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Spruce Budworm Defoliation Dynamics and its Influence on the Acadian Forest

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SPRUCE BUDWORM DEFOLIATION DYNAMICS AND ITS INFLUENCE ON THE ACADIAN FOREST

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A DISSERTATION

Submitted in Partial Fulfillment of the

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December 2019

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Dissertation Advisor: Dr. Aaron Weiskittel

An Abstract of the Dissertation Presented
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Spruce budworm (SBW; *Choristoneura fumiferana* (Clem.)) is the primary forest defoliator in North America. SBW defoliation has affected tens of millions ha of forests during its periodic outbreaks and caused severe growth reduction and mortality of spruce-fir (*Picea-Abies*) species. Evaluating these damaging effects of SBW defoliation requires understandings of the variation and dynamics of defoliation, as well as trees' variable responses to defoliation in consideration of various tree- stand-, and site-level factors. In this dissertation, we developed statistical models to 1) evaluate influences of SBW defoliation on spruce-fir stand dynamics of annual volume net growth, mortality, and ingrowth, 2) quantify effects of SBW defoliation on annualized diameter and height increment, crown recession, and mortality, and 3) assess patterns and temporal development of SBW defoliation on individual trees. Measurements of individual trees and their defoliation collected from 560 permanent sample plots in Maine and New Brunswick during the last SBW outbreak in the 1970s-1980s, which covered > 40 000 km^2 as well as 10 years of varying ranges of defoliation and forest conditions were used in the analyses. Our results strongly demonstrated that 1) even relatively low levels of cumulative defoliation were significantly related to stand-level mortality and ingrowth, while net growth was more competition driven, 2) effects of defoliation on diameter increment, crown recession, and mortality were highly significant but relatively moderate depending on species, and 3) variation in individual tree defoliation was predominantly dependent on species. In addition, defoliation of each host species analyzed developed towards their respective converged trajectories. Based on these findings, we developed annualized modifiers for the Acadian variant of the Forest Vegetation Simulator (FVS-ACD) to account for effects of SBW defoliation on forest development, which consistently had smaller biases and prediction errors than FVS-ACD refined by STAMAN (a Canadian growth model) SBW modifiers. Overall, our findings highlight the high variability in SBW defoliation and trees' responses to defoliation, which were consistent between Maine and New Brunswick despite varying forest management history and species composition. We believe the developed modeling framework should also be extendable to analyzing other forms of defoliation in broader regions.

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CHAPTER 1

THE ACADIAN FOREST AND THE SPRUCE BUDWORM: A PROLOGUE

1.1. The Acadian Forest

From a broad point of view, the Acadian forest covers the inland parts of New England states of the United States along with the Maritime Provinces and southern Quebec of Canada by the demarcation of the World Wildlife Fund (Davis et al. 2018), which is similar to the northeastern highlands ecoregion in the classification of Omernik (1987). This region is a transition zone from the maple-beech-birch (*Acer-Fagus-Betula*) characterized northern hardwood forest in the south to the spruce-fir (*Picea-Abies*) characterized boreal softwood forest in the north. While the spruce-fir forest is the subject of this dissertation, its geographical extent thus reflects a historical perspective of the Acadian region that contains northern Maine, southern Quebec, and the Maritime Provinces of Canada (Williamson 1832), where spruce-fir dominates the forest.

Although the Acadian region includes thousands of km of coastline, the region does not experience a typical oceanic climate because the prevailing winds are from the west and blow off the continent (Loo and Ives 2003). Nevertheless, the Atlantic Ocean has a significant humidifying and moderating effect on both precipitation and temperature regimes. Consequently, this region has warm and moist summers along with cold and snowy winters, which are milder than those in the middle of the continent (Simmons 1984). Mean annual precipitation is generally above 1 000 mm in this region (Seymour 1995). Mean annual temperature is 6.8 ºC in Bangor, Maine and 5.2 ºC in Fredericton, New Brunswick, while mean frost-free days are 141 and 125 days in these two respective locations.

The Acadian region is a part of the Appalachian Mountain Range with elevations ranging from sea level to 1 605, 807, and 560 m in Maine, New Brunswick, and Nova Scotia, respectively.

Erosion and glaciation have shaped the characteristic topography of mountains, plateaus, and valleys, and also determined the mosaic of soil and forest types of this region. The mountains and plateaus are thinly covered by glacial till underlain by granite and metamorphic rocks, which is acidic and low in fertility. In comparison, valleys are relatively more fertile but poorly drained with large numbers of swamps and lakes. The way that glacial drift was deposited has largely determined that the best soils for forest development are often found on mid-slopes of hills and mountains (Degraaf 1991).

Forest dominates the Acadian landscape and covers about 90%, 85%, and 73% of the lands of Maine, New Brunswick, and Nova Scotia, respectively (Seymour 1995, Loo and Ives 2003). Forest species distribution was more even before the large-scale exploitation of the Acadian forest in the past centuries than it is today (Lutz 1997). Lorimer (1977) states that much of the northern Maine forest was tolerant mixedwood mainly consisting of spruce (*Picea* spp.), American beech (*Fagus grandifolia* Ehrh.), balsam fir (*Abies balsamea* L.), white cedar (*Thuja occidentalis* L.), and yellow birch (*Betula alleghaniensis* Britt.) about 200 years ago. However, spruce and balsam fir have large increases in abundance, e.g., from being about 25% of the forest 200 years ago to about 50% today in New Brunswick (Loo and Ives 2003), and dominate the softwood inventory (Seymour 1995). In the meantime, red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marshall) become increasingly common among hardwood in this region (Seymour 1995). These changes in species distribution have been attributed to a number of courses including: 1) agricultural clearing and subsequent abandonment, 2) waves of removal of individual species such as white pine (*Pinus strobus* L.) and spruce, and 3) changes in the regimes of natural disturbances such as fire and insect outbreaks.

Major natural disturbance agents in the Acadian region include wind, fire, and insect. While red spruce (*Picea rubens* Sarg.) and balsam fir are both shallow-rooted, wind damage becomes a chronic phenomenon but is generally limited to small scales (Seymour 1992). On the other hand, stand-replacing wind damages occur at intervals from hundreds to thousands of years similar to those of fire (Lorimer 1977, Seymour et al. 2002). In addition, continued fire suppression will likely further reduce the frequency and extent of fire (Wein and Moore 1977). In comparison, a number of insects like spruce bark beetle (*Dendroctonus rufipennis* Kirby), balsam fir sawfly (*Neodiprion abietis* Harris), and spruce budworm (*Choristoneura fumiferana* (Clem.); SBW) are known to have influenced the Acadian forest for as long as records have been kept. Among the above mentioned disturbances, SBW outbreaks are more important in that they have a larger spatio-temporal scale, shorter return interval, and greater influence on forest productivity. In addition, Periodic SBW outbreaks have not been suppressed while appear to be better synchronized and increasing in extent and severity (Blais 1983).

1.2. The Spruce Budworm and Its Outbreaks

SBW is endemic to broad areas of eastern North America ranging from Yukon, Canada to the Atlantic coast, where spruce-fir forest presents (Webb et al. 1961, Irland et al. 1988). SBW has a life cycle of one year. Its Moths emerge from July to August and lay eggs mainly on the foliage of spruce-fir trees over several days. These moths lay an average of 200 eggs at a number of places with each egg-mass containing an average of 20 eggs. After these eggs hatch in about 10 days, the first-instar larvae hanging on silken threads disperse by wind within and between trees without feeding. Surviving larvae spin hibernacula, within which they molt to the second instars that emerge in April or May of the following year. The second to sixth instar larvae feed on current-year shoots of a number of conifers with balsam fir, white spruce (*Picea glauca* (Moench) Voss), red spruce, and black spruce (*Picea mariana* (Mill.) B.S.P.) being the major hosts. This feeding lasts for 6-7 weeks, and only occurs on older foliage when current-year shoots are depleted. Finally, Pupation of SBW normally takes place on the foliage in early July (Talerico 1984).

An important feature of SBW, which probably has contributed to the widespread outbreaks of defoliation, is its ability of dispersal. In addition to the dispersal of young larvae by wind, SBW moths normally fly 50-100 km downwind and as far as 450 km from mainland Canada to Newfoundland (Greenbank et al. 1980). After laying a part of their egg complements at places of emergence, female moths take obligatory flights and deposit their eggs where they land over several nights. These dispersal flights are governed by meteorological conditions such that they only take place when temperature is at 14-30 ºC (Royama 1984).

SBW outbreak is a predominant natural disturbance of the spruce-fir forest distributed over broad areas of eastern North America. Three SBW outbreaks in these areas in the 20th century starting in the 1910s, 1940s, and 1970s have been well documented. On the other hand, reconstruction of outbreak history has been based on the comparison of radial growth patterns between non-host and host trees that survived SBW defoliation (Blais 1962). For example, outbreaks began about 1770, 1806, and 1878 have been identified in New Brunswick (Webb et al. 1961); Blais (1965) found evidence of outbreaks in the Laurentide Park region of Quebec beginning about 1710, 1755, 1812, and 1838; and Fraver et al. (2007) identified outbreaks beginning about 1709, 1762, and 1808 but found little or no evidence for the 1830s and 1870s outbreaks. Consequently, Fraver et al. (2007) concluded return interval of SBW outbreaks to be about 60 years. However, Royama (1984) argued that the missing indications of outbreaks in dendrochronological analyses were possibly because defoliation did not reach levels high enough to affect tree rings at places. Therefore, return interval of SBW outbreaks is close to 30 years.

SBW outbreaks starting in the 1910s, 1940s, and 1970s each lasted for about 15 years and had extents of about 10, 25, and 57 million ha, respectively (Blais 1983). An estimated 55 million m^3 of timber was lost due to defoliation in eastern Canada during the 1910s-1920s (Swaine and Craighead 1924), while this timber loss during the same period in Maine was estimated to be 8.3 million m^3 by McLintock (1955) and 98 million m^3 by Seymour (1992). As these outbreaks extending over increasingly larger areas in the 20th century, timber losses also increased to 32-43 million m^3 $year^{-1}$ in Canada during 1978-1987, which accounted for 41-53% of Canada's total annual timber losses (Sterner and Davidson 1982, Power 1991). However, the 1940s outbreak caused little tree mortality in Maine, which resembles a hidden outbreak outlined by Royama (1984).

Two important features of SBW population dynamics have limited our understandings of influences of SBW defoliation and management options to control it. First, SBW populations fluctuate between extreme levels (e.g., from <5 to 20 000 larvae per tree; Irland et al. 1988) among trees, stands, and forests over the durations of outbreaks. On the other hand, SBW populations have been changing in synchrony at a regional scale over the 30-60 year outbreak cycles (Royama 1984). Three major hypotheses of SBW population dynamics have been postulated over the 20th century (Royama 1984, Pureswaran et al. 2016), and likely will affect how findings of this dissertation are interpreted and utilized.

The silviculture hypothesis considers that outbreaks were driven by forest management practices. Specifically, SBW's major host balsam fir was little utilized and its regeneration was promoted by the harvesting of competing species, which consequently accumulated food sources for large populations of SBW. The double-equilibria hypothesis suggests that warm weather conditions released SBW populations from the low density equilibrium at epicenters (hot spots). These populations subsequently dispersed to large areas and finally reached the high population density equilibrium. Finally, the second-order oscillation hypothesis argues that SBW population dynamics follow a second-order density-dependent process such that SBW populations reached outbreak levels because the density-dependent survival of larvae was high. Outbreaks were synchronized by independent but highly correlated weather conditions, which governed the ratio of all eggs laid to the number of locally emerged moth (a measure of immigration and emigration).

1.3. Structure of This Dissertation

This dissertation focuses on the dynamics of SBW defoliation and its influence on the development of spruce-fir forest. Consequently, the rest of this dissertation is divided into the following four chapters: Chapter 2 — assessing the influence of SBW defoliation on forest stand dynamics, Chapter 3 — evaluating the influence of SBW defoliation on individual tree growth and mortality, Chapter 4 — modeling variation and temporal dynamics of individual tree defoliation caused by SBW, and Chapter 5 — refining the Forest Vegetation Simulator (FVS) for projecting the effects of SBW defoliation.

