, and windthrow, had the most significant impact on balsam fir in terms of % plot and maximum % mortality (damage severity), overall.

Table 2.6 Summary of plot numbers affected by mortality as a function of known causes and measurement periods.

Known Causes	Number of Plots				
	M2	M3	M4	M5	M6
Measurement Period					
Insect damage	175	58	15	3	0
Windthrow	103	140	133	35	2
Broken Top	245	65	50	1	0
Stem Breakage	185	153	143	0	1
Suppression	260	198	125	34	5
Over mature	55	43	50	25	1

2.3.4 Temporal variations of maximum percentages of known causes of mortality

Mortality due to insect- and wind-related causes exhibit temporal variations that express a “legacy effect” of SBW-caused mortality to be highly susceptible to subsequent wind disturbance events, leading to substantial blowdown and stand decline. The shift in mortality caused by insect damage to wind-related causes is evidenced in Figure 2.7, with a peak in windthrow in M4.

The shift in maximum % mortality from insect damage is evident as an increase in maximum % mortality caused by windthrow between M2 and M3 measurement period (8.3%) and maximum % mortality caused by suppression increased between M2 and M3 by 4.0%. The important causes with respect to maximum mortality are windthrow (33.3%), stem breakage (33.3%), and insect damage (22.8%).

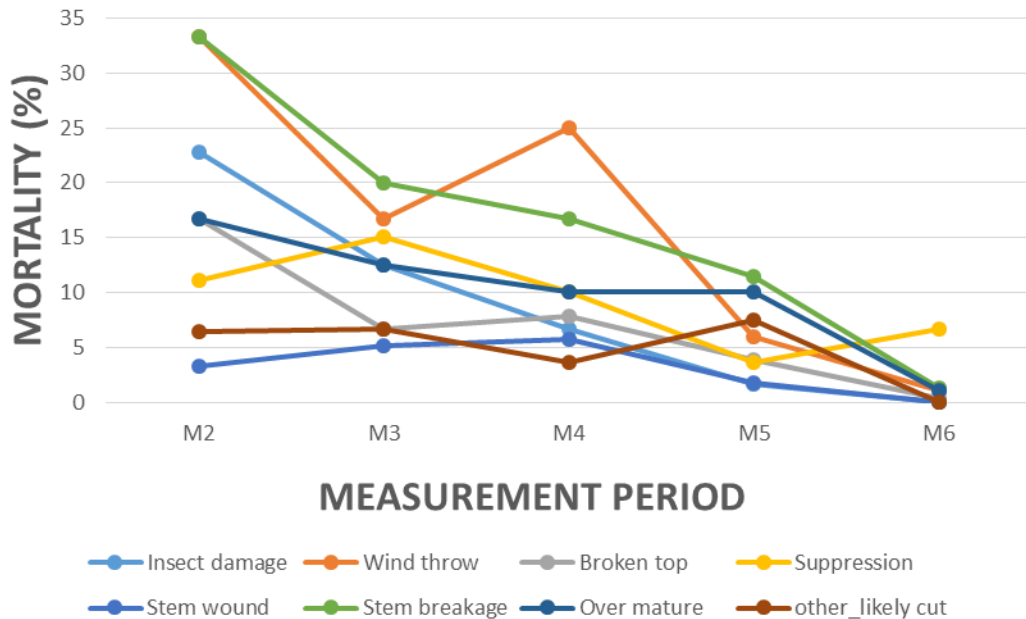


Figure 2.7 Time series of maximum % tree mortality as a function of known causes.

2.3.5 Temporal variations of percentage of plot affected by mortality of known causes

Suppression caused mortality was predominant, covering 27.8% of all sampled inventory plots. This suggests that competition for resources is persistent across the measurement periods. The spatial distribution decreased steadily from the SBW-outbreak to the post-outbreak period, until a sharp increase occurred between the fifth and sixth measurement periods. Stem breakage-caused mortality was the next most important in terms of spatial distribution, recording 19.7%, slightly higher in insect damage-related mortality (18.6%) during the SBW outbreak (Figure 2.8). The steady decrease in spatial distribution of mortality is apparent in both stem breakage and insect damage, following suppression. However, the influences on insect damage-related mortality on suppression is evident during M6, windthrow during M3, over mature during M4, and the least significant on anthropogenic causes (i.e., stem wound and likely cut; Figure 2.8). Influence of spatial distribution of mortality caused by insect damage was evident in windthrow, with an increase in severity of 3.8% between M2 and M3, and suppression, with an increase of 5.3% between M5 and M6.

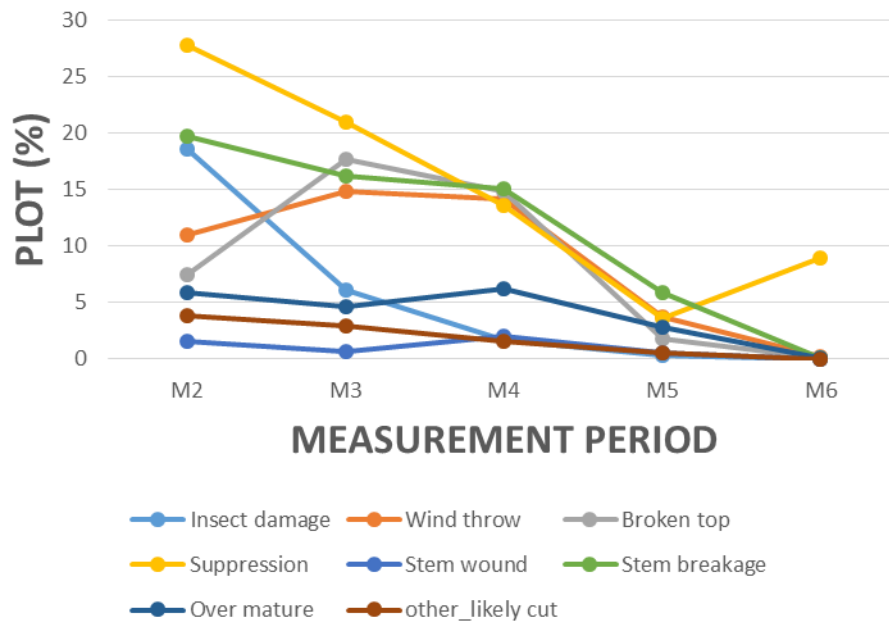


Figure 2.8 Time series of % sample plots affected by mortality (i.e., at least one tree dying for a given mortality cause within a given plot).

2.3.6 Temporal variations of percentage of plots with maximum percentages of mortality

In evaluating the different levels of impact of mortality in terms of timing rates, extent, and spatial distribution due to the known causes, I assessed the variation of spatial distribution in comparison with maximum % mortality to generalize and validate the integrity of the interactive effect of each of the known causes.

Maximum % constitute the highest % values recorded for all sampled plots in each measurement period for each of the causes of mortality. Results of this comparative

analysis are given in Figure 2.9. The plots show that there is a general agreement (correlation) between the spatial distribution (% plots) and the quantity of trees (maximum %) for the same measurement periods. This validates the interrelation between the impact of mortality on plot area and the quantity of trees.

The temporal decline in mortality expressed by the eight known causes is partly due to the trees dying younger during the earlier measurement years as a result of their inability to compete for resources (self-thinning). As they grow bigger during the latter measurement periods, their resilience increases resulting in a reduction in self-thinning (Oliver & Larson, 1996). The correlation between the quantity of trees and spatial distribution also reaffirms the declining pattern of mortality which is in agreement with the plot area distribution.

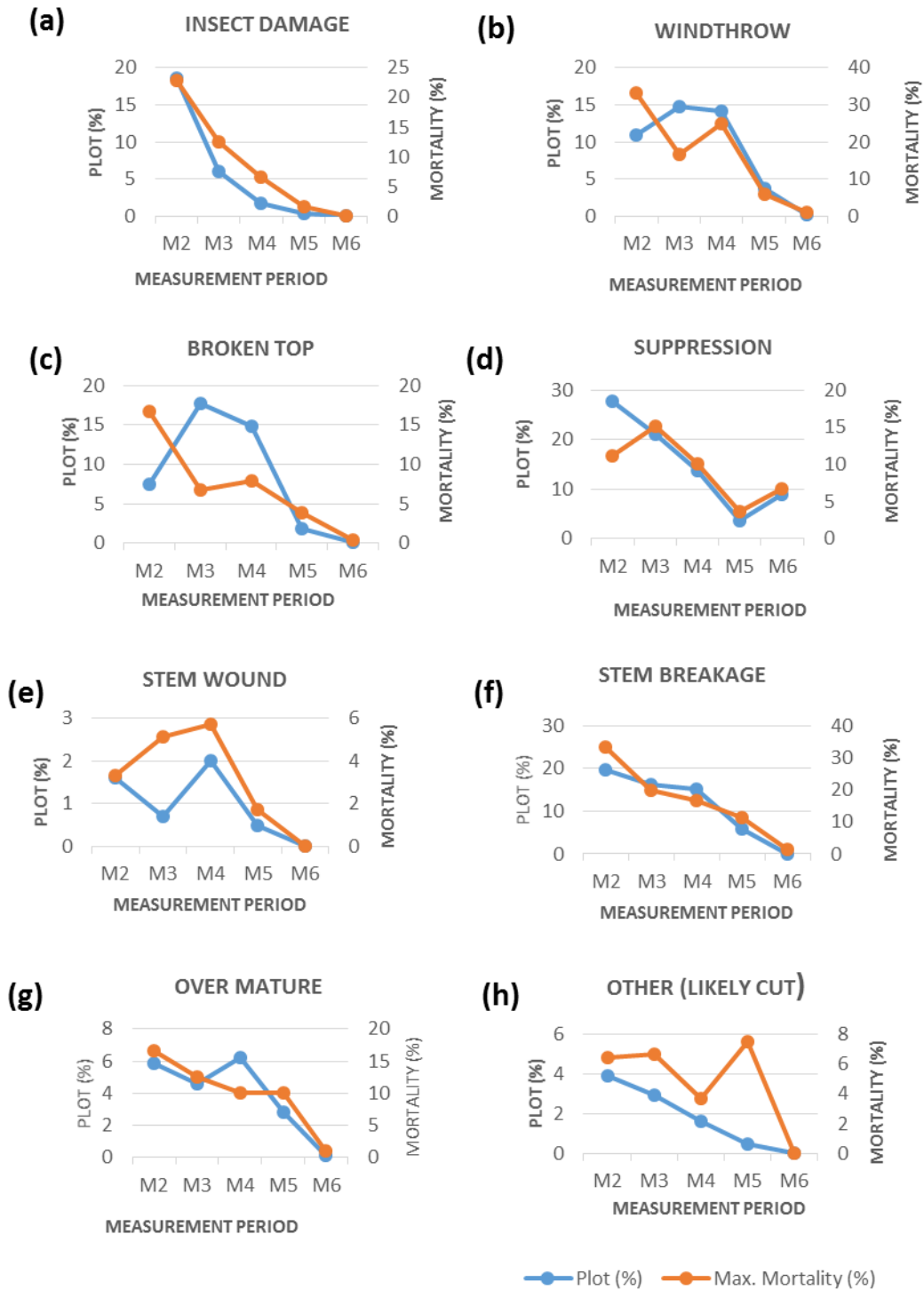


Figure 2.9 Comparison of % plots affected by mortality (i.e., at least one tree dying for a given mortality cause within a given plot) per measurement period with maximum % mortality across plots for the same measurement periods, for the different known causes, (a) through (h). For actual values, refer to Tables 2.4 and 2.5.