Many studies have evaluated the influence of SBW defoliation on the growth and mortality of trees by species (e.g., Blais 1958; MacLean 1980; Reams et al. 1988; MacLean and Ostaff 1989; Piene 1989; MacLean et al. 1996; Solomon et al. 2003; Pothier et al. 2012). These evaluations have been conducted at cumulative defoliation levels ranging from 336% to 840% (Blais 1958; MacLean and Ostaff 1989; Piene 1989; MacLean et al. 1996), and have not explicitly assessed the potential compounding effects of stand structure and composition, site potential productivity, and topography. Consequently, Chapter 2 aims to comprehensively assess the influence of SBW defoliation on stand dynamic variables of net growth, mortality, and ingrowth under cumulative defoliation levels mainly below 300%, which were typical during the 1970s-

1980s outbreak in Maine and New Brunswick. In addition, Chapter 2 will also try to identify the most important stand and site factors on the above variables of stand dynamics.

While the stand-level assessment of Chapter 2 provides useful information for making forest management decisions at large scales to mitigate the influence of SBW defoliation, it is unable to provide information on the intrinsic differences in responses of individual trees to defoliation, which are the theoretical basis of cyclic SBW outbreaks (Holling 1973) and silvicultural methods proposed to alleviate influences of defoliation (Baskerville 1975, Blais 1983). However, previous studies as those identified above have performed evaluations mostly by species (i.e., aggregating trees of the same species over a large spatial and temporal extent) with a few by size-class (e.g., Steinman and MacLean 1994, MacLean 1996). In addition, these evaluations have been primarily focused on mortality caused by defoliation. Therefore, the primary objective of Chapter 3 is to develop a rather comprehensive set of individual tree models of diameter and height increments, crown recession (height to crown base increment), and mortality to quantify the effects of SBW defoliation, meanwhile evaluate their interplay with various stand and site factors.

Host trees' capacities in supporting defoliator populations, i.e., the susceptibility of these trees (Mott 1963), partly decide the varying levels of defoliation these trees likely sustain. While such variations in SBW defoliation have long been observed (e.g., MacLean and Lidstone 1982, Gray et al. 2000, Doran et al. 2017), their patterns have been little examined or modeled. In Chapter 4, we propose evaluations of the variation and temporal dynamics of SBW defoliation from a cross-scale approach, which would allow potential causal effects to be evaluated at suitable scales (e.g., specific effects may be better assessed at tree-level to separate structural and compositional effects of stands, while diversity can be analyzed at larger scales). As a result, coarse observations of defoliation obtained from remote sensing may potentially be leveraged to provide detailed defoliation predictions of individual trees and consequently replace the costly and time-consuming on-site measurements of defoliation.

Based on the findings in previous chapters, influences of SBW defoliation on individual tree diameter and height increments, crown recession (height to crown base increment), and mortality, as well as stand dynamic variable of ingrowth will be synthesized with predictions of individual tree defoliation and its temporal dynamics to generate projections of forest growth and yield in Chapter 5. Specifically, annualized modifiers that adjust annual predictions of the above mentioned growth and mortality variables will be developed to be used in the Acadian variant of FVS (FVS-ACD; Weiskittel et al. 2017), which offers flexibility in accounting for the specific effects of management activities and disturbance agents on individual trees at an annual resolution, and better represents forests in the Acadian region. Consequently, the work of Chapter 5 will potentially provide the well-established FVS with the capability of accounting for the potential effects of SBW defoliation on forest development and provide information for forest management and protection planning.

Overall, we believe that our work will be a valuable complement to previous studies on the influences of SBW defoliation, which have been focused on higher levels of severe defoliation. The large spatial and temporal extents of our work will make it extendable to larger areas, while the findings of the underlining relationships between SBW defoliation and tree as well as stand dynamic variables may also help evaluate the influences of defoliation on landscapes. Besides predictions of forest growth and yield, the refined FVS-ACD may also be used to provide variable information on the forest ecosystem such as changes in carbon storage as well as fire and wind hazards. Finally, our work has the potential of providing a flexible modeling framework for extensions to other forms of defoliation.

CHAPTER 2

EVEN LOW LEVELS OF SPRUCE BUDWORM DEFOLIATION AFFECT MORTALITY AND INGROWTH BUT NET GROWTH IS MORE DRIVEN BY COMPETITION[1]

2.1. Introduction

Loss of photosynthetic material through insect defoliation results in reduced growth and survival of trees, and is one of the most important natural disturbances influencing forests (e.g., Kulman 1971, MacLean 2016). Spruce budworm (SBW; *Choristoneura fumiferana* (Clem.)) is the primary defoliating insect in North America and has affected over 58 million ha of forests during its last major outbreak in 1970s and 1980s (Blais 1983, USDA Forest Service 2009). Consequently, approximately 44 million m^3 of timber was lost annually during this outbreak period in Canada alone (Sterner and Davidson 1982). On the other hand, SBW has co-evolved with spruce-fir (*Picea-Abies*) forests for hundreds of years with periodic outbreaks 30-60 years apart (Fraver et al. 2007), and these forests are still abundant in the region (McWilliams et al. 2005, Power and Gillis 2006). Therefore, evaluating the influence of SBW defoliation on stand dynamics is critical in predicting future supply of forest products and in understanding stand dynamics and succession under varying disturbance regimes.

SBW larval emergence is synchronized with the bud burst of its hosts balsam fir (*Abies balsamea* L.) and white spruce (*Picea glauca* (Moench) Voss), and these larvae feed primarily on current year foliage despite the species' retention of multiple years of foliage (Irland et al. 1988). Additionally, SBW defoliation has cumulative effects on growth and mortality. For example, Blais (1958) noted that growth reduction was often observed after two years of defoliation, while MacLean (1980) suggested that trees usually started to die only after four or five years of severe

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[1] This chapter previously appeared as an article as follows: Chen, C., Weiskittel, A., Bataineh, M., and MacLean, D.A. 2017. Even low levels of spruce budworm defoliation affect mortality and ingrowth but net growth is more driven by competition. Canadian Journal of Forest Research 47: 1546-1556.

defoliation. Consequently, cumulative sums of the defoliation of current-year foliage (cumulative defoliation) have long been considered a suitable metric in measuring the severity of SBW defoliation.

There is a vast literature on the influence of SBW defoliation on forest development (e.g., Blais 1958, MacLean 1980, Osawa et al. 1986, Reams et al. 1988, MacLean and Ostaff 1989, Piene 1989, MacLean et al. 1996, Solomon et al. 2003, Pothier and Mailly 2006, Pothier et al. 2012), with reported tree mortality between 73-100% for balsam fir and between 27-66% for spruce (*Picea* spp.) and growth reductions in balsam fir up to 83%. The cumulative defoliation that caused the above mortality and growth reductions have largely ranged between 336-840% (Blais 1958, MacLean and Ostaff 1989, Piene 1989, MacLean et al. 1996). Obviously, the influence of SBW defoliation on forest development has generally been assessed at rather high levels of defoliation, and was largely overlooked for cumulative defoliation levels below 300%. Furthermore, studies on SBW defoliation have often been confined in space (1-73 sample plots; Blais 1958, MacLean 1980, Reams et al. 1988, MacLean and Ostaff 1989, Piene 1989, MacLean et al. 1996, and Solomon et al. 2003) or rather coarse in temporal resolution (~ 10 years between measurements; Pothier and Mailly 2006, Pothier et al. 2012). Hence, their representativeness of the dynamic process of defoliation hinged on the premise that this process was comparable at various spatial and temporal scales. However, defoliation is heterogeneous and varies greatly over space and time during a SBW outbreak (Supplemental Materials A.1, Baskerville and MacLean 1979, Irland et al. 1988, Hennigar et al. 2013). Consequently, the influence of SBW defoliation on forest development is also likely to be heterogeneous at different scales. For example, Osawa et al. (1986) was restricted to a portion of Baxter State Park (~ 800 km^2) in Maine and recorded mortality for balsam fir from mid-1970s to 1982 of 74%, while Brann et al. (1985) summarized data from across northern Maine (> 40

000 km^2) during the same period and reported such mortality of ~15%. Therefore, it is critical to evaluate whether this influence is an artifact of scaling of the defoliation process, or is consistent over large areas.

Besides the high variation in defoliation, evaluating the influence of SBW defoliation on forest development is challenging because forest stand and site characteristics, which are indicators of resource availability (productivity) and competition, are also expected to vary considerably within the vast areas affected by SBW defoliation. While productivity and competition regulate forest development in the absence of disturbances, they most likely interact with defoliation and confound their effects on forest development. For example, while defoliation directly reduces tree growth, it may also cause mortality of the neighboring trees and hence reduce competition and promote growth of the surviving trees. On the other hand, some stand and site characteristics may be favorable to SBW, e.g., a higher content of a preferred host, thus intensifying the influence of defoliation. Therefore, evaluating the influence of SBW defoliation and its potential interactions with a variety of stand and site characteristics is necessary to provide a more comprehensive understanding of the influence of defoliation. Identifying the relative importance of productivity, competition, and defoliation in forest development is critical for prioritizing forest management activities to address the influence of defoliation.

This study utilized comprehensive defoliation data collected at short time intervals (1-3 years) from extensive networks of permanent sample plots (PSP; 560 in total) that covered a longitudinal range of ~ 490 km and a latitudinal range of ~ 340 km. These data comprised a wide range of cumulative defoliation observations accompanied by detailed tree and site measurements, which provided opportunities to evaluate how varying levels of SBW defoliation (especially lower levels that have been largely overlooked in previous studies) influenced forest development, and to assess how the effects of defoliation on growth, mortality, and ingrowth interacted with stand and site characteristics. The above data were used to quantify the influence of SBW defoliation on key forest stand dynamics since stand development is considered the linkage between pest incidence and forest development (Erdle and MacLean 1999) and evaluating stand dynamics generally requires less information (Weiskittel et al. 2011a). This analysis was applied separately to two rather distinct regions with contrasting forest management and SBW outbreak histories to test whether it was valid and consistent over a broad geographical area with varying stand, site, and defoliation conditions.

Specific research objectives were to: 1) model annual stand volume net growth, mortality, and ingrowth using variables derived for SBW defoliation, stand structure and composition, potential productivity, and topography from long-term, remeasured permanent plots across both of the regions; 2) evaluate the varying influences of SBW defoliation and identify the most important stand and site factors on the above variables of stand dynamics; and 3) perform the above modeling and evaluation in Maine and New Brunswick, which differ in forest management and SBW outbreak histories, to better verify the robustness and consistency of our findings. It was expected that our findings would indicate that defoliation, even at relatively low levels, had an important role in all of the stand dynamic variables examined, but this effect would depend largely on stand structure and composition as well as important site factors like soil drainage. In addition, our models were expected to indicate these effects of defoliation, as well as its interaction with stand and site characteristics, were comparable between the two regions, despite differences in their forest management and SBW outbreak histories. This would provide support to the general robustness and consistency of the models.

2.2. Material and Methods

2.2.1. Study Area

The combined study area (44°56'-48°00' N, 64°28'-70°44' W) in Maine and New Brunswick mainly belongs to the temperate broadleaf mixed forest biome (Figure 2.1). The most common forest types in Maine include maple-beech-birch (*Acer-Fagus-Betula*) of 2.9 million ha and spruce-fir of 2.4 million ha in 2003 (McWilliams et al. 2005). Growing stocks of SBW's major hosts of balsam fir, red spruce (*Picea rubens* Sarg.), black spruce (*Picea mariana* (Mill.) B.S.P.), and white spruce were 117, 146, 14, and 17 million m^3, respectively, in 1982, and 65, 100, 15, and 17 million m^3, respectively, in 2003 (McWilliams et al. 2005). New Brunswick had 2.5, 1.8, and 1.4 million ha of softwood, mixedwood, and hardwood forests, respectively, in 2001 (Power and Gillis 2006). Growing stock of balsam fir and spruce was 118 and 154 million m^3, respectively, in 1981, and 91 and 174 million m^3, respectively, in 2001 (Bonnor 1982, Power and Gillis 2006). Soils in Maine and New Brunswick are generally infertile, acidic, and low in permeability (Ferwerda et al. 1997; Rees et al. 2005). Maine has a humid continental climate with warm, humid summers, and cold, snowy winters. Annual precipitation varies from 909 to 1 441 mm and is distributed evenly year-round. Climate in New Brunswick is similar to that of Maine with annual precipitation ranging from 889 to 1 143 mm, evenly distributed through the year. Elevation of the study areas in Maine and New Brunswick ranged from 41-691 m and 0-578 m, respectively. These two areas have similar SBW outbreak histories as both experienced an outbreak in the 1970s-1980s.

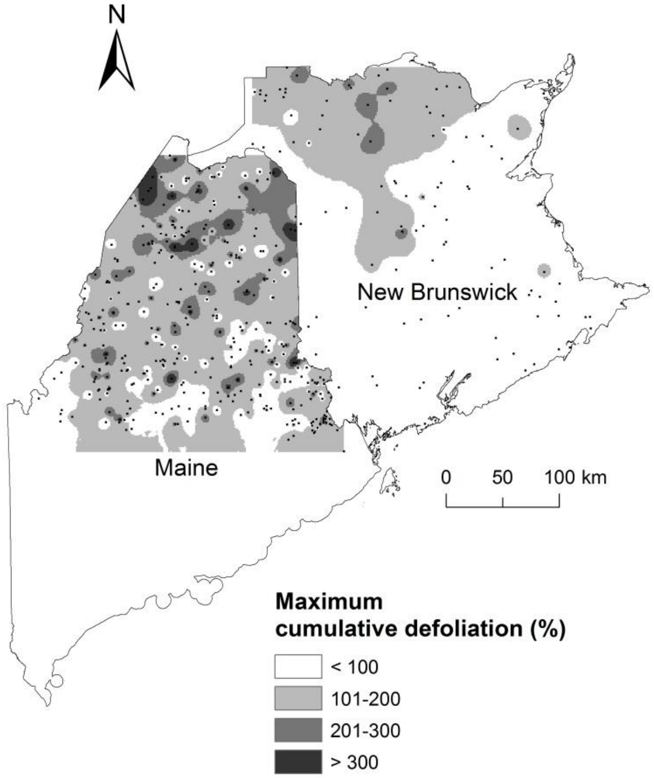

Figure 2.1. Locations of the study area and sample plots included in this analysis with interpolated plot-level maximum cumulative defoliation. Cumulative defoliation is the cumulative sums of the percentage defoliation of current-year foliage from all previous years until current year (%). Data collected in Maine during 1975-1985 covered most of the temporal extent of the last SBW outbreak, while the New Brunswick analysis period of 1986-1991 was in the declining years of the SBW outbreak.

2.2.2. Data

The data used in this study came from the University of Maine Cooperative Forestry Research Unit Growth Impact Study data collected in northern Maine, USA (Solomon and Brann 1992) and Canadian Forest Service permanent sample plots data collected in New Brunswick, Canada (MacLean and Erdle 1986). The most significant difference between the two regions in the data was species composition, which Fraver et al. (2007) considered to be the reason behind the differences in their SBW outbreak histories, in addition to the dynamics of SBW outbreaks. Specifically, balsam fir, red spruce, black spruce, white spruce, and hardwood accounted for 37%, 23%, 2%, 3%, and 19% of all trees in stems, respectively, in Maine, and 37%, 21%, 11%, 9%, and 14% of all trees in stems, respectively, in New Brunswick. Each of the datasets used in this study is described in detail below.

2.2.2.1. Growth Impact Study of Maine

The Growth Impact Study was initiated in 1975 (after SBW activity reached epidemic level in 1974) as a cooperative effort among federal and state forest agencies, as well as private forestry companies to document the impact of SBW on growth and mortality of the Maine forest. Data were collected at 424 ~0.2 ha circular plots including 8 762 trees ≥ 11.4 cm in diameter at breast height (DBH) throughout northern Maine during 1975-1985 (most of the temporal extent of the last SBW outbreak in Maine). The data included annual records of species, DBH, crown position, cause of death, total height, crown length, and degree of defoliation. Each year during the study period, current-year and previous-years foliage on each host tree within the plot were visually examined for the degree of defoliation, and categorized separately into one of five classes (before 1982; 0, 1-5%, 6-20%, 21-50%, and 51-100%) or eleven classes (after 1982; 0-10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90%, 91-99%, and 100%) of defoliation.

2.2.2.2. Permanent Sample Plots of New Brunswick

Approximately 1 500 random PSPs were established between 1976-1979 as part of the New Brunswick Department of Forests, Mines and Energy Forest Inventory. Of these plots, 136 were selected for SBW related studies based on stratification by species, maturity, and degree of insecticide use for protection. Each PSP consisted of three permanent prism points (basal area factor = 2 m^2 ha^{-1}) located 40 m apart, on which species, DBH, crown class, year of death, initial height, and degree of defoliation of each tree were recorded. The above data were collected during 1976-1993, with DBH initially measured between 1976 and 1979 and remeasured in 1980, 1983, 1985, 1988, and 1991. Current year and total defoliation (defoliation on all age classes of foliage) were measured annually during 1984-1993 (when the SBW outbreak was declining), while height was measured once during 1976-1979. For all of the 6 316 sample trees in the PSP data set, only the 5 503 trees compatible in size with the Growth Impact Study dataset (i.e. DBH ≥ 11.4 cm) were included in this study. Both current-year and total defoliation in the New Brunswick PSPs was estimated for each host tree each year by scanning the crowns with binoculars. The results of both types of defoliation were separately put into seven percentage classes of 0-10%, 11-20%, 21-40%, 41-60%, 61-80%, 81-99%, and 100%.

2.2.2.3. Data Compilation

All measurements in the two datasets were converted to metric units. Since annual measurements of DBH were not available for the PSP dataset, spline and linear functions were used to impute DBH values for years between measurements. Height values for the PSP dataset were obtained through imputation using a species- and plot-specific mixed effects model outlined by Robinson and Wykoff (2004). Given the difficulty in accurately measuring heights on an annual basis, height increments of > 0.9 m yr^{-1} in the Growth Impact Study dataset (1.1% of the total observations) were replaced by values obtained using the above modeling approach. All individual tree total volumes were estimated using a species-specific taper equation for the region (Li et al. 2012; Weiskittel and Li 2012). As SBW prefers sun foliage and hence causes frequent top-kill (Ostaff and MacLean 1989), tree height increment was greatly reduced and nearly ceased from the beginning of our data. Therefore, top-kill was an implicit factor in consecutive measurements of height, which were inputs to the taper equation that was used to predict consecutive volumes. Consequently, top-kill likely had a minimal effect in predicting volume growth, which was derived by subtracting these consecutive predictions of volume.

At the plot-level, several attributes describing structure and composition were derived. Stand density index was estimated using the additive method and relative density values were computed using an equation proposed by Woodall et al. (2005) that predicts maximum stand density index using average species specific gravity (USDA 2010). Preliminary analysis indicated that this measure of relative density outperformed more traditional stand structural metrics like stem density and total basal area. Additionally, stand species composition was represented by the proportions of balsam fir (BF), black spruce (BS), red spruce (RS), white spruce (WS), and hardwood species (HW). Site productivity was estimated through dominant height and several other metrics including biomass growth index (Hennigar et al. 2017), climate site index (Weiskittel et al. 2011b), topographic wetness index, and other site attributes like slope, aspect, and elevation as well as their transformations (Stage 1976).

A variety of defoliation metrics were evaluated including those presented in Hennigar et al. (2013). For this analysis, severity of defoliation was presented as cumulative sums of the percentage defoliation of current-year foliage from all previous years until current year, which was rather commonly used in previous studies and the most effective metric indicated by our preliminary analysis. The observed cumulative defoliation varied between 0-586% and averaged 85 ± 86% (mean ± SD) and 64 ± 53 % in Maine and New Brunswick, respectively. Cumulative defoliation was primarily concentrated towards the lower end of the above range in the data. Specifically, there were 3 250, 935, 295 and 119 stand-level observations of 0-100%, 101-200%, 201-300%, and >300% defoliation, respectively. Although the defoliation levels were generally lower than reported in previous studies, a large range of defoliation values observed and the wider geographic region examined may explain these trends. In addition, as described below, both areas had varying levels of aerial spraying of insecticide.

During the last outbreak, portions of both regions underwent aerial spraying of insecticide against SBW. This protection activity included most of New Brunswick's forested areas in certain years (MacLean et al. 1984). From 1970 to 1974, an average of 160 000 ha of forests was sprayed annually in Maine. This resulted in nearly 17% of the Growth Impact Study plots being sprayed at least once during this period. As the spraying extended to over 400 000 ha year^{-1} through the outbreak, and peaked at 1.6 million ha in 1976 (Seegrist and Arner 1982), it is reasonable to assume that the majority of these plots received some spraying. However, preliminary analysis found no identifiable relationships between spraying and the examined stand dynamics, so additional analyses using information on spraying were not explored further (Supplemental Materials A.2). Likely, the effects of spraying are implicitly accounted for in the observed cumulative defoliation values, which would have been probably higher without spraying.

For this analysis, several components of stand dynamics, namely, annual volume net growth, mortality, and ingrowth were included. Values of standing volume, mortality, and ingrowth were derived by summing the per ha volumes of each tree at each measurement period by status (live, dead, or ingrowth). Ingrowth was defined as all (host and non-host) trees ≥ 11.4 cm DBH that were not present in the previous measurement. Since trees in the understory are more sensitive to defoliation and often die first during an outbreak (Blais 1958), defoliation was expected to directly affect ingrowth, while the plot-level cumulative defoliation was considered a suitable representation of understory defoliation severity. The response variable of annual volume net growth was obtained by subtracting subsequent standing volume from the previous one (volume increment of surviving trees); and the response variables for annual volume mortality and ingrowth were taken as the percentage of corresponding standing volume. For the variable-radius plots in the NB PSP dataset, tree expansion factors at the first measurement were fixed for subsequent measurements to ensure compatibility as suggested by Myers and Beers (1968). A summary of the attributes derived from the data used in this analysis is presented in the Supplemental Materials A.3.

2.2.3. Analysis

The above response variables were related to various stand structure, species composition, site productivity, and defoliation variables, and fitted with nonlinear mixed effect models by setting a random effect across plots. Model selections (of suitable model formulations and predictors) were based on a combined consideration of biological interpretability, Akaike Information Criterion (AIC), coefficient of determination (R^2), and mean bias (predicted - observed). The selected models best depicting stand dynamics in response to defoliation are all described in more detail below. All analyses were conducted in R v3.2.2 (R Development Core Team 2015). In particular, the R package "nlme" (Pinheiro et al. 2016) was used for constructing the nonlinear mixed effect models.

2.2.3.1. Net Growth

In general, the growth of trees likely exhibits a sigmoidal behavior, which both logistic and Gompertz functions are suitable to model this expected trend. A major difference between these two functions lies in that logistic and Gompertz functions reach their inflection points (maximum acceleration in growth) at *K*/2 (*K* is the asymptote in yield) and *K*/*e*, respectively. The latter better matches the relatively short period of accelerated growth of trees in their early stage, and can be parameterized as follows:

$$(1)\ y(t) = Kexp\left(ln\left(\frac{y(0)}{K}\right)exp(-rt)\right)$$

where *y*(*t*) is the yield at time *t*; *K*, *y*(0), and *r* are parameters, of which *K* is the asymptote of yield, *y*(0) is the initial volume, and *r* is the growth rate.

Differentiating Equation (1) on *t*, substituting functions of *t* with Equation (1) so to avoid explicitly including time *t* as a covariate (since its relationship with growth may be distorted by forest management activities and disturbances like SBW), and expanding *K* and *r* such that the former is density dependent and the latter is affected by potential productivity (β4), species composition (β3, β5, and β7), and defoliation (β5 and β7) generates the following growth function:

$$(2)\ y'(t) = y(t) ln\left(\frac{K}{y(t)}\right) r$$

$$= y(t) ln\left(\frac{exp\big((\beta 1 + \gamma 1) + \beta 2 \cdot RD\big)}{y(t)}\right)\left(\begin{array}{c} \beta 3 \cdot exp(BS + RS + WS) \cdot HW \\ + \beta 4 \cdot HT_{DOM} \\ + \beta 5 \cdot (BS + RS + WS) \cdot CDEF + \beta 6 \cdot BF \\ + \beta 7 \cdot BF \cdot CDEF \end{array}\right) + \varepsilon$$

where *y'*(*t*) is net growth at time *t* ($m^3\ ha^{-1}\ yr^{-1}$); *RD* is relative density; *BF*, *BS*, *RS*, *WS*, and *HW* are proportions of balsam fir, black spruce, red spruce, white spruce, and hardwood in terms of volume, respectively; HT_{DOM} is dominant height (m); *CDEF* is cumulative defoliation (%); β1 - β7 are parameters for fixed effects (β7 was not applied to the New Brunswick data); γ1 is a parameter for plot-level random effect; and ε is the error of the model. Since considerable variation was found in *K* and the standard deviation of *r* was less than 0.01% of its mean in both datasets, only random effects for the intercept of *K* (β1) were considered in the models.