2.3.7 Interaction between known causes as a function of time

Analysis by Taylor (2007) on a subset of 50 plots indicated that the highest accumulation of dead wood was from fir-spruce stands ($196 \text{ m}^3 \text{ ha}^{-1}$) compared with spruce-fir and non-declining fir-spruce stands (122 and $77 \text{ m}^3 \text{ ha}^{-1}$, respectively). Further analysis of mortality between two measurement periods (1990-92 and 1999-2003) related mortality to tree size and growth rate (Taylor, 2007). Results showed a shift from insect to wind-related causes following the end of the SBW outbreak in 1993.

2.3.8 Distribution of causes of mortality at the beginning of the SBW outbreak (1987-1990)

The interacting effect of one cause of mortality on the other starts after the beginning of the SBW outbreak, thus between M1 and M2. It is, therefore, essential to examine the proportion of severity of mortality caused by each of the eight known causes during the first period of the SBW outbreak, corresponding to the second measurement year, M2.

The period of death attributed to insect defoliation at the beginning of the SBW-outbreak (1987) is 18.6% (Figure 2.10). This result is consistent with Taylor (2007) as the proportion of dead balsam fir trees caused by insects. During this period, suppression (27.8%) causing mortality predominates the remaining causes, e.g., stem breakage (19.7%) and windthrow (11%).

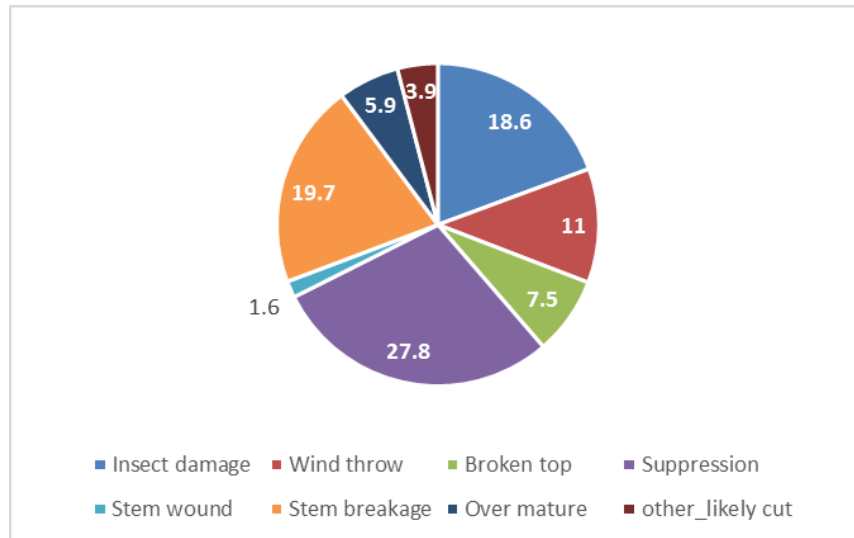


Figure 2.10 Percentage of plots with some level of mortality at the onset of measurement period (1987) as a function of eight known causes.

Decreasing rate of mortality as exhibited by the eight known causes, as illustrated in Figure 2.12, is affected by SBW defoliation. Most severe defoliation was experienced in measurement periods M2 and M3. A general reduction in mortality began in M3, persisting through M6, with the exception of mortality caused by suppression. There is generally a proportional decline in maximum % mortality from one measurement period to the next. A slight deviation from this decline is the maximum % mortality caused by suppression and windthrow. This is not surprising, as observed in Figure 2.11. The influence of mortality caused by insect damage is most significant in windthrow and suppression. Stem breakage causing mortality (33.3%), windthrow (33.3%), and insect damage (22.8%) were the most important in maximum % during the second measurement period and also remained the highest across all other measurement periods. Mortality in suppressed trees, although persistent across measurement periods, is the least important of natural causes (Figure 2.11). The maximum % mortality from anthropogenic causes was

significantly lower across all measurement periods (i.e., 1.6 and 3.9% for stem wound and cut damage, respectively; Table 2.4).

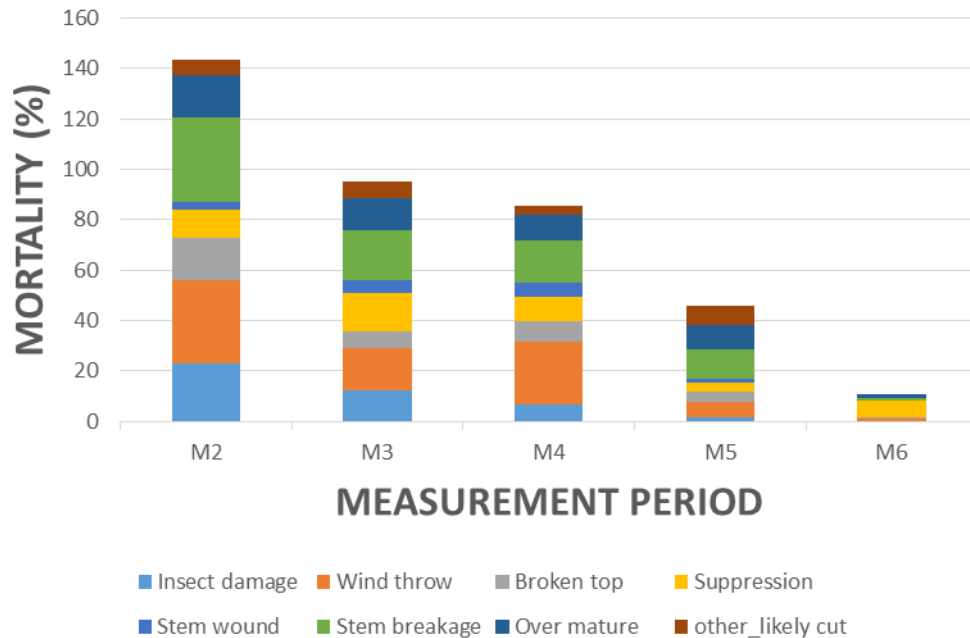


Figure 2.11 Maximum % mortality as a function of eight known causes (legend) and measurement period.

2.3.9 Percentage of total sampled plots affected by mortality

In agreement with the interactions observed in maximum values of mortality caused by each of the eight known causes, as observed in Figure 2.11, the severity of mortality due to suppression was most persistent across the measurement periods. Suppression is high when stands are densely populated and through self-thinning, the suppressed trees die through natural processes. Proportional decrease in severity of mortality is observed except for broken top-caused mortality, which experienced an increase during the third and fourth measurement period. Stem breakage, broken top,

suppression, and insect damage caused mortality remain the most important during the SBW outbreak.

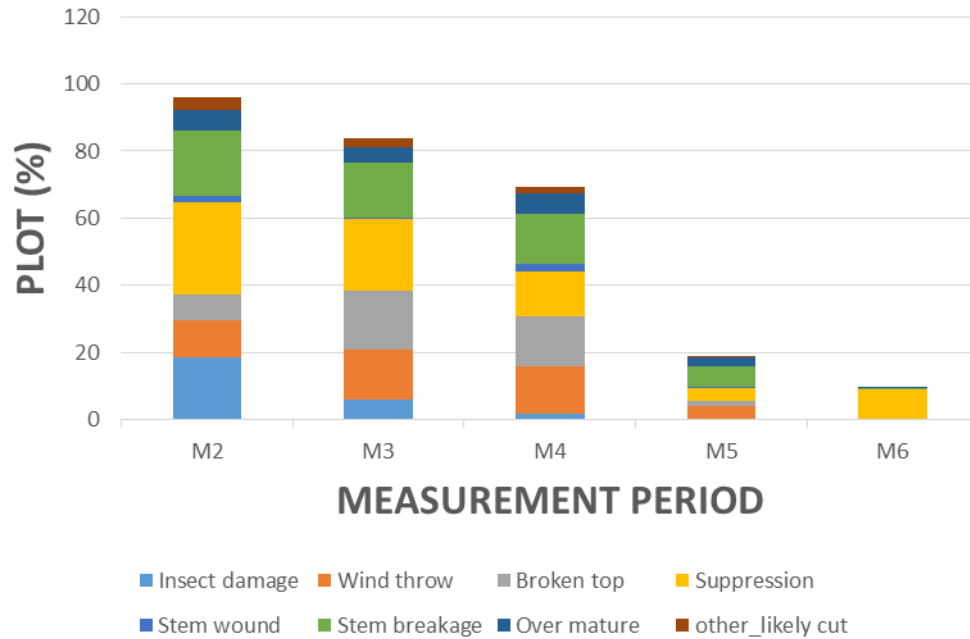


Figure 2.12 Percentage plots affected by some level of mortality (i.e., at least one tree dying for a given mortality cause within a given plot) as a function of eight known causes and measurement period.