2.2.3.2. Mortality

Zero-inflated models have been used for modeling rare events like tree mortality, and were tested in this analysis in both frequentist and Bayesian settings assuming a beta distribution for mortality/ingrowth (as the ratio between mortality/ingrowth volume and standing volume expressed as a percentage through this analysis; Supplemental Materials A.4). It was found that these models yielded fewer close-to-zero predictions for actual zero observations and smaller predicted values for over-dispersed observations than the models proposed below. Consequently, to address both excessive zeros and over-dispersion in the observations, a model of % mortality in volume of the following form, which had a goodness-of-fit at least as good as the zero-inflated models, was used:

$$(3)\ y = \frac{1}{1 + exp\left(-\begin{pmatrix} \beta 1 + \gamma 1 \\ +\beta 5 \cdot HT_{DOM} \end{pmatrix}\right)} \cdot \frac{1}{1 + exp\left(-\begin{pmatrix} \beta 6 + \beta 2 \cdot BF \cdot CDEF + \beta 3 \cdot VOL \\ +\beta 4 \cdot (BS + RS + WS) \cdot CDEF \end{pmatrix}\right)} + \varepsilon$$

where *VOL* is standing volume ($m^3\ ha^{-1}$); β1 - β6 are parameters for fixed effects (β4 - β6 were not applied to the New Brunswick data); γ1 is a parameter for random effect; and the other notations are the same as defined above. Equation (3) can be considered as a modification of the zero-inflated model in that $1/1 + exp\big(-(\beta 1 + \gamma 1 + \beta 5 \cdot HT_{DOM})\big)$ can be treated as the probability of belonging to the distribution of actual mortality values in a zero-inflated model. However, the mass of zeros were removed from the parameter estimation of a zero-inflated model (so mortality estimated using Equation (3) would not be reduced by a < 1 probability of not being zero) to allow for more dispersed estimates. Preliminary analysis showed significant effect of *VOL* on mortality independent of stand development stage, such that mortality rate monotonously decreased over the increase of various formulations of *VOL*, of which the one used in Equation (3) was highly significant and most parsimonious.

2.2.3.3. Ingrowth

The ingrowth data and the modeling approach for it shared common features with mortality. However, an even greater number of zeros was observed in ingrowth (87% of plot observations), which also exhibited a higher level of variability than mortality. In this case, the probability of belonging to the distribution of actual ingrowth values as in Equation (3) practically went to zero in the modeling process. For this reason, % ingrowth in volume was modeled using a single logistic function as follows:

$$(4)\ y = \frac{1}{1 + exp\left(-\begin{pmatrix}\beta 1 + (\beta 2 + \gamma 2) \cdot BF \cdot CDEF + \beta 3 \cdot HT_{DOM} \\ +(\beta 4 + \gamma 4) \cdot VOL + \beta 5 \cdot (BS + RS + WS)\end{pmatrix}\right)} + \varepsilon$$

where β1 - β5 are parameters for fixed effects (β3 and β5 were not applied to the New Brunswick data); γ2 and γ4 are parameters for random effects; and the other notations are the same as defined above. Similar to the mortality model, ingrowth rate monotonously decreased over the increase of various formulations of *VOL*, of which the one used in Equation (4) was highly significant and most parsimonious.

2.3. Results

2.3.1. Net Growth

Models for annual volume net growth (volume increment of surviving trees) as well as mortality and ingrowth were built using 3 846 and 753 observations for Maine and New Brunswick, respectively. The fixed effects of the net growth models explained 64 and 64% (79 and 88% when random effects were also considered) of its variation for Maine and New Brunswick, respectively. The mean predicted net growth was 3.79 and 5.43 $m^3\ ha^{-1}\ yr^{-1}$ with mean biases (predicted - observed) of +0.09 and +0.07 $m^3\ ha^{-1}\ yr^{-1}$ for Maine and New Brunswick, respectively. All parameter estimates were significant at $p < 0.05$ level (except for β5 in the New Brunswick model), and strictly in accordance in direction, comparable in magnitude and relative importance, and ecological interpretability for the two regions (Table 2.1).

Table 2.1. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual volume net growth models ($m^3 ha^{-1} yr^{-1}$) by region. RD is relative density; BF, BS, RS, WS, and HW are proportions of balsam fir, black spruce, red spruce, white spruce, and hardwood in volume, respectively; HT_{DOM} is dominant height (m); CDEF is cumulative defoliation (%).

Parameter and Fit Statistic	**Maine (n = 3 846)**			**New Brunswick (n = 753)**		
	Value	**SE**	**p-value**	**Value**	**SE**	**p-value**
β1 (Intercept)	4.95690	0.03553	< 0.0001	4.69726	0.06315	< 0.0001
β2 (RD)	2.77830	0.07094	< 0.0001	3.09574	0.15507	< 0.0001
β3 (exp(BS+RS+WS)·HW)	-0.01351	0.00305	< 0.0001	-0.03197	0.01253	0.0110
β4 (HT_{DOM})	0.00234	0.00013	< 0.0001	0.00363	0.00046	< 0.0001
β5 ((BS+RS+WS)·CDEF)	-0.00007	0.00001	< 0.0001	-0.00013	0.00008	0.0984
β6 (BF)	0.01919	0.00414	< 0.0001	0.04738	0.01107	< 0.0001
β7 (BF·CDEF)	-0.00011	0.00001	< 0.0001	--	--	--
γ1 (Random effects on β1)		0.1524			0.1617	
R^2 (Fixed effects)	0.64			0.64		
R^2 (Incl. random effects)	0.79			0.88		
Mean bias ($m^3 ha^{-1} yr^{-1}$) (Fixed effects)	-0.06			-0.32		
Mean bias ($m^3 ha^{-1} yr^{-1}$) (Incl. random effects)	+0.09			+0.07		

Our analysis showed an inverse relationship between net growth and defoliation, and this relationship was dependent on the proportion of host species in that net growth was significantly lower with higher spruce and balsam fir content (Table 2.1). Specifically, when cumulative defoliation increased from 100 to 200%, net growth decreased from 3.43 to 3.00 $m^3 ha^{-1} yr^{-1}$ (equivalent to a relative decrease of 13%), while a 0.1 increase in the proportion of spruce and hardwood content decreased net growth by 0.03 and 0.15 $m^3 ha^{-1} yr^{-1}$, respectively, without the influence of defoliation (cumulative defoliation equals zero) in Maine. In addition, none of the site factors tested significantly affected net growth. Net growth was predominantly controlled by stand density (indicated by relative density and standing volume) and potential productivity (indicated by dominant height), while moderately influenced by defoliation and species composition during a SBW outbreak (Figure 2.2).

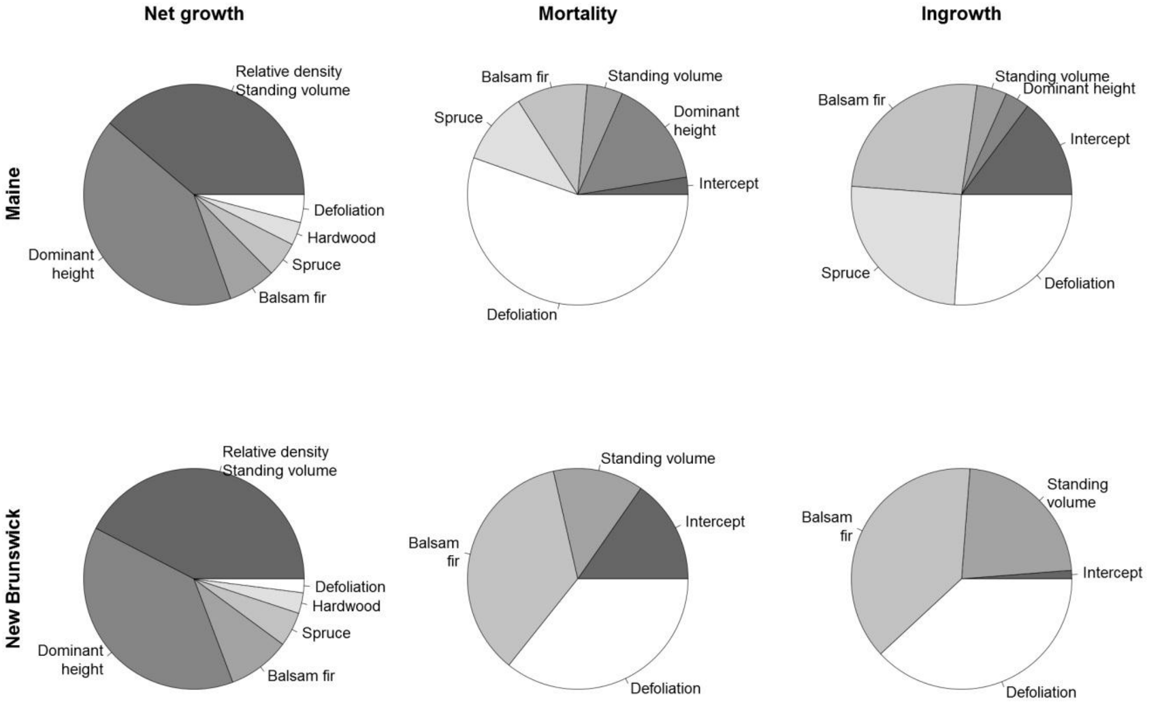

Figure 2.2. Relative importance of various variables (at their mean values; Achen 1982) on different stand dynamic components examined in this analysis (net growth, mortality, ingrowth) by region.

Similar results were found in New Brunswick, where the same specific growth reductions as shown above were from 4.89 to 4.52 m^3 ha^{-1} yr^{-1} (equivalent to a relative decrease of 8%) due to the increase in defoliation as well as 0.04 and 0.34 m^3 ha^{-1} yr^{-1} related to the increases in spruce and hardwood content. Furthermore, the above relationships were presented at the mean values of the other variables in these nonlinear models, and consistent between the two regions, although both the observed and predicted net growth was generally higher in New Brunswick than in Maine (Supplemental Materials A.3 and Figure 2.3).

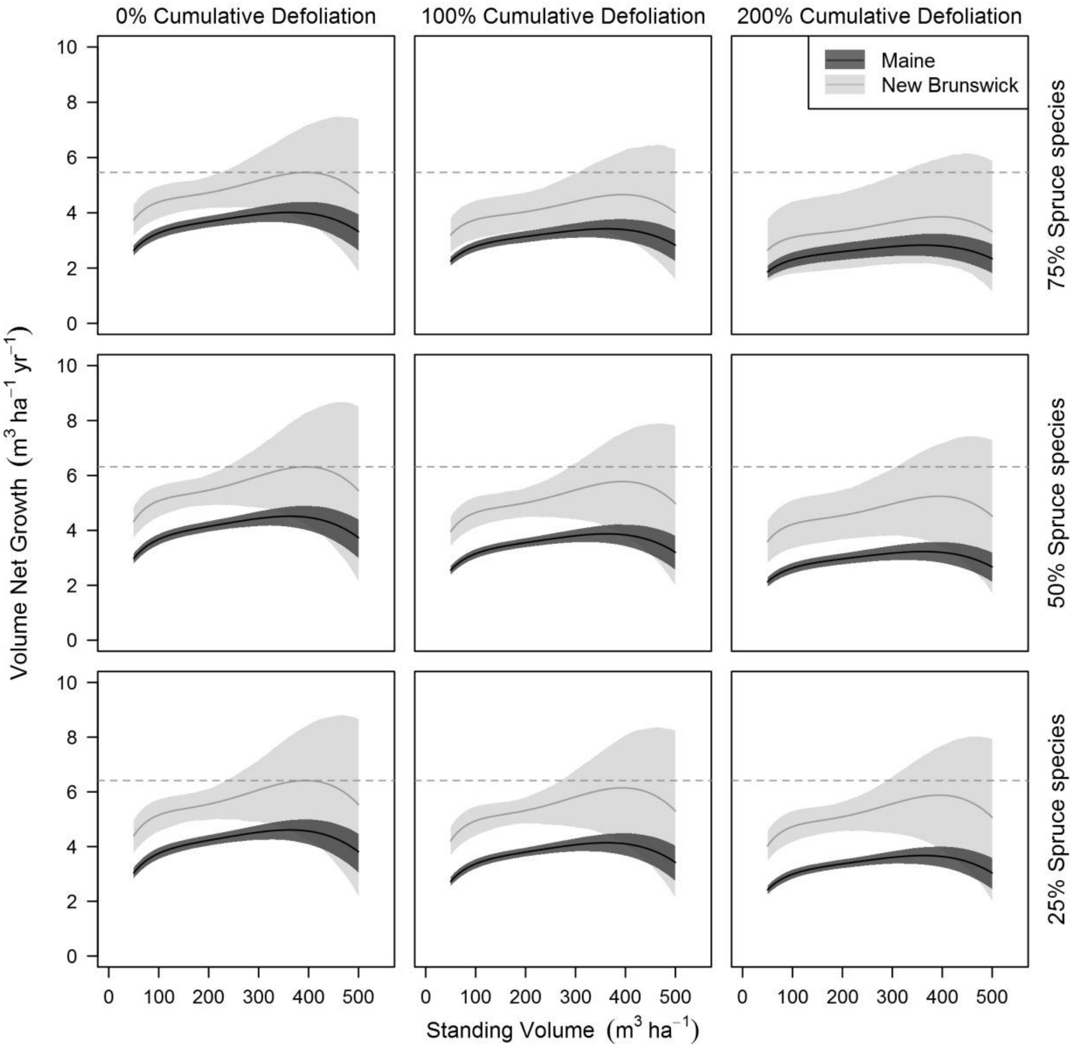

Figure 2.3. Predictions of annual volume net growth (m^3 ha^{-1} yr^{-1}) as a function of standing volume (m^3 ha^{-1}) under different levels of cumulative defoliation and spruce species content by region. All the other covariates were set at their mean values except relative density was set based on its correlation with standing volume. The observed net growth was closest to that shown in the lower-left graph. Dashed lines that pass the maxima of the curves in the first column from left are used to help show the differences in growth under different levels of defoliation. The shaded areas are the 95% confidence interval of the predictions.

2.3.2. Mortality

A total of 28% (47%) and 34% (54%) of the variation in annual volume mortality rate was explained by the fixed effects (and random effects) in the models for Maine and New Brunswick, respectively. The mean predicted annual volume mortality rate was 2.32% and 1.83% with mean biases of -0.10 and +0.14% for Maine and New Brunswick, respectively. All parameter estimates were significant at $p < 0.01$ level, and consistent in direction, magnitude, relative importance, and ecological interpretability between the two regions (Table 2.2).

Table 2.2. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual volume mortality rate models (% yr^{-1}) by region. BF, BS, RS, and WS are proportions of balsam fir, black spruce, red spruce, and white spruce, respectively; VOL is standing volume ($m^3\ ha^{-1}$); HT_{DOM} is dominant height (m); CDEF is cumulative defoliation (%).

Parameter and Fit Statistic	Maine (n = 3 846)			New Brunswick (n = 753)		
	Value	**SE**	**p-value**	**Value**	**SE**	**p-value**
β1 (Intercept)	-5.1686	0.5095	< 0.0001	-2.6356	0.1863	< 0.0001
β2 (BF·CDEF)	0.0158	0.0018	< 0.0001	0.0088	0.0034	0.0095
β3 (VOL)	-0.0038	0.0006	< 0.0001	-0.0071	0.0010	< 0.0001
β4 ((BS+RS+WS)·CDEF)	0.0149	0.0017	< 0.0001	--	--	--
β5 (HT_{DOM})	0.1725	0.0273	< 0.0001	--	--	--
β6 (Intercept)	-1.8256	0.1643	< 0.0001	--	--	--
γ1 (Random effects on β1)		0.7203			0.7269	
R^2 (Fixed effects)	0.28			0.34		
R^2 (Incl. random effects)	0.47			0.54		
Mean bias (%) (Fixed effects)	-0.03			+0.05		
Mean bias (%) (Incl. random effects)	-0.10			+0.14		

Both observed and predicted mortality rates were relatively low, even under the higher levels of defoliation observed across the regions (Supplemental Materials A.3 and Figure 2.4; defoliation was generally lower in this study compared to previous studies). Besides decreasing with an increase in standing volume and reduction in host content, mortality rate was most sensitive to defoliation, especially in Maine (Figure 2.2). Specifically, when cumulative defoliation increased from 100 to 200%, annual mortality rate increased from 1.9 to 3.8% and from 1.7 to 2.1% in Maine and New Brunswick, respectively, which were equivalent to relative increases of 101 and 23%, respectively. There was also a slight difference in the response of mortality rate to the increase of the various host species such that a 0.1 increase in the proportion of balsam fir and spruce content increased annual mortality rates by 0.27 and 0.26%, respectively, at 100% cumulative defoliation in Maine. Furthermore, the above relationships were presented at the mean values of the other variables in the nonlinear models, and consistent between the two regions (Supplemental Materials A.3 and Figure 2.4).

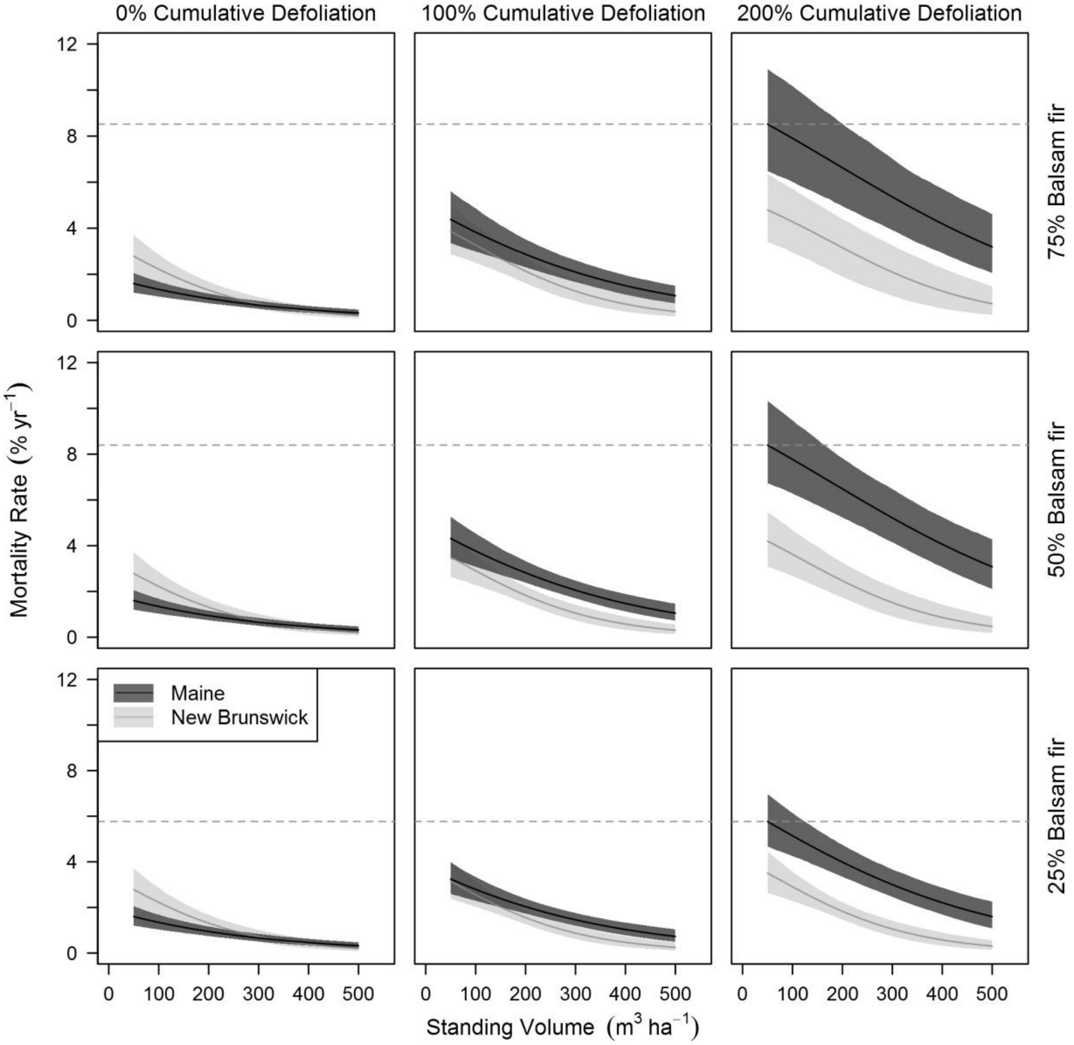

Figure 2.4. Predictions of volume mortality rate (% yr^{-1}) as a function of standing volume (m^3 ha^{-1}) under different levels of cumulative defoliation and balsam fir content by region. All the other covariates were set at their mean values. The observed mortality was closest to that shown in the lower-left graph. Dashed lines that pass the maxima of the curves in the third column from left are used to help show the differences in mortality rate under different levels of defoliation. The shaded areas are the 95% confidence interval of the predictions.

2.3.3. Ingrowth

Models for annual volume ingrowth rate accounted for 20% (33%) and 21% (37%) of its variation by the fixed effects (and random effects) for Maine and New Brunswick, respectively. The mean predicted annual volume ingrowth rate was 0.42% and 0.59% with mean biases of ~ 0.00% and +0.13% for Maine and New Brunswick, respectively. All parameter estimates were significant at $p < 0.01$ level (except for β2 in the New Brunswick model). The effects of all of the covariates were comparable across the regions, and consistent with ecological expectations (Table 2.3).

Table 2.3. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual volume ingrowth rate models (% yr^{-1}) by region. BF, BS, RS, and WS are proportions of balsam fir, black spruce, red spruce, and white spruce respectively; HT_{DOM} is dominant height (m); VOL is standing volume (m^3 ha^{-1}); CDEF is cumulative defoliation (%).

Parameter and Fit Statistic	**Maine (n = 3 846)**			**New Brunswick (n = 753)**		
	Value	**SE**	**p-value**	**Value**	**SE**	**p-value**
β1 (Intercept)	-1.0239	0.1841	< 0.0001	-4.1678	0.2683	< 0.0001
β2 (BF·CDEF)	-0.0063	0.0023	0.0063	-0.0062	0.0040	0.1251
β3 (HT_{DOM})	-0.1400	0.0171	< 0.0001	--	--	--
β4 (VOL)	-0.0110	0.0015	< 0.0001	-0.0050	0.0017	0.0033
β5 (BS+RS+WS)	-0.6455	0.1977	0.0011	--	--	--
γ2 (Random effects on β2)		0.0085			< 0.0001	
γ4 (Random effects on β4)		0.0065			0.0039	
R^2 (Fixed effects)	0.20			0.21		
R^2 (Incl. random effects)	0.33			0.37		
Mean bias (%) (Fixed effects)	-0.04			+0.07		
Mean bias (%) (Incl. random effects)	~ 0.00			+0.13		

Both observed and predicted ingrowth rates were low across the regions, although consistently higher in New Brunswick than in Maine (Supplemental Materials A.3 and Figure 2.5). The factors of defoliation, proportion of host species, standing volume, and dominant height all appeared to negatively affect ingrowth rate (Table 2.3) with the first two factors being most influential

(Figure 2.2). In particular, when cumulative defoliation increased from 100 to 200%, annual ingrowth rate would decrease from 0.14 to 0.12% and from 0.48 to 0.39% in Maine and New Brunswick, respectively, which were equivalent to relative decreases of 15 and 18%, respectively. In addition, the above relationships were presented at the mean values of the other variables in the nonlinear models, and consistent between the two regions (Supplemental Materials A.3 and Figure 2.5).