2.4 Conclusions

Permanent sample plot data has shown to be a reliable resource for tracking balsam fir mortality relevant to understanding balsam fir survivability in NB forests. This fosters a better understanding of balsam fir mortality dynamics with and without insect disturbances. The plot area impact of mortality by natural causes was most prominent in suppressed trees, represented by 27.8% of plots per measurement period. The highest records of maximum mortality were manifested in windthrow (33.3%) and stem breakage (33.3%). The impact of mortality on plot area and the extent of impact generally declined

over time. Results show a direct correlation between the impact (% plots) and the extent of impact/severity (by way of maximum % mortality).

Results of this study support our hypothesis that SBW defoliation and wind-related causes had varying impact on the eight known causes of mortality. The interaction between the different causes of mortality re-expresses the extended effect as already weakened, defoliated trees are exposed to secondary stressors brought on by wind. When acting individually, each of these causes is unlikely to cause widespread mortality as observed here. The extended effect of the SBW outbreak was most prominent in mortality caused by tree suppression.

Ecoregion influence on balsam fir mortality for the eight known causes is most prominent in the Highlands and Southern Uplands of the province. These areas coincide with the northern and central SBW zones of Royama et al. (2005).

Evidence from this study supports the results of other studies:

- Higher mortality of smaller balsam fir trees during the SBW outbreak was noted in studies by Blais (1958) and Baskerville & Maclean (1979). Early in an outbreak, there is tendency for smaller and suppressed trees to be killed. Later after the outbreak, some of the older trees give up their resilience and die.
- The proportion of death attributed to insect damage during the SBW-outbreak period M2 was 18.6% (Figure 2.11). This result is consistent with the 18% reported by Taylor (2007), as the proportion of dead balsam fir trees caused by insect damage.

3 SURVIVAL OF BALSAM FIR IN NEW BRUNSWICK AS A FUNCTION OF MICROCLIMATE

3.1 Introduction

In Chapter two, balsam fir mortality attributed to known causes was the primary focus. This chapter investigates tree mortality that has no known causes (Appendix C). I suspect that this component of mortality may be attributed to environmental constraints. To address this aspect of mortality, I examine the regions where mortality occurred using environmental data to assess the site conditions of mortality-affected neighborhoods. Surviving trees within the same regions are examined based on knowledge of tree size (DBH) and tree vigor (DGR). Environmental data are incorporated with tree data to determine how environmental factors can explain the variations in tree size and vigor. Data used to account for environmental variation is addressed through spatial re-constructions of landscape-level SWC, PAR, and GDD (Chapter 1). This chapter presents an account of balsam fir survival in NB to explain how the environmental variables may have contributed to tree survival and, conversely, tree mortality.

3.2 Methods

3.2.1 Derivation of modelled biophysical surfaces

Bourque & Gullison (1998), Bourque et al. (2000), and Hassan et al. (2007) developed methods to map PAR, GDD, and SWC using the LandSET model and remotely sensed thermal data. Using their methods, biophysical surfaces of PAR, GDD, and SWC at 30-m resolution were derived for the study area.

LanDSET is a grid-based terrain analysis and process-based model, which integrates several components to compute long-term biophysical attributes of complex landscapes. It consists of (i) topographic analysis, (ii) hydrological network extraction, (iii) radiation, and (iv) soil water content modules. Topographic representation of complex landscapes is introduced in the model by a terrain analysis module. This module computes primary terrain attributes of slope, aspect, horizon angle, view factor, and terrain configuration factor for individual grid cells of a digital elevation model (DEM). The output from the terrain analysis module is used by the hydrological network extraction module to create a depressionless DEM, using the pit-filling algorithm of Planchon & Darboux (2001). This procedure enables computation of flow directions, flow accumulation, and subsequent application towards drainage network identification and delineation (Isaac & Bourque, 2001; Hassan & Bourque, 2009). The radiation module uses output from the terrain analysis to evaluate PAR as a function of (i) DEM-based terrain attributes (i.e., slope, aspect, view factors, horizon angle, and terrain configuration factors), (ii) sun-earth geometry and solar illumination angles, and (iii) solar-flux calculations at the top of the atmosphere. Radiation calculations take into consideration incoming and reflected shortwave radiation and incoming and outgoing longwave radiation. Incident PAR is assumed unaffected by changes in atmospheric composition and climate (Hassan et al., 2007). Generated PAR surfaces presume non-cloudy conditions, and, therefore, represent fields of potentially available PAR.

Long term SWC in the landscape is simulated per grid-cell assessments of hydrological fluxes and storage by LanDSET. The calculation of SWC includes available solar radiation and hydrological inputs of annual mean precipitation and lateral flow from

upslope regions. Hydrological outputs include infiltration, evapotranspiration, surface runoff, and percolation (Bourque & Gullison 1998; Bourque et al., 2000). Generated SWC values range between 0 and 1, with 0 associated with the drier sites at or slightly above the permanent wilting point, and 1 associated with the wetter sites at field capacity. A GDD map from thermal data for the study area was based on the standard definition of GDD proposed by McMaster & Wilhelm (1997), i.e.

$$[3.1] \quad GDD = \sum_{i=1}^{i=n} T_{avg} - T_{base}; \text{ when } T_{avg} - T_{base} > 0,$$

where T_{avg} is the average daily temperature, T_{base} is the base temperature set at 5.6°C, $i=1, \dots, n$, where 1 and n represent the start- and end-day number of the growing season. Remote sensing data used in the development of the GDD surface includes (i) MODIS-based 8-day composites of surface temperature (T_s ; at 1-km resolution) and 16-day composites of enhanced vegetation index (EVI; at 250-m resolution) for the April-through-October period of 2003-2005, (ii) tower-based 30-minute emitted infrared (thermal) radiation to estimate canopy T_s , and (iii) point-estimates of 30-year averages of GDD (1971-2000) from 101 climate stations situated across the Atlantic Maritime ecozone for GDD-surface calibration (Hassan et al., 2007).

Biophysical surfaces of PAR, GDD, and SWC were generated in raster format. All non-LandSET data were pre-processed in ESRI ArcGIS™. A more in-depth review of the methodology, including modeling of biophysical variables, can be found in Bourque & Gullison (1998), Bourque et al., (2000) and Hassan et al. (2007), and references herein.

Derived surface data of the environmental variables showing low and high variations is presented in Figure 3.1.

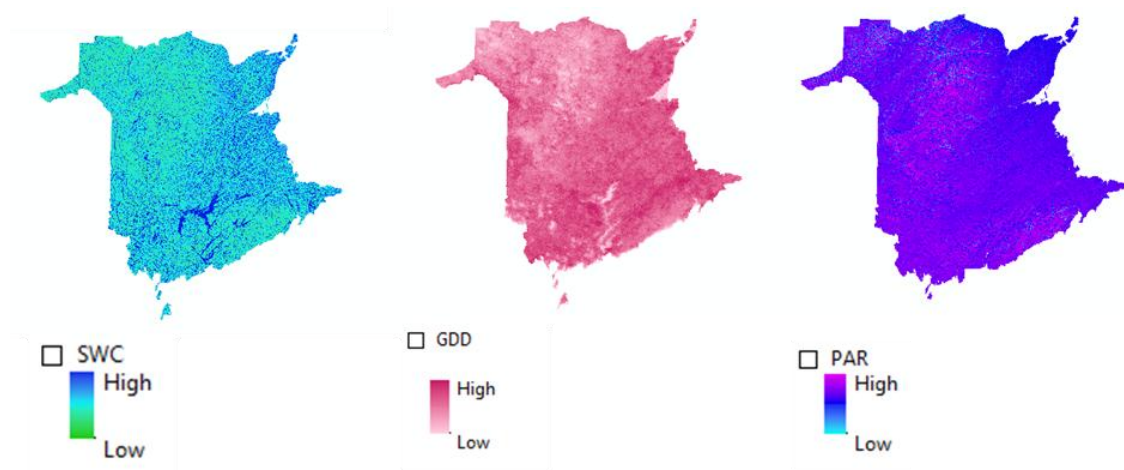


Figure 3.1 Surface data of environmental variables, i.e., GDD, SWC, and PAR, at 30-m resolution.

MODIS-based GDD values ranged from 800 for the coolest to 2071.8 for the warmest sites of the province. The lowest to the highest incident PAR ranges from 2000-4134.1 MJ m⁻² and SWC, from 0-1 (non-dimensional) representing dry to wet conditions.

Highest GDD values are in the south, southwest, and southeastern parts of the province, whereas low GDD are concentrated in the north and northwestern parts. Soil water content is generally high around the northeastern and eastern parts of the province above and below the St. John River, while the low SWC areas are concentrated in the northwestern part of the mid-west and southern parts of the St. John River basin. High PAR is concentrated in the northwestern, middle, and southern parts of NB.

3.3 Environmental variables at PSP locations

Each point in the PSP shapefile database represents a plot of 11.28 m radius. Data for the environmental variables are continuous raster of 30 m × 30 m resolution. Computing a buffer of the zonal area with radius of 900 m to incorporate the average pixel values falling within the buffer using zonal statistics. The resulting mean pixel values are extracted at the PSP point locations.

3.4 Results and discussion

A summary of the component of balsam fir whose mortality is not identified with any particular cause is recorded in Table 3.1. There is a general decline in both maximum % mortality and % plots affected across the measurement periods. The decrease suggests that as trees age, they potentially become more resilient to environmental constraints, leading to an overall increase in survival.

Table 3.1 Temporal variation of balsam fir mortality without identified causes.

Period	Maximum %	Minimum % > 0.0	No. Plots with 0.0 Mortality	Plot count > 0.0 Mortality	% Plots with Some Level of Mortality
M2	16.67	0.1	786	153	16
M3	12.25	0.1	821	118	12.6
M4	20	0.2	864	75	8
M5	3.43	0.2	921	18	1.9
M6	10	0	937	2	0.2

3.4.1 Spatial distribution of balsam fir mortality without recorded causes:

Variation as a function of elevation

During measurement period M2, 153 plots were affected by mortality. The number of plots affected successively decreased from 118, 75, 18 to 2, through measurement periods M3 through to M6, respectively (Figure 3.2).

Unlike mortality with identified causes, as discussed in Chapter 2, regions where balsam fir mortality was not identified are usually in low elevation terrain. Low-elevation terrain is generally characterized as having a warmer climate relative to high-elevation areas (see Figure 3.2).