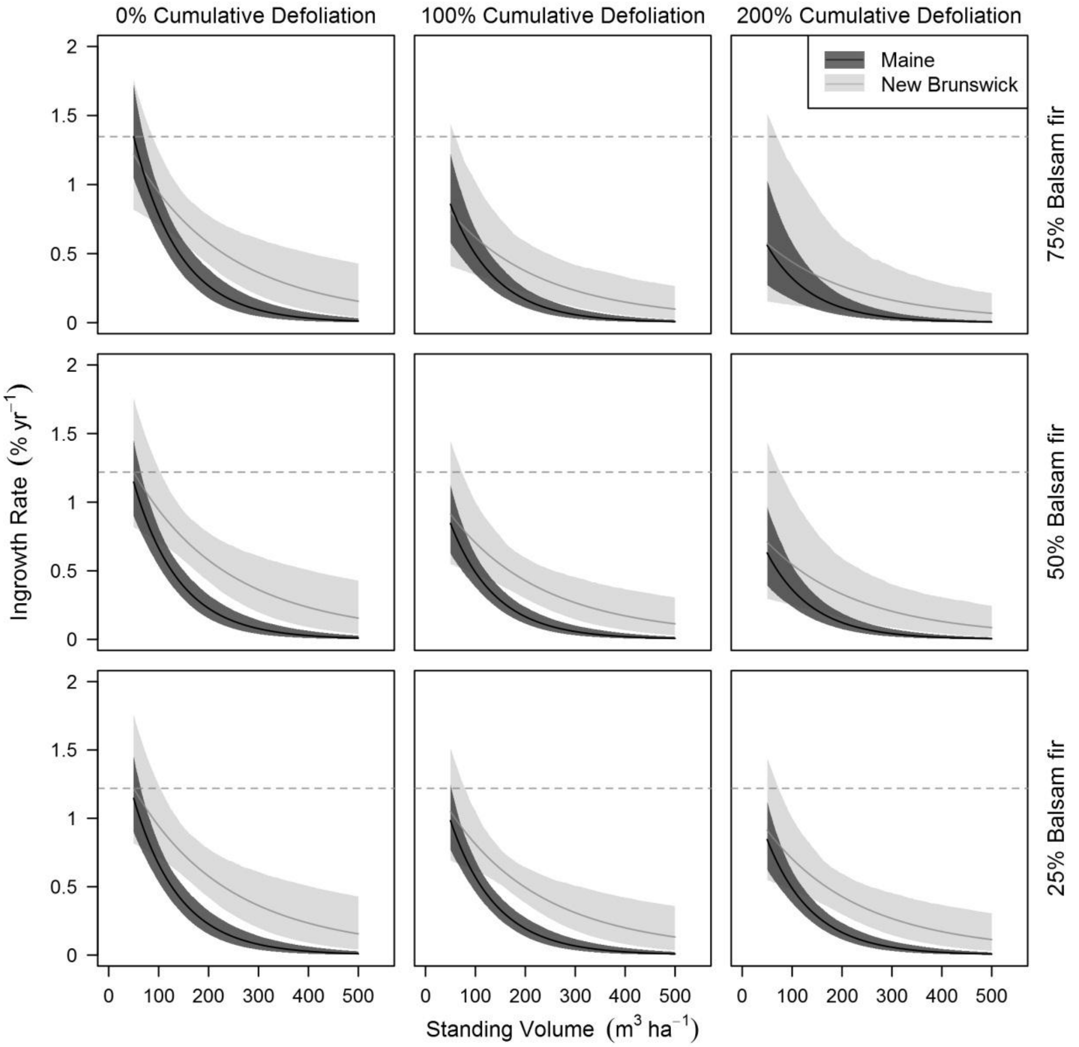

Figure 2.5. Predictions of volume ingrowth rate (% yr^{-1}) as a function of standing volume (m^3 ha^{-1}) under different levels of cumulative defoliation and balsam fir content by region. All the other covariates were set at their mean values. The observed ingrowth was closest to that shown in

the lower-left graph. Dashed lines that pass the maxima of the curves in the first column from left are used to help show the differences in ingrowth rate under different levels of defoliation. The shaded areas are the 95% confidence interval of the predictions.

2.4. Discussion

Defoliation, despite being generally lower in this study when compared to previous studies, was found to have a significant influence on all of the stand dynamic responses examined. Consistent with our initial expectations, these influences of defoliation were found to be most dependent on stand species composition, with balsam fir stands experiencing higher levels of growth reduction and mortality, and less ingrowth than spruce stands. As cumulative defoliation increased from 0 to 100%, net growth reduction averaged 0.90 and 0.67 m^3 ha^{-1} yr^{-1} for stands with 75% balsam fir and 25% hardwood versus 75% spruce and 25% hardwood, respectively. Although these reductions in net growth were only moderate, it is a bit surprising that cumulative defoliation at such a low level had any significant effect. Since our models showed much higher normal growth rates of balsam fir than spruce or hardwood species, and the difference in net growth reduction influenced by defoliation between balsam fir and spruce stands was small, balsam fir dominated stands would likely maintain relatively higher rates of growth when compared to spruce dominated stands under the same levels of defoliation. This agreed with the higher growth rates of balsam fir mixed stands than spruce mixed stands following SBW defoliation reported by Colford-Gilks et al. (2012). However, both Hennigar et al. (2008) and our analysis indicated that balsam fir tended to experience higher levels of defoliation (i.e. more susceptible) than spruce species.

Many studies mentioned above have reported the influence of defoliation on mortality of individual trees by species, which ranges from 73-100% for balsam fir and 27-66% for spruce species under 336-840% cumulative defoliation. There was no obvious way to directly compare these tree-level statistics with our stand-level estimates that were conditional on a variety of characteristics. However, it was likely that our mean predicted annual volume mortality rates of 2.32 and 1.83%, which are approximately equivalent to ten-year cumulative mortality rates of 21 and 17% for Maine and New Brunswick, respectively, were below those reported by studies identified above. The relatively low mortality rates in this study were likely related to the mean observed cumulative defoliation of 85 and 64% for Maine and New Brunswick, respectively, which could also be a major cause behind the discrepancy in mortality between this study and some previous studies. It was also found in this study that both observed and predicted mortality rates decreased with the increase in standing volume. A test of the interaction between standing volume and relative density confirmed this effect of standing volume on mortality for a given relative density, as well as indicated that mortality rate and relative density were positively related for a given standing volume.

Several limitations that influence interpretation of our findings should be recognized. First, the temporal extent of our data did not cover the full duration of the last SBW outbreak. SBW activity reached epidemic levels in 1974 in Maine (Irland et al. 1988), but the data began in 1975. The New Brunswick SBW outbreak spanned 1965-1993 in different parts of the province, and the analysis period in this study was 1986-1991, which was when SBW populations and defoliation were declining. Second, the effect of insecticide spraying was tested based on spraying records of the sample plots in Maine during 1970-1974 and found to be highly insignificant in this analysis (Supplemental Materials A.2). MacLean et al. (1984) also found that spraying did not significantly change mortality rates of black and red spruce. Likely, the effects of spraying were essentially captured in our cumulative defoliation data, which would have been higher if spraying had not been conducted. Third, sampling differences occurred between the two datasets, such as the use of variable-radius sampling in New Brunswick versus fixed-area plots in Maine. However, such sampling inconsistencies were likely small in comparison to the observed effects of defoliation as well as the broad spatial and temporal span of the sample plots.

The stand dynamics examined in this study exhibited a large amount of variation, with coefficients of variation (CV) for annual volume mortality and ingrowth of 277 and 331% for Maine, and 188 and 329% for New Brunswick, respectively. This was much higher than the 11% CV of mortality from Cape Breton Island, Canada (e.g., MacLean and Ostaff 1989), which had uniformly high mortality (mean 87%) caused by severe defoliation. Observed variations in these stand dynamic responses were higher than those usually associated with typical stands. Consequently, relationships between these responses and site characteristics were not significant and none of the characteristics examined accounted for more than 1% of the variation in the response variables in either of the regions (Supplemental Materials A.5). This observation is in agreement with MacLean et al. (1984) and MacLean and MacKinnon (1997), who found spruce-fir growth and mortality were not related to site characteristics, and could suggest that the effects of site characteristics found on SBW defoliation caused growth reduction and mortality (e.g., Blais 1958, Osawa et al. 1986) may have been location specific as in reflecting local limiting factors on growth and mortality.

A considerable amount of variations in stand dynamics was accounted for by random effects among sample plots in our models. This could be an indication of important factors affecting stand dynamics not being included in the models. However, this is less likely given that many common stand and site factors were tested and failed to show statistically significant relationships. It therefore was more likely that the random effects reflected autocorrelation in stand dynamics. Spatial clustering of mortality over a small extent found in this study and reported by Baskerville and MacLean (1979) could reflect this autocorrelation. Inclusion of a spatial or temporal autocorrelation error structure did not improve model fit significantly. Likely, a complex and dedicated research effort involving a denser sample plot network over a broader area and a longer time series would be necessary to fully investigate this potential autocorrelation.

The same models fit the data from both Maine and New Brunswick well, with parameter estimates of all covariates strictly in accordance in signs, and comparable in magnitudes and relative importance. These consistent effects of SBW defoliation and its interaction with stand characteristics across a broad region provide support for the models' general applicability. However, the models also showed some regional differences such that predictions of net growth, regular mortality (without the influence of SBW defoliation), and ingrowth were generally higher, while predictions of irregular mortality (under the influence of SBW defoliation) were generally lower for New Brunswick. These differences could reflect general differences in age, composition, and productivity of forests between these regions. More variation in stand dynamics tended to be explained by the models for New Brunswick, which may be related to the stratification applied in its sampling process such that differences in stand dynamics were likely to be more substantial among strata of more distinct stand, site, and defoliation conditions.

Overall, our results strongly demonstrated that even relatively low levels of cumulative defoliation were significantly related to mortality and ingrowth, while net growth was primarily competition driven. Defoliation level and species composition largely determined differences in mortality and ingrowth between Maine and New Brunswick, while site potential productivity and topographic characteristics had little influence. This study clearly highlights the variability in net growth, mortality, and ingrowth following SBW defoliation and suggests that an improved understanding at the individual tree-level may be necessary to fully understand this variability (e.g., Chen et al. 2017). Fully evaluating the developed models from this analysis during the next SBW outbreak will be an important test of their overall representativeness.

CHAPTER 3

EVALUATING THE INFLUENCE OF VARYING LEVELS OF SPRUCE BUDWORM DEFOLIATION ON ANNUALIZED INDIVIDUAL TREE GROWTH AND MORTALITY IN MAINE, USA AND NEW BRUNSWICK, CANADA[1]

3.1. Introduction

Of all the major natural disturbances in forests in northeastern North America, spruce budworm (*Choristoneura fumiferana* (Clem.); SBW) outbreaks are more important than fire or wind in that they have a larger spatio-temporal scale (Blais 1983), shorter return interval (40-60 years; Fraver et al. 2007), and greater influence on forest productivity (Morin et al. 2007). Periodic SBW outbreaks have occurred for hundreds of years in northeastern North America (Fraver et al. 2007). In particular, over 58 million ha of forests were defoliated in one year during the last outbreak between the 1970 and 1980s (Blais 1983, USDA Forest Service 2009) with approximately 44 million m^3 of timber lost annually in Canada alone (Sterner and Davidson 1982). Forty years since the last outbreak, the spruce-fir (*Picea-Abies*; major host species of SBW) forests are still abundant in the region with high economic and ecological importance (McWilliams et al. 2005; Erdle et al. 2008).

Interplaying with SBW, spruce-fir (*Picea-Abies*) forests are considered an example of highly unstable yet enormously resilient ecosystems such that a SBW outbreak kills mature balsam fir (*Abies balsamea* L.) and leads to the development of new mature balsam fir stands, which favors another SBW outbreak to perpetuate this cycle (Holling 1973). This resilience is conditional on the premise that balsam fir tends to out-regenerate and outgrow spruce (*Picea*) in the absence of SBW, which compensates for its higher mortality caused by SBW (Baskerville 1975) and

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[1] This chapter previously appeared as an article as follows: Chen, C., Weiskittel, A., Bataineh, M., and MacLean, D.A. 2017. Evaluating the influence of varying levels of spruce budworm defoliation on annualized individual tree growth and mortality in Maine, USA and New Brunswick, Canada. Forest Ecology and Management 396: 184-194.

implies intrinsic differences in the growth and mortality of SBW's host species. Blais (1983) considered that the frequency, extent, and severity of SBW outbreaks were on the rise in the 20th century, and attributed this to the high rates of red spruce (*Picea rubens* Sarg.) harvesting for pulpwood among other factors. Therefore, it is ecologically important to quantify such differences in species growth and mortality in order to better understand the resilience of spruce-fir forests and to improve the prediction of future ecosystem dynamics given ongoing changes in environment and disturbance regimes.

Control of SBW has largely relied on the application of insecticide in the past. Meanwhile, various silvicultural methods have been proposed and tested as long-term solutions to alleviating the influence of SBW on forest development (Baskerville 1975; Blais 1983). These methods largely depend on the perceived differences in various host species' responses to SBW in relation to stand structure and composition, as well as site conditions. For example, balsam fir is widely recognized as more vulnerable to SBW defoliation than spruce (e.g., Osawa et al. 1986; Pothier et al. 2012), hence the influence of defoliation on forest development may be mitigated by reducing balsam fir through stand conversion and thinning. Thinning targeting balsam fir has also been thought to reduce vulnerability of remaining hosts by stimulating their growth and improving their vigor (Irland et al. 1988). Similarly, increasing the non-host hardwood species is considered to reduce the influence of SBW on host trees due to increased dispersal and migration losses of SBW (Mott 1963; Baskerville 1975).

However, observations on the potential of these silvicultural strategies to reduce host vulnerability and mitigate SBW impacts during the last outbreak in Maine suggested a less than optimum outcome (Irland et al. 1988), especially under severe defoliation pressure. Irland et al. (1988) reported that 10 out of 14 of their expert respondents felt that balsam fir and spruce were equally vulnerable. Budworm-caused mortality (i.e., total minus natural) was similar (31-

49% and 11-32%) in spaced and un-spaced young balsam fir plots, respectively, but reached 94-100% in severely defoliated spaced plots (MacLean and Piene 1995). Irland et al. (1988) indicated that mortality appeared to be higher in spaced and thinned stands where more crowns were exposed. All of these past studies indicate that a large amount of variation existed in tree response to defoliation such that more comprehensive data are necessary to show the full range of this response. Furthermore, tree response to defoliation interacts with various stand and site factors, which further complicates the observed relationships.