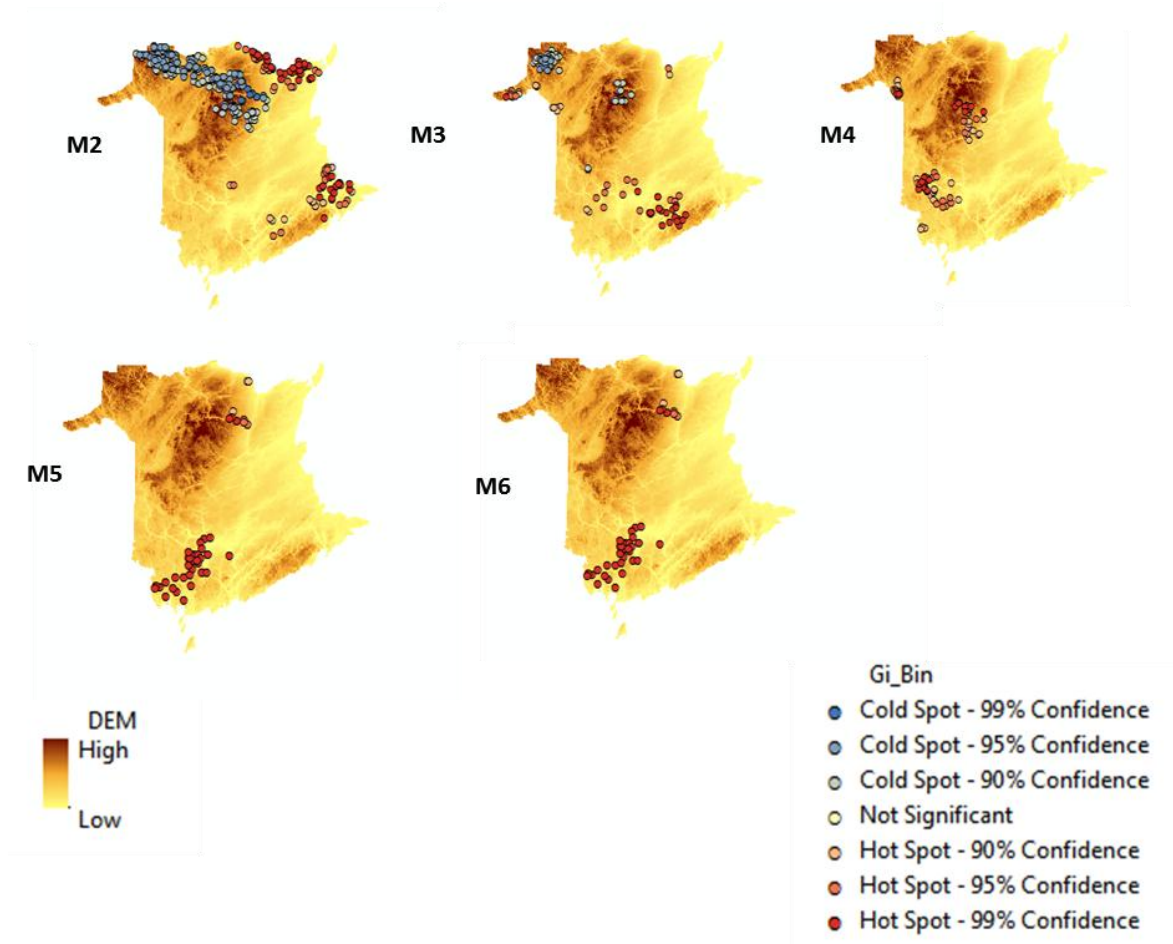


Figure 3.2 Spatiotemporal distribution of balsam fir mortality without known causes as a function of elevation.

3.4.2 Summary statistics of environmental data representing high and low survival

The parameters representing the environmental variables are encoded as pixel values of gridded rasters. In this work, I aggregate the pixel values over hot and cold spot areas of balsam fir tree survival to allocate the average GDD, PAR and SWC values coinciding with these regions. Given the Gi_Bin values range from -3 to 3, the statistically significant values are rated as -3 to -1, representing low survival, whereas values ranging from 1 to 3 represent high survival. The ratings are summarized in Table 3.2 below.

Table 3.2 Hot and cold spot ratings and their confidence level.

Feature	Rating	Associated Confidence Level (CL)
Low values (cold spot)	-1 to -3	-3 (99% CL) -2 (95% CL) -1 (90% CL)
High values (hot spot)	+1 to +3	+1 (90% CL) +2 (95% CL) +3 (90% CL)

The environmental values of PAR, SWC, and GDD that coincide with the -3 and +3 ratings of balsam fir survival across measurement periods are evaluated. Results of these ratings are summarized in Figure 3.3. According to Mann-Whitney rank sum tests, the difference in the median values between the two groups in each case is greater than would be expected by chance alone ($p < 0.001$), and as a result are taken as statistically different.

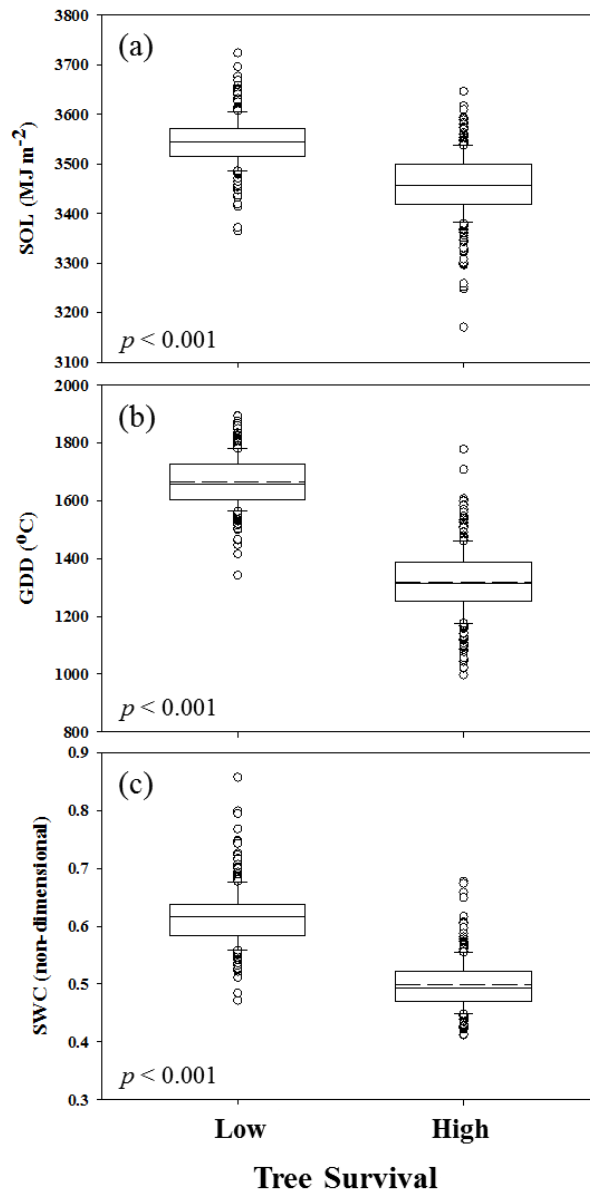


Figure 3.3 Box plots of environmental variables (SOL=PAR) associated with balsam fir survival hot and cold spots at the 99% confidence level (i.e., +3 and -3 ratings, respectively; Table 3.2). The solid and dashed lines in the middle of the boxes represent the median and mean of plotted values. The upper and lower extremities of the boxes represent the 75th and 25th percentile of the data; upper and lower whiskers represent the 90th and 10th percentile. Open circles represent data points beyond the 90th or 10th percentile.

3.4.3 Variation with soil water content

The highest unexplained mortality during M1 occurred in regions of moderately high SWC (0.5-0.6). Most of the trees are relatively young during this period and have lower resilience to wet conditions. The resilience to wetness increases during the later measurement periods M3, M4, M5 and M6 (Figure 3.3) as the trees increase in size. This results in a geographic shift in survival to wetter soil conditions (> 0.6), occurring mainly in regions close to the St. John River. Soil moisture conditions that are favorable to high survival are generally lower (≤ 0.5) compared to conditions (≥ 0.6) that promote lower survival (high mortality; Figures 3.3 and 3.4). Resilience to wetter conditions are manifested mostly in older trees, as shown in Figure 3.4, particularly during measurement periods M5 and M6.

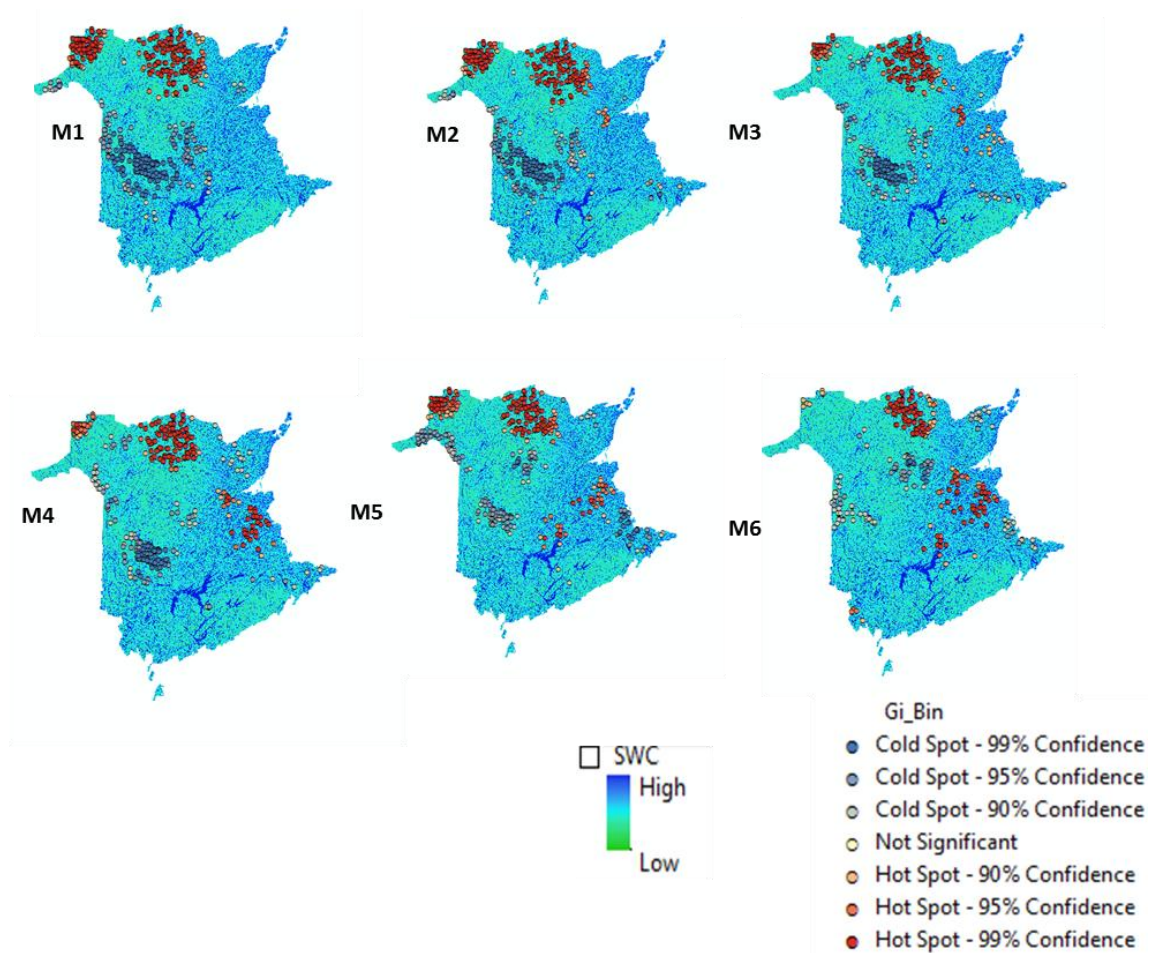


Figure 3.4 Spatial variation of survival as a function of soil water content.

3.4.4 Variation with photosynthetically active radiation

Photosynthesis is a light-dependent process in which the rate of photosynthesis depends on carbon dioxide and solar light intensity. Excessive light can often lead to overheating of the leaf surface causing damage to the photosynthetic apparatus. Continuous exposure to high sunlight may cause entire trees to be affected over the trees' growing cycle to the point of affecting its height growth and survival (Figure 3.3).

Low to medium regions of solar radiation coincides with high unexplained mortality. Essential to balsam fir survival is how well light resources essential to photosynthesis are utilized. Lack of resilience to low PAR conditions in the relatively younger trees during M2 caused many of them to die. Through measurement periods M3 to M6, the living trees acquire greater resilience, resulting in a shift in mortality in higher PAR regions, where other prevailing environmental conditions (most likely high GDD) cause some trees to die. Generally, high survival is evident in moderate PAR conditions as opposed to lower survival (high mortality) in areas of high PAR (Figures 3.3 and 3.5).

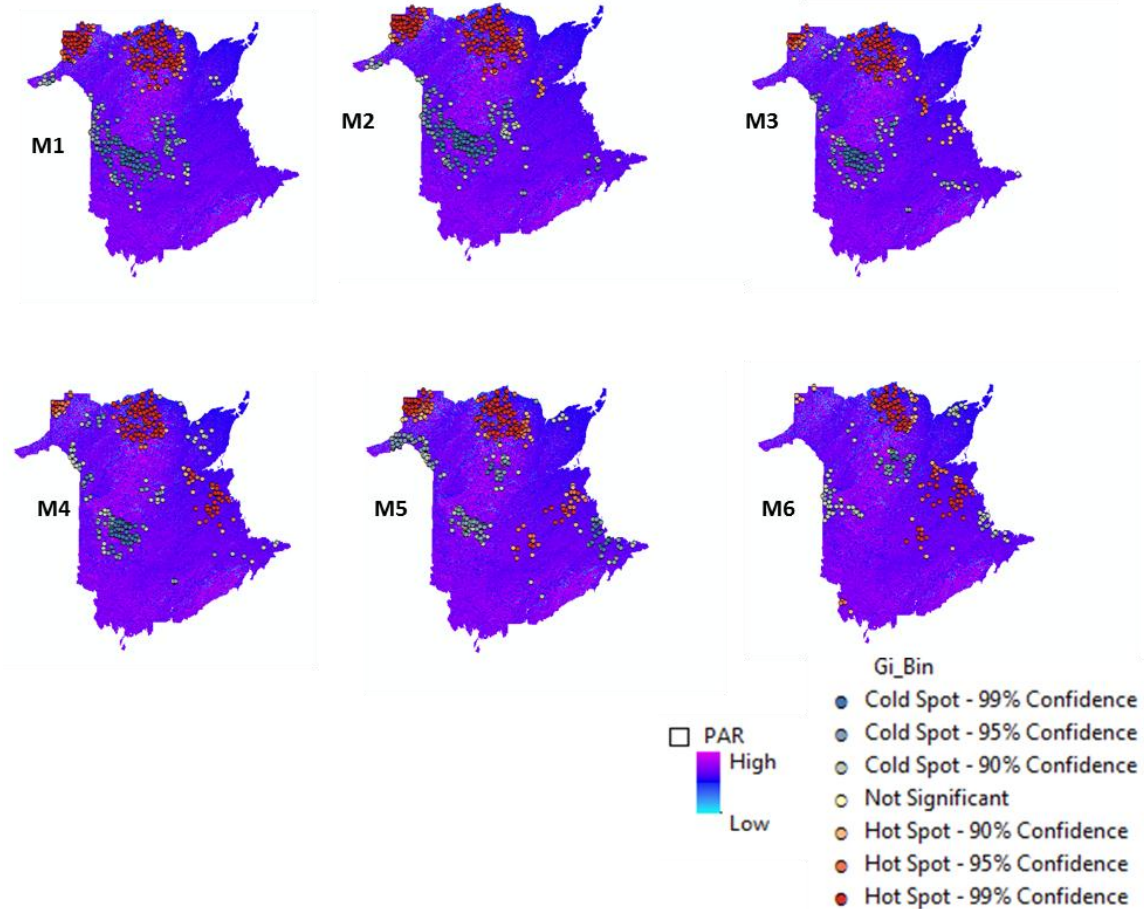


Figure 3.5 Spatiotemporal variation of survival as a function of photosynthetically active radiation.

3.4.5 Variation with growing degree days

Regions of high growing degree days are evidently unfavorable for balsam fir survival. Unexplained mortality is largely prominent in high growing degree-day areas of the landscape. Relatively young trees with less resilience to unfavorable PAR and SWC also succumbed in areas of high GDD during M2. The shift in mortality generally persists in other warm regions across measurement periods M3 through M6. This pattern of mortality in all regions of the province shows that temperature is an important environmental factor for balsam fir survival. In some cases, older trees show resilience to

high GDD as shown in Figure 3.6, where trees in M6 exhibit high survival. Results suggest that high survival of balsam fir trees generally occur in lower GDD areas relative to lower surviving areas (high mortality), where GDD are higher (Figures 3.3 and 3.6).

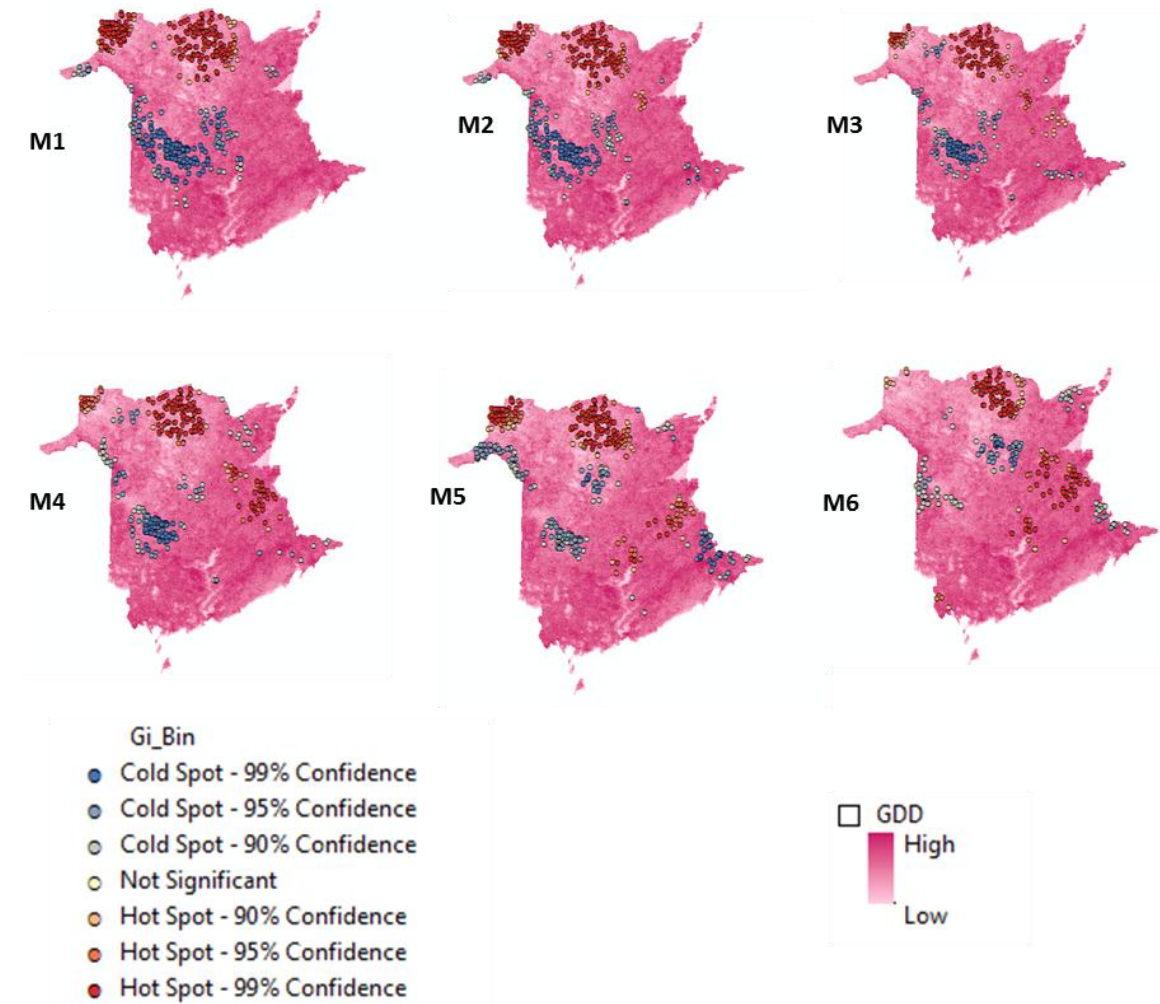


Figure 3.6 Spatiotemporal variation of survival as a function of growing degree days.