Forest growth models that consider the influence of SBW defoliation are limited. Chen et al. (in review) evaluated the influence of SBW defoliation on forest stand dynamics and indicated that defoliation, in connection with species composition and other stand and site conditions, modified both stand-level net growth and mortality in Maine and New Brunswick, with some regional differences. By aggregating individual trees, these models provided useful information for making forest management decisions at large scales aimed to mitigate the influence of SBW defoliation. However, they were unable to provide detailed information on the intrinsic differences in individual tree as well as host species' responses to defoliation. Such a limitation commonly exists in the few studies that have examined the influence of SBW defoliation, e.g., the cohort model employed by the SBW decision support system (SBW-DSS), which is widely used in Canada (MacLean 1996) and the conceptual diameter-class model proposed by Steinman and MacLean (1994), which both update growth projection at 5-year intervals across a range of size classes.

While forest growth models may be constructed at hierarchical levels of tree, stand, and landscape, models with less bias constructed at one level are more useful in prediction at a higher level in that accurate predictions can be achieved with increasingly small errors as sample size increases. Therefore, an individual-tree model capable of utilizing detailed information for individual trees is not only more likely to better characterize impacts of damaging agents, but to better predict stand responses to management practices (Weiskittel et al. 2011a). In particular, an individual tree approach may be necessary for depicting differences in host species' growth responses to the complex and variable influence of SBW defoliation interplaying with various stand and site factors. Unfortunately, previous studies on the influence of SBW defoliation were primarily focused on mortality (e.g. MacLean 1979, 1988, Osawa et al. 1986, Reams et al. 1988, MacLean and Ostaff 1989, Solomon et al. 2003), except for a limited number of stand-level and size-class models such as those mentioned above.

For this analysis, our goal was to develop a set of species- and region-specific individual-tree growth and mortality models that quantify the effects of SBW defoliation. Specific objectives of this study were to: 1) model annual diameter and height increment, crown recession (height to crown base increment), and mortality of major host species using key site, stand, and tree variables; 2) evaluate the influence of SBW defoliation on these attributes; and 3) compare differences in these attributes and the influence of SBW defoliation between Maine and New Brunswick.

3.2. Material and Method

3.2.1. Study Area

The combined study area (44°56'-48°00' N, 64°28'-70°44' W) in Maine and New Brunswick mainly belongs to the temperate broadleaf mixed forest biome (Figure 3.1). The most common forest types in Maine include maple-beech-birch (*Acer-Fagus-Betula*) of ca. 2.9 million ha and spruce-fir of ca. 2.4 million ha (McWilliams et al. 2005). In New Brunswick, the public forest is 55% spruce-fir, 14% other softwood species, and 32% hardwood species. Black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir are the two most abundant species, each making up 20% of the forest (Erdle and Ward 2008). Soils in Maine and New Brunswick are generally infertile, acidic, and low in permeability (Ferwerda et al. 1997; Rees et al. 2005). Maine has a humid continental climate with warm, humid summers, and cold, snowy winters. Annual precipitation varies from 909 to 1 441 mm and is distributed evenly year-round. Climate in New Brunswick is similar to that of Maine with annual precipitation ranging from 889 to 1 143 mm, evenly distributed through the year. Elevation of the study areas in Maine and New Brunswick ranged from 41-691 m and 0-578 m, respectively. These two areas have a similar SBW outbreak history and both experienced a severe outbreak in the 1970s-1980s.

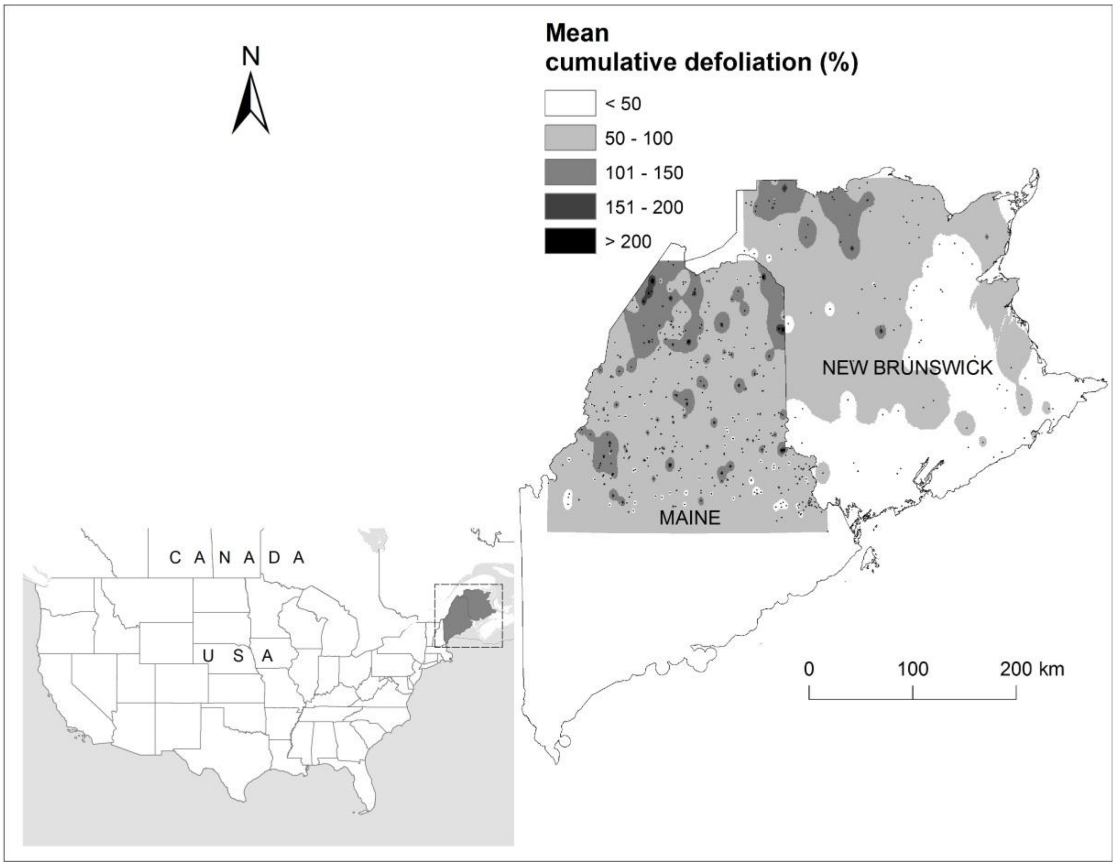

Figure 3.1. Locations of the study area and sample plots included in this analysis with interpolated plot-level mean cumulative defoliation (cumulative sums of the percentage defoliation of current-year foliage from all previous years until current year; %). Data collected in Maine during 1975-1985 covered most of the temporal extent of the last SBW outbreak, while

the New Brunswick analysis period of 1986-1991 was either in the declining years or after the end of the SBW outbreak.

3.2.2. Data

The data used in this study came from the University of Maine Cooperative Forestry Research Unit Growth Impact Study data collected in northern Maine, USA (Solomon and Brann 1992) and Canadian Forest Service permanent sample plots (PSP) data collected in New Brunswick, Canada (MacLean and Erdle 1986). Each of the datasets used in this study is described in detail below.

3.2.2.1. Growth Impact Study of Maine

The Growth Impact Study was initiated in 1975 (after SBW activity reached epidemic level in 1974) as a cooperative effort among federal and the State of Maine forest agencies, as well as private forestry companies to document the impact of SBW on growth and mortality of the Maine forest. Data were collected at 424 ~0.2 ha circular plots including 8 762 trees ≥ 11.4 cm in diameter at breast height (DBH) throughout northern Maine during 1975-1985 (most of the temporal extent of the last SBW outbreak in Maine). The data included annual records of species, DBH, crown position, cause of death, total height, crown length, and degree of defoliation. Each year during the study period, current-year and previous-years foliage on each host tree within the plot were visually examined for the degree of defoliation, and categorized separately into one of five (before 1982) or eleven (after 1982) classes representing 0-100% defoliation of current-year and previous-years foliage.

3.2.2.2. Permanent Sample Plots of New Brunswick

About 1 500 random PSPs were established between 1976-1979 as part of the New Brunswick Department of Forests, Mines and Energy forest inventory. Of these plots, 136 were selected for SBW related studies based on stratification by species, maturity, and degree of insecticide use for protection. Each PSP consisted of three permanent prism points (basal area factor = 2 m^2 ha^-

^{1}) located 40 m apart, on which species, DBH, crown class, year of death, initial height, and degree of defoliation of each tree were recorded. The above data were collected during 1976-1993, with DBH initially measured between 1976 and 1979 and remeasured periodically in 1980, 1983, 1985, 1988, and 1991. Current year and total defoliation (defoliation on all age classes of foliage) were measured annually during 1984-1993 (when the SBW outbreak was declining), while height was measured once during 1976-1979. For all of the 6 316 sample trees in the PSP data set, only the 5 503 trees compatible in size with the Growth Impact Study dataset (i.e. DBH ≥ 11.4 cm) were included in this study. Both current-year and total defoliation in the New Brunswick PSPs was estimated for each host tree each year by scanning the crowns with binoculars. The results of both types of defoliation were separately put into seven percentage classes ranging from 0-100%.

3.2.2.3. Data Compilation

For this analysis, several components of individual-tree growth, namely annual diameter increment, height increment, crown recession (height to crown base increment), and mortality rate (including blowdown, which is a major secondary impact from SBW defoliation) were modeled using covariates derived from a variety of attributes of the measurements. DBH, height, and crown ratio were used as measures of tree and crown size (hence vigor); basal area of larger trees; and ratio between tree height and the mean height of softwood trees in a plot was used to represent tree social status; and dominant height was considered as an indicator of site productivity. Other measures of site conditions such as biomass growth index (Hennigar et al. 2017), climate site index (Weiskittel et al. 2011b), and topographic attributes were not considered due to their general lack of appreciable relationship with growth and mortality under the influence of SBW defoliation (Chen et al. In review). The primary hardwood species in this analysis were red maple (*Acer rubrum* L.) and white birch (*Betula papyrifera* Marsh.) accounting for 7% and 3% of all trees, respectively, in Maine, and 5% and 3% of all trees, respectively, in New Brunswick.

The severity of defoliation was presented as cumulative sums of the percentage defoliation of current-year foliage from all previous years until current year for each individual tree, which averaged 136 ± 139% (mean ± SD) and 82 ± 89% in Maine and New Brunswick, respectively. This is a relatively moderate cumulative defoliation level, equivalent to the removal, on average, of about one to one and one-half age classes of foliage. All above mentioned models accounted for specific differences in growth and mortality of the major host species of balsam fir, red spruce, black spruce, and white spruce (*Picea glauca* (Moench) Voss) by including interactions between species and key covariates. Natural hybridization between red and black spruce may have caused identification problems during the data collection (Gordon 1976; Bobola et al. 1992), and the sample size of black spruce in Maine was relatively small, so red and black spruce were combined into one species group in this analysis. In this analysis, presence of broken tops was noted and these observations were not included in the analysis. All measurements were converted to metric units. Summaries of the data for individual-tree measurements by species as well as stand and site characteristics are shown in Supplemental Materials B.1.

During the last outbreak, portions of both regions underwent aerial spraying of insecticide against SBW. This protection activity included most of New Brunswick's forested areas in certain years (MacLean et al. 1984). From 1970 to 1974, an average of 160 000 ha of forests was sprayed annually in Maine. This resulted in nearly 17% of the Growth Impact Study plots being sprayed at least once during this period. As the spraying extended to over 400 000 ha year^{-1} through the outbreak, and peaked at 1.6 million ha in 1976 (Seegrist and Arner 1982), it is reasonable to assume that the majority of these plots received some spraying and it was a variable included in the original dataset. However, previous analysis found no identifiable relationships between spraying and the examined stand dynamics, so additional analyses using information on spraying were not explored further (Chen et al. 2017b).