3.4.6 Survival and growth

The diameter growth rate (DGR) is obtained by subtracting the DBH of trees (followed by tree ID) from their DBH in subsequent measurement years. The DGR values obtained are divided by the number of years between measurement periods in annualizing tree vigor. Average annual tree vigor per plot is given in Figures 3.7-3.9.

3.4.7 Diameter changes across measurement years

A change in DBH from the measurement years' t to $t+1$ gives DGR (or Δ DBH) for each consecutive measurement interval (3 or 5 years; Figures 3.7-3.9). Mean DGR's are significantly high during the first and second measurement year, M1 to M2. At M3, mean DGR's begin to decline. The level of cambial growth does not reflect the same probability of survival for all trees of a given species (Bachman et al., 1983). As trees become larger, an ever-increasing fraction of total dry weight exists as wood that is photosynthetically non-productive (Kramer & Kozlowski, 1979); i.e., relative growth rate decreases with increasing tree size. Thus, DGR patterns in young trees differ from those in mature trees and in trees under different environmental constraints. The environmental conditions are more important for younger trees, where high DGR's (vigor) are prominent in regions of moderately high GDD ($\sim 1400^{\circ}\text{C}$), medium PAR (3200-3400 MJ m⁻²), and moderately wet soil conditions (SWC=0.3-0.5).

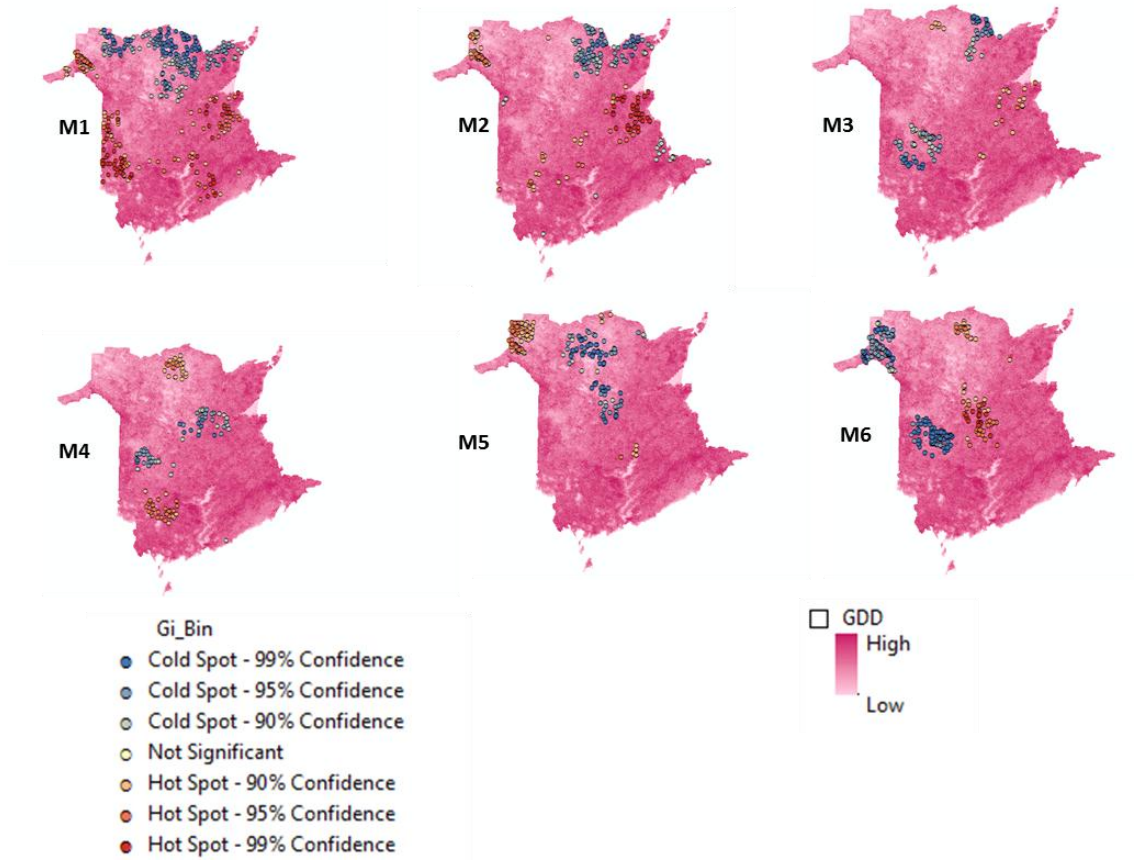


Figure 3.7 Spatiotemporal distribution and variation of annual DGR as a function of GDD.

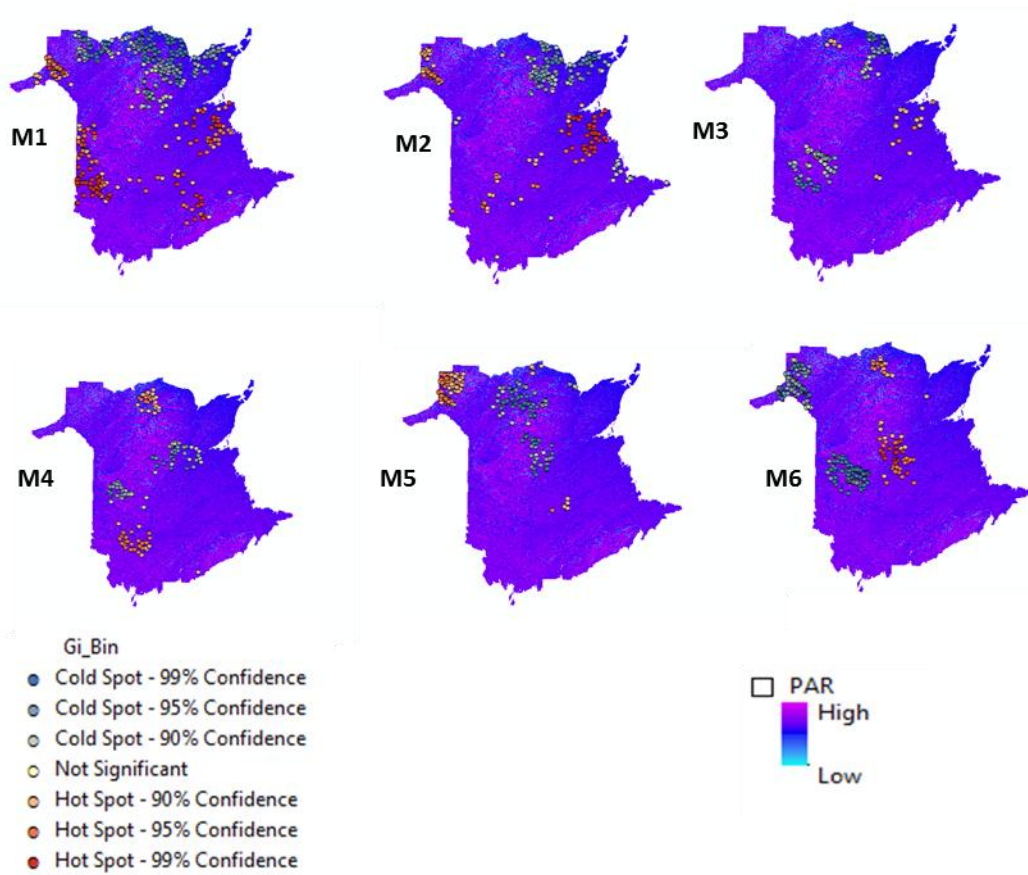


Figure 3.8 Spatiotemporal distribution and variation of annual DGR as a function of PAR.

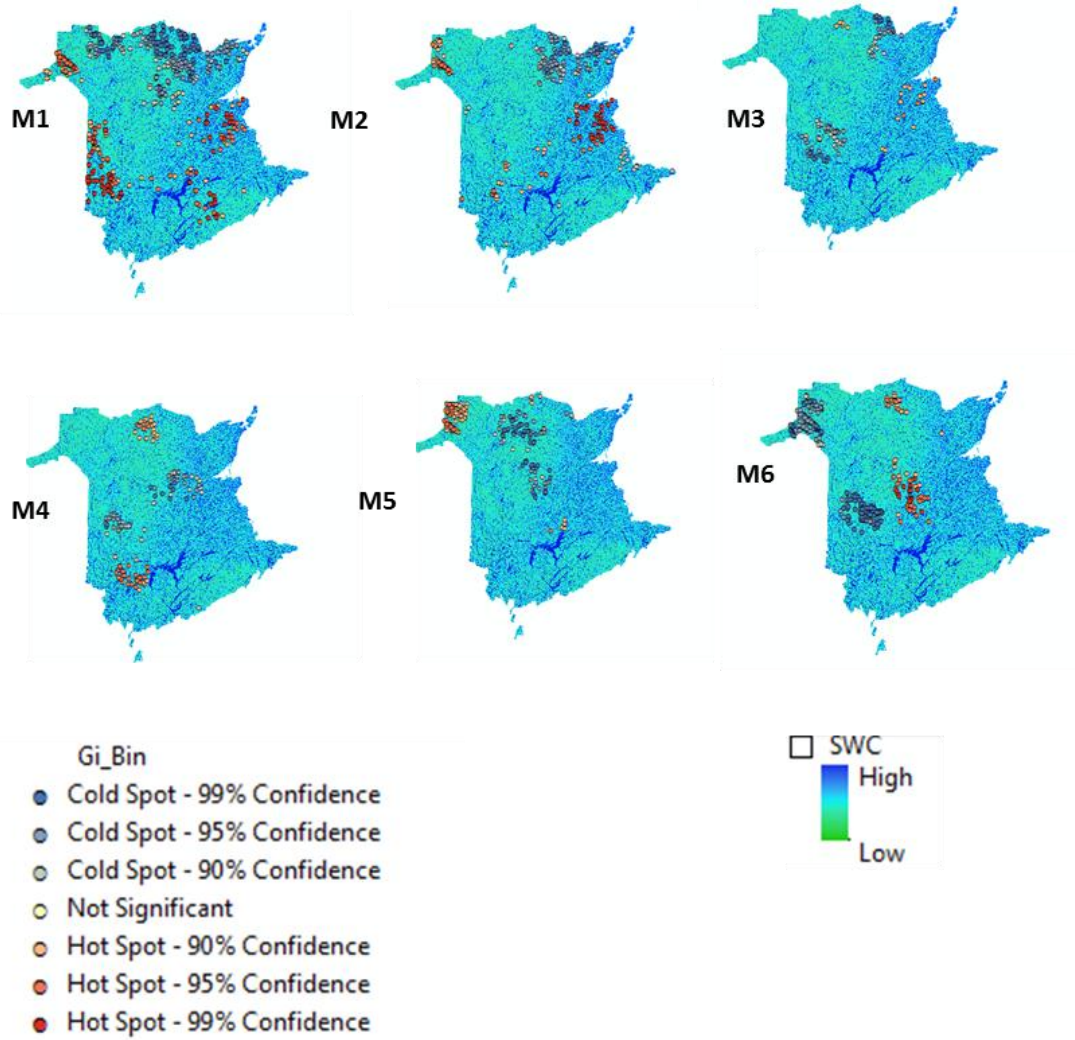


Figure 3.9 Spatiotemporal distribution and variation of annual DGR as a function of SWC.

3.4.8 Spatiotemporal distribution of mean annual DGR as a function of environmental variables

In order to have a better understanding of factors behind the observed spatial patterns of mean annual DGR of surviving trees, I explore the spatiotemporal variations with respect to the environmental variables. High values of PAR span a maximum of 27% of sampled plots. Relative SWC is lowest with a maximum of 11% of sampled plots. Growing degree days are generally evenly distributed spanning a maximum of 8.5% of sampled plots.

Distribution of DGR during measurement period M1 constitutes lower DGR values, occupying a maximum of 12.8% of sampled plots. The environmental conditions favorable to this distribution are SWC and GDD. Lower DGR's, however, generally occur when PAR is low.

A shift in this pattern occurred during measurement period M2 where DGR's increased in proportion to plot coverage under high PAR, low SWC, and high GDD. There is a general reduction in low DGR's under high PAR after a shift from low to high DGR's between M1 and M2. This increasing trend in DGR's show an increase in plot distribution from 10.6 to 74.5% of sample plots between M3 to M6.

Proportion of younger trees (lower DGR) that become older (higher DGR) suggest that a smaller % of the younger trees died under low PAR, high SWC, and moderately high GDD. In contrast, older trees generally survived under high PAR, low SWC, and low GDD favorable for balsam fir diameter growth.

3.4.9 Spatial distribution of surviving trees as a function of environmental variables

Percentage of surviving trees show significant variation in timing and extent with respect to the maximum % survival. Distribution generally increases across measurement year M2, M3, and M4, showing high survival rates in areas with high PAR, low SWC, and low GDD.

The trend of increasing survival with increasing PAR and decreasing SWC and GDD is consistent from M2 to M4. However, maximum plot % coverage decreases across measurement periods M2 (13%), M3 (10.6%), and M4 (5%), respectively. This trend is proportional to the maximum % coverage of the environmental variables PAR (27%), SWC (11%), and GDD (8.5%). Decrease in maximum plot % coverage of surviving trees across measurement periods M2, M3, and M4 is in response to environmental thresholds in balsam fir trees.

3.4.10 Comparative evaluation of maximum DGR with maximum mortality rate

To support inferences about timing rates of DGR as a function of environmental variables, I evaluated correlation between DGR and survival rate (Figures 3.10 and 3.11).

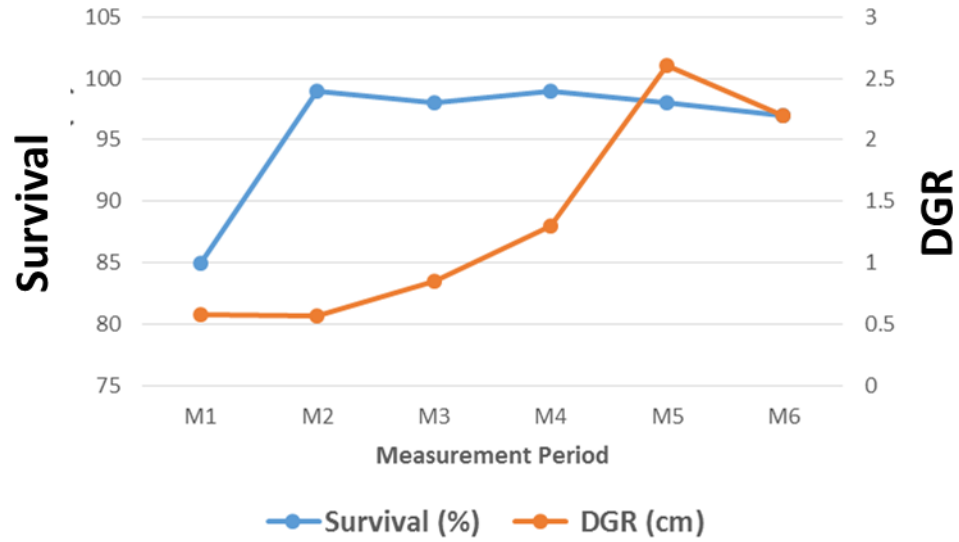


Figure 3.10 Temporal variation of maximum mean annual DGR with maximum % survival.

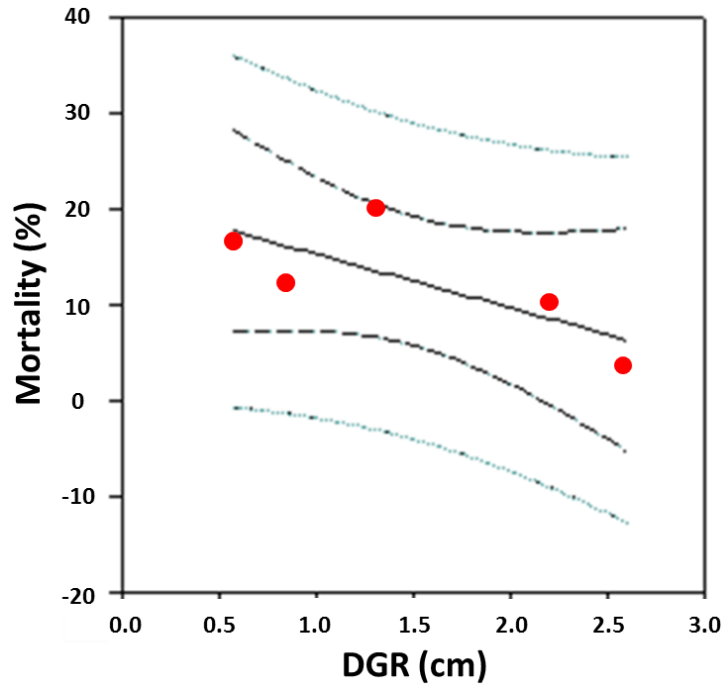


Figure 3.11 Maximum % mortality (or % survival, as inverse) as a function of maximum mean annual DGR; Mortality = $20.887 - (5.596 * DGR)$, with $R^2 = 0.59$.

3.4.11 Implication of climatic influence on balsam fir survival

Evaluation of fir survival as a function of climatic variables is based on (a) species distribution; (b) growth and vigor; (c) resistance and resilience; and (d) variation in unexplained mortality. Growth and vigor are evaluated with respect to the DGR response to the environmental factors. Resistance and resilience are assessed by evidence of increasing survival through growing and growing conditions evaluated in this study, which in turn explains the mortality rate of balsam fir trees from unknown causes.

Maximum DGR tends to correlate with maximum survival % across measurement periods. In agreement to this correlation, maximum mean annual mortality indirectly

correlates with maximum DGR, as depicted in Figure 3.11 ($R^2 = 0.59$). This suggests DGR is a reasonably good indicator of species vigor and survival.

Balsam fir survival increases across the measurement periods in proportion with increasing PAR at non-damaging levels. Increasing PAR is an indication of increasing energy for tree-physiological processes.

In contrast, survival increases across measurement periods with decreasing GDD and SWC. As GDD and SWC are controlled by temperature and precipitation, an increase in these variables will directly impact growing potential, causing balsam fir survival to potentially diminish.

Results of this work highlight the importance of photosynthetic processes in tree growth and survival. Data used in the evaluation of photosynthetic response to diameter growth is clearly captured with increasing PAR to non-destructive levels. Results show a decrease in DGR with increasing age (older trees). Younger trees use more photosynthesis for growth than do older trees, resulting in a decrease in the mean annual DGR. Photosynthetic resources are allocated in the maintenance of older trees as respiration increases and the demand on stored photosynthetic substances increases, leading to reduced growth and a decrease in DGR, as observed in Figures 3.7-3.9 (also, see Appendix D).

3.5 Conclusions

Generally, unexplained tree mortality occurred in areas of relatively high GDD, SWC, and PAR relative to trees that are known to have fared much better (surviving trees). Diameter growth rate (DGR) variation agrees with balsam fir survival variations. These results were evident as the maximum DGR is inversely correlated with mean annual mortality rate and directly correlated with survival rate. Results of hot spot analysis of unexplained mortality across the measurement periods coincides with lower elevations in the New Brunswick landscape. Climatic influence of these variables further supports the fact that these regions can potentially experience high levels of mortality in the event of temperature and precipitation increases projected to occur with climate change (Bourque, 2015). There is a general temporal decline in mean annual DGR indicating that growth rate decreases as trees age. Microclimates in NB can lead to differential survival dynamics in balsam fir.

4 GENERAL CONCLUSIONS

A species-specific understanding of stand dynamics, with and without insect disturbances, is needed to determine impacts and potential benefits of mixed wood management in order to protect softwood supplies from widespread losses due to spruce budworm outbreaks. An approach to addressing the interaction of a combination of environmental factors that cause damage and mortality to softwood and temperature-sensitive species, such as balsam fir, is crucial; understanding the combination of these interacting factors, rather than addressing them individually, is an important guide to management decisions.

This thesis has two main objectives. The first objective is to determine the quantity and spatial distribution of mortality caused by eight recorded factors in balsam fir under the influence of SBW. These causes were specifically under the influence of insect and wind, as well as anthropogenic disturbances, such as harvesting and cutting. The second objective was to explain the mortality of balsam fir trees of which the causes were not documented using another component of the environment that is known to satisfy their water, energy, and light requirements.

In Chapter 2, the spatiotemporal investigation of the effect of the latest SBW outbreak (1972-1993) is described. Results indicate variation in impact of SBW on each of the eight known causes of mortality. Data used were obtained from PSP's measured consecutively during the 1987-2014 period.

Spatial distribution of mortality is observed through the interaction of topography, temperature, aspect, sunlight, and moisture availability with climate and SBW emergence.

Statistically significant hot spots of mortality caused by insect damage coincide with the northern affinity of balsam fir, due to their prominence in cooler and moderately dry environments (Figure 2.3).

Temporal variations of mortality due to insect- and wind-related causes show a vulnerability to SBW-caused mortality to be highly susceptible to subsequent wind disturbance events, leading to substantial blowdown and stand decline in balsam fir. Suppression-caused mortality affected the greatest number of plots, accounting for 27.8% of all sampled plots.

Proportion of tree death attributed to insect during the first SBW outbreak period was 18.6%. This result is consistent with Taylor (2007). Interaction between different causes of mortality re-expresses the vulnerability in already weakened, defoliated trees that are exposed to secondary stresses brought on by wind. Acting individually, the causes are unlikely to cause widespread mortality.

Ecoregion influence on balsam fir mortality with known causes is most prominent in the Highlands. Compounded by the impact of climate could potentially lead to different levels of stress on forests.

Temporal decline of mortality to some degree is consistent with the fact that high probability of mortality typically occurs in small individual trees (DBH < 10 cm), as a result of self-thinning due to competition for resources.

In Chapter 3, the component of mortality that did not match any of the eight known causes is further investigated to attribute the possible causes. Water, energy, and light

requirements of trees are evaluated using surface data of PAR, SWC, and GDD. In this context, balsam fir survival is shown to be influenced by climatic variables. The energy component is based on light and heat, and accounts for the amount of energy available for tree-physiological processes. Survival is evaluated on species distribution, growth and vigor, and resistance and resilience to environmental factors.

The direct relationship between DGR and survival concurs with the fact that trees must grow in order to survive. This interaction is useful in validating the DGR relation to the environmental variables with survival. Utilization of environmental resources by balsam fir is evidence that survival and growth is a response to the environment as represented by PAR, SWC, and GDD.

The temporal decline in DGR could be due to the fact that as trees grow older, their growth processes decline as photosynthetic resources acquired from the environment are used for maintenance. Spatiotemporal distribution of both mean annual DGR and survival rate demonstrate a similar response to climatic variables, generally confirming that the conditions favorable to balsam fir survival are regions of low PAR ($\sim 3400 \text{ MJ m}^{-2}$), low GDD (~ 1400), and low SWC (≤ 0.5).

Environmental disturbances in the form of insect damage, wind, and anthropogenic disturbances collectively impact balsam fir survival. Mortality due to self-thinning is more pronounced in younger trees. Under favorable environmental conditions of PAR, SWC, and GDD, mean annual DGR decreases with tree age. The multiplicity of causes affect the physiological condition and vigor of trees during their lifetime; these stresses accumulate

over time, wearing down the trees' defenses until they eventually die. Maximum and minimum mean annual DGR is recorded at 2.6 and 0.6 cm yr⁻¹ (Appendix E, Table E1).

Unexplained mortality dominates in regions of low elevation, indicating that water and high energy levels are undesirable for balsam fir in these regions. This study has shown that tree mortality during and after uncontrolled SBW outbreak is not solely a function of defoliation; site and stand characteristics also have an influence. This thesis has outlined a better understanding of survival dynamics with and without SBW defoliation at the scale of microclimates. The methods of this study are portable to other species, in expansion of the scope of investigation. Results of this work can potentially be applied to larger scales across Canada to improve upon species response model for balsam fir and other species.

Recommendations based on this study are:

1. Further investigations should be conducted on other catastrophic mortality events, such as fire to assess the relative impact on mortality.
2. A survival model that utilises the combination of all factors affecting tree survival into account and reflecting the actual distribution of tree species should be constructed and simulated. This type of model could help optimize predictions of actual species distribution.
3. Further investigation of survival as a function of growth could be carried out by incorporating other growth parameters to improve the fit between % survival and DGR (increasing R²).

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6 APPENDICES

Appendix A: Summary statistics of other known causes of balsam fir mortality

Table A1. Broken top.

Measurement Period	Total # Balsam Fir Trees	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	25,269	16.67	0.1	721	7.5
M3	19,771	6.67	0.12	611	17.7
M4	16,451	7.83	0.21	456	14.8
M5	8,252	3.85	0.26	329	1.8
M6	4,955	0.36	0.36	202	0.1

Table A2 Insect damage.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	22.81	0.13	616	18.6
M3	12.5	0.22	620	6.1
M4	6.67	0.36	579	1.7
M5	1.67	1.11	343	0.3
M6	0	0	203	0

Table A3 Stem wound.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	3.33	0.13	776	1.6
M3	5.13	0.33	661	0.7
M4	5.71	0.31	576	2
M5	1.74	0.39	341	0.5
M6	0	0	203	0

Table A4 Windthrow.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	33.33	0.09	688	11
M3	16.67	0.1	538	14.8
M4	25	0.25	462	14.2
M5	6	0.26	311	3.7
M6	1.09	0.53	201	0.2

Table A5 Other, likely cut.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	6.4	0.38	754	3.9
M3	6.67	0.2	650	2.9
M4	3.64	0.2	580	1.6
M5	7.5	1.7	341	0.5
M6	0	0	203	0

Table A6 Over mature.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	16.67	0.3	736	5.9
M3	12.5	0.32	634	4.6
M4	10	0.18	537	6.2
M5	10	0.25	320	2.8
M6	1.09	1.09	202	0.1

Table A7 Suppression.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	11.11	0.12	530	27.8
M3	15.09	0.17	480	21
M4	10	0.18	467	13.6
M5	3.64	0.25	312	3.6
M6	6.67	0.61	119	8.9

Table A8 Stem breakage.

Measurement Period	Max (%)	Min % > Zero	# Plots with Zero Mortality	% Plots with Some Level of Mortality
M2	33.33	0.1	606	19.7
M3	20	0.16	525	16.2
M4	16.67	0.22	453	15.1
M5	11.43	0.29	291	5.9
M6	1.33	1.33	202	0.1

Appendix B: Algorithm for tracking tree mortality

for each plot(P) in plots:

for each measurement year(Yr) i in measurement years-1 (1...n-1):

where n is the last measurement year for the current plot

TreeInYear_i = All trees in current Yr(i)

TreeNextYear_i+1 = All trees in next measurement Yr(i+1)

LivingTrees = TreeInYear_i (Intersection) TreeNextYear_i+1

Year_i compliment or Trees that did not show up in Year_i+1

Mortality_inYear_i = TreeInYear_i (Difference) LivingTrees # Year_i compliment

Total_Number_Trees_Year_i = Size(TreeInYear_i)

Number_Mortality_i = Size(Mortality_inYear_i)

Mortality_Percentage_In_Year_i = (Number_Mortality_i / Total_Number_Trees_Year_i)
* 100

#group by cause codes

#=====

cause_group = dictionary{code: number of trees that died by this cause}

#classify mortality by cause

for trees in Mortality_inYear_i:

cause = get cause of death

add to cause to cause_group

#unknown cause are grouped as : cause code == -1 or cause code == 9

#e.g.

#cause group {code: #number of trees}

{1: 2, 2: 6, 3: 0, 4: 0, 5: 0, 6: 3, 7: 0, 8: 0, -1: 9}

#get the year interval between year i and year i+1

Year_interval_i = Year(i+1) - Year(i)

#group by mortality by cause percentage per year

#=====

for each cause (c) in cause_group:

```

#percentage of trees that died as a result of cause c / number of trees in the plot
#cause as a percentage of trees in the plot
percentage_by_cause_c = Size(cause_c in cause group) / Total_Number_Trees_Year_i
#normalize cause by year interval between Year_i and Year_i+1
percentage_by_cause_c_per_year (i to i+1) = percentage_by_cause_c / Year_interval_i
#group classes ranges
# e.g. [(0.5, 5.5), (5.6, 10.6), (10.7, 15.7), (15.8, 20.8), (20.9, 25.9), (26.0, 31.0)]
# this finds for each class how much mortality occurred
Mortality_Per_Class = {class1: [trees], class2:[trees]}
for each class in classes_year_i :
trees_in_class = get_trees_in_class(class)
mortality_in_class = trees_in_class (Intersection) Mortality_inYear_i
add mortality_in_class to Mortality_Per_Class

```

Appendix C: Summary statistics of mortality without known causes

Table C1 Mean annual % mortality of undocumented causes.

Measurement Period	Total Number of Balsam Fir trees	Max (%)	Minimum % > Zero	% Count = Zero	Number of Plots with Zero Mortality	Percentage of Plots with Some Level of Mortality
M2	25269	16.67	0.1	786	153	16
M3	19771	12.25	0.1	821	118	12.6
M4	16451	20	0.2	864	75	8
M5	8252	3.43	0.2	921	18	1.9
M6	4955	10	0	937	2	0.2

Appendix D: Summary statistics of mean annual diameter growth rate (DGR)

Table D1 Summary of mean annual diameter growth rate of surviving trees.

Measurement Period	Max (CM)	Count=Zero	Count< Zero	Count>Zero	% Plot
M1	0.58	55	1	883	94
M2	0.57	153	10	776	82.6
M3	0.85	284	36	619	66
M4	1.3	361	35	543	58
M5	2.6	598	42	299	32
M6	2.2	738	27	174	19

VITA

Candidate's full name: Christian Kwaku Akpanya

Universities attended:

BSc in Physics, University of Cape Coast, Ghana, 2002

MSc in Atmospheric Science, (Course work), Creighton University, Omaha NE, USA, 2011

Diploma in University Teaching (DUT), University of New Brunswick (UNB), 2013

MScF Candidate University of New Brunswick

Presentations:

Akpanya, C.K., & Bourque, C.P.-A. 2017. Mortality risk of balsam fir to variations in solar radiation. Graduate seminar, Faculty of Forestry and Environmental Management (UNB). Fredericton, NB

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