3.2.3. Model Development

3.2.3.1. Model fitting and Validation

Individual-tree growth components of annual diameter increment, height increment, crown recession (height to crown base increment), and mortality rate were related to various variables representing individual-tree measurements, stand structure and species composition, site productivity, and defoliation, and fitted with nonlinear mixed effect models by setting random effect across plots and by using a recursive annualization technique similar to that used by Weiskittel et al. (2007). Model selections (of suitable model formulations and predictors) were based on a combined consideration of biological interpretability, Akaike Information Criterion (AIC), and coefficient of determination (R^2). The annualization technique and the selected models best depicting individual-tree growth response to defoliation are described in detail below. All analyses were conducted in R v3.2.2 (R Core Team 2015). In particular, the R package "nlme" (Pinheiro et al. 2016) was used for constructing the nonlinear mixed effect models. Systematic deviation of these developed estimators from the observed mean values was also monitored in the model fitting process for diameter and height increments and crown recession, and presented as the statistic of percentage bias: $\frac{\sum(\hat{y}-y)}{\sum y} \cdot 100$. Percentage form of this statistic was taken to ensure their comparability to other studies using different units or under contrasting conditions. This statistic was not applied to the mortality model since it was of no practical meaning in such context, and was largely decided by the proportions of observations in the two categories (dead or alive).

3.2.3.2. Annualization

To reduce cost and measurement error, sample plots are often measured on periodic intervals instead of annually. This however hinders the development of growth and yield models, which are built as functions of these primary measurements, at a finer resolution than the measurement interval. A conventional method to convert interval measurements to annual measurements is to average the former over the interval (linear interpolation), which likely produces linear increments contradicting the results from the growth model being developed. Instead, a recursive annualization technique proposed by Cao (2000) and Weiskittel et al. (2007) in the form of Equation [1] was used to make annual growth and mortality predictions in this study:

$$[1]\ x_j = x_i + \sum_{t=i}^{j-1} f(x_t, w)$$

where x_j is the value of the variable of interest (e.g., DBH, height, or status of being dead or alive) at the end of the measurement cycle (year *j*); x_i is the corresponding value at the beginning of the cycle (year *i*); $f(x_t, w)$ is the growth models developed in this study, which utilizes *x* along with some other variables *w* as predictors.

Obviously, this procedure generates interpolated (annualized) values of variables in close agreement with their predicted values. It also provides an additional advantage of increased model validity with its ability to utilize data of various intervals to increase sample size. Instead of modeling growth based on successive measurements, measurements of all possible intervals were used as preliminary results indicated a significant improvement in model behavior. Overall, a total of 191 277 and 7 161 measurements from Maine and New Brunswick, respectively, were available for this analysis. Approaches used for each attribute examined are further described below.

3.2.3.3. Diameter Increment

Two general approaches of model formulation, namely potential growth multiplied by a modifier and a single unified equation, have been used to predict individual tree growth (Weiskittel et al. 2011a). However, it can be difficult to estimate such potential growth, especially under the influence of SBW defoliation, and the unified approach generally outperforms the potential by modifier approach (e.g., Russell et al. 2014). Based on this, unified equations for diameter increment in the form of Equation [2] and [3] with components from equations proposed by Holdaway (1984), Weiskittel et al. (2011b), and Garcia et al. (2012) were developed for Maine and New Brunswick, respectively:

$$[2]\ \ \Delta DBH = \beta 1 \cdot SPP \cdot DBH \cdot \exp\begin{pmatrix} (\beta 2 + \gamma 2) \cdot DBH + \beta 3 \cdot BAL + \beta 4 \cdot \exp(BA_{SW}/BA) \\ + \beta 5 \cdot HT_{DOM} + \beta 6 \cdot SPP \cdot \log(CDEF + 1)/\exp(CR) \end{pmatrix} + \varepsilon$$

$$[3]\ \ \Delta DBH = \beta 1 \cdot SPP \cdot DBH \cdot \exp\begin{pmatrix} (\beta 2 + \gamma 2) \cdot DBH + \beta 3 \cdot BAL \\ + \beta 6 \cdot SPP \cdot \log(CDEF + 1)/DBH \end{pmatrix} + \varepsilon$$

where *DBH* and *ΔDBH* are initial diameter at breast height (cm) and annual *DBH* increment (cm yr^{-1}), respectively; *SPP* is species (balsam fir, red/black spruce, or white spruce); *BAL* is basal area of trees larger than the subject tree in *DBH* ($\text{m}^2\ \text{ha}^{-1}$); *BA* and BA_{SW} are basal area and that of softwood trees ($\text{m}^2\ \text{ha}^{-1}$), respectively; HT_{DOM} is dominant height (m); *CR* is crown ratio; *CDEF* is cumulative defoliation (%); β1-β6 are model parameters; γ2 is a parameter for plot-level random effects; and *ε* is the error of the model.

3.2.3.4. Height Increment

For the same reasons given above, height increment was modeled using Equation [4] in a similar form to the diameter increment model, as height itself was sufficiently expressed as a function of DBH based on a fairly clear relationship between them. This model was not developed for New Brunswick due to the lack of available repeated height measurements.

$$[4]\ \ \Delta HT = \beta 1 \cdot SPP \cdot DBH \cdot \exp\begin{pmatrix} (\beta 2 + \gamma 2) \cdot DBH + \beta 3 \cdot HT_{DOM} \\ + \beta 4 \cdot SPP \cdot \log(CDEF + 1)/\exp(CR) \end{pmatrix} + \varepsilon$$

where *ΔHT* is annual height increment (m yr^{-1}); β1-β4 are model parameters; γ2 is a parameter for plot-level random effects; and the other notations are as defined above.

3.2.3.5. Crown Recession

Crown recession was modeled as annual height to crown base increment by Equation [5] in a mixed form of the incremental and static equations proposed by Russell et al. (2014) such that it was modeled directly by using initial height instead of predicted height increment. Since height increment was predicted in part as a function of defoliation in this analysis, using predicted height increment as a predictor would artificially separate and reduce the effect of defoliation on crown recession. This model was also not developed for New Brunswick due to the lack of available crown measurements.

$$[5]\ \Delta HCB = \frac{HT}{1 + \exp\begin{pmatrix} -\beta 1 \cdot SPP \cdot DBH^2 - (\beta 2 + \gamma 2) \cdot HT/DBH - \beta 3 \cdot BAL \\ -\beta 4 \cdot BA_{SW}/BA - \beta 5 \cdot SPP \cdot \log(CDEF + 1)/\exp(CR) \end{pmatrix}} + \varepsilon$$

where *ΔHCB* is annual height to crown base increment (m yr^{-1}); *HT* is initial height (m); β1-β5 are model parameters; γ2 is a parameter for plot-level random effects; and the other notations are as defined above.

3.2.3.6. Mortality

Logistic and probit (specifically on the cumulative distribution function of a standard normal distribution) models are widely used to model binary variables such as tree mortality (e.g., Liang et al. 2005; Maguire et al. 2011). In our data, mortality was a relatively low-probability event (mortality on stem counts in general never exceeded 8% in any given year for both Maine and New Brunswick). Consequently, the more flexible and asymmetric cumulative distribution function of an extreme value distribution (i.e. complementary log-log function) was used to model individual tree mortality to account for the fact that most trees lived through wide ranges of conditions such as defoliation and competition. Equations [6] and [7] were used to model mortality in Maine and New Brunswick, respectively:

$$[6]\ \ MORT = 1 - \exp\left(- \exp\left(\begin{array}{c} (\beta 1 + \gamma 1) + \beta 2 \cdot SPP \cdot \log(DBH) + \beta 3 \cdot MHT_{SW} \\ + \beta 4 \cdot HT/MHT_{SW} + \beta 5 \cdot BAL + \beta 6 \cdot \exp(BA_{SW}/BA) \\ + \beta 7 \cdot HT_{DOM} + \beta 8 \cdot SPP \cdot \log(CDEF + 1)/\exp(CR) \end{array} \right) \right) + \varepsilon$$

$$[7]\ \ MORT = 1 - \exp\left(- \exp\left(\begin{array}{c} (\beta 1 + \gamma 1) + \beta 6 \cdot HT/DBH + \beta 7 \cdot HT_{DOM} \\ + \beta 8 \cdot SPP \cdot \log(CDEF + 1) \cdot HT/MHT_{SW} \end{array} \right) \right) + \varepsilon$$

where *MORT* is the annual probability of mortality; MHT_{SW} is mean height of softwood trees (m); β1-β8 are model parameters; γ1 is a parameter for plot-level random effects; and the other notations are as defined above.

3.3. Results

3.3.1. Diameter Increment

A total of 89 976, 92 147, and 9 154 observations for balsam fir, red/black spruce, and white spruce, respectively, from Maine, and 2 819, 3 497, and 845 observations, respectively, from New Brunswick were available for this analysis. The observed mean annual diameter increments were 0.13 ± 0.13 (mean ± SD), 0.14 ± 0.14, and 0.15 ± 0.16 cm yr^{-1} for balsam fir, red/black spruce, and white spruce, respectively, in Maine, and 0.27 ± 0.19, 0.21 ± 0.17, and 0.29 ± 0.19 cm yr^{-1}, respectively, in New Brunswick (Supplemental Materials B.1). The annual diameter increment models explained 61% (77%) and 68% (78%) of the variation (including random effects) in the Maine and New Brunswick data, with percentage mean biases (including random effects) of -9.28% (+2.72%) and -2.90% (+1.34%), respectively (Table 3.1). Most parameter estimates were highly significant ($p < 0.0001$) and logical in their direction and magnitude. Parameter estimates were also consistent between the two regions.

Table 3.1. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual diameter increment models (cm yr^{-1}) by region. BF, BS, RS, and WS are balsam fir, black spruce, red spruce, and white spruce, respectively; DBH is initial diameter at breast height (cm); BAL is basal area of trees larger than the subject tree in DBH (m^2 ha^{-1}); BA and BA$_{SW}$ are basal area and that of softwood trees (m^2 ha^{-1}), respectively; HT$_{DOM}$ is dominant height (m); CR is crown ratio; CDEF is cumulative defoliation (%).

	Maine (n = 191 277)			**New Brunswick (n = 7 161)**		
Parameter and Fit Statistic	**Value**	**SE**	**p-value**	**Value**	**SE**	**p-value**
β1 (DBH·BF)	0.0465	0.0015	< 0.0001	0.1364	0.0135	< 0.0001
β1 (DBH·BS/RS)	0.0376	0.0012	< 0.0001	0.1284	0.0140	< 0.0001
β1 (DBH·WS)	0.0420	0.0014	< 0.0001	0.1467	0.0183	< 0.0001
β2 (DBH)	-0.0639	0.0015	< 0.0001	-0.0780	0.0032	< 0.0001
β3 (BAL)	-0.0293	0.0003	< 0.0001	-0.0353	0.0019	< 0.0001
β4 (exp(BA$_{SW}$/BA))	-0.2473	0.0076	< 0.0001	--	--	--
β5 (HT$_{DOM}$)	0.0330	0.0015	< 0.0001	--	--	--
β6 (log(CDEF+1)/exp(CR)·BF)	-0.1834	0.0054	< 0.0001	--	--	--
β6 (log(CDEF+1)/exp(CR)·BS/RS)	-0.0057	0.0052	0.2708	--	--	--
β6 (log(CDEF+1)/exp(CR)·WS)	-0.3094	0.0940	0.0010	--	--	--
β6 (log(CDEF+1)/DBH·BF)	--	--	--	-1.2271	0.2161	< 0.0001
β6 (log(CDEF+1)/DBH·BS/RS)	--	--	--	-1.8329	0.3160	< 0.0001
β6 (log(CDEF+1)/DBH·WS)	--	--	--	-2.1061	0.3879	< 0.0001
γ2 (Random effects on β2)		0.0292			0.0177	
R^2 (Fixed effects)	0.61			0.68		
R^2 (Incl. random effects)	0.77			0.78		
%Bias (Fixed effects)	-9.28			-2.90		
%Bias (Incl. random effects)	+2.72			+1.34		

As shown in Figure 3.2, diameter increment increased, soon peaked, and decreased over initial DBH, and was at much higher rates in New Brunswick. In both regions, diameter increment displayed an inverse relationship with defoliation, which varied among species. In particular, diameter increment of balsam fir was significantly more sensitive to defoliation than that of red/black spruce in Maine, while such sensitivity to defoliation among different species was less distinguishable in New Brunswick. Specifically, when comparing no and relatively high defoliation (200% cumulative defoliation, equivalent to removal of two age classes of foliage), predicted mean diameter increments for balsam fir, red/black spruce, and white spruce decreased from 0.13, 0.09, and 0.09 cm yr^{-1} to 0.06, 0.09, and 0.03 cm yr^{-1}, equivalent to 54, 2, and 68%, respectively, in Maine, while decreased from 0.21, 0.21, and 0.17 cm yr^{-1} to 0.15, 0.13, and 0.11 cm yr^{-1}, equivalent to 29, 36, and 37%, respectively, in New Brunswick. In addition, larger BAL and proportion of softwood trees both led to reduced diameter increment, which was otherwise enhanced with higher dominant tree height (potential productivity).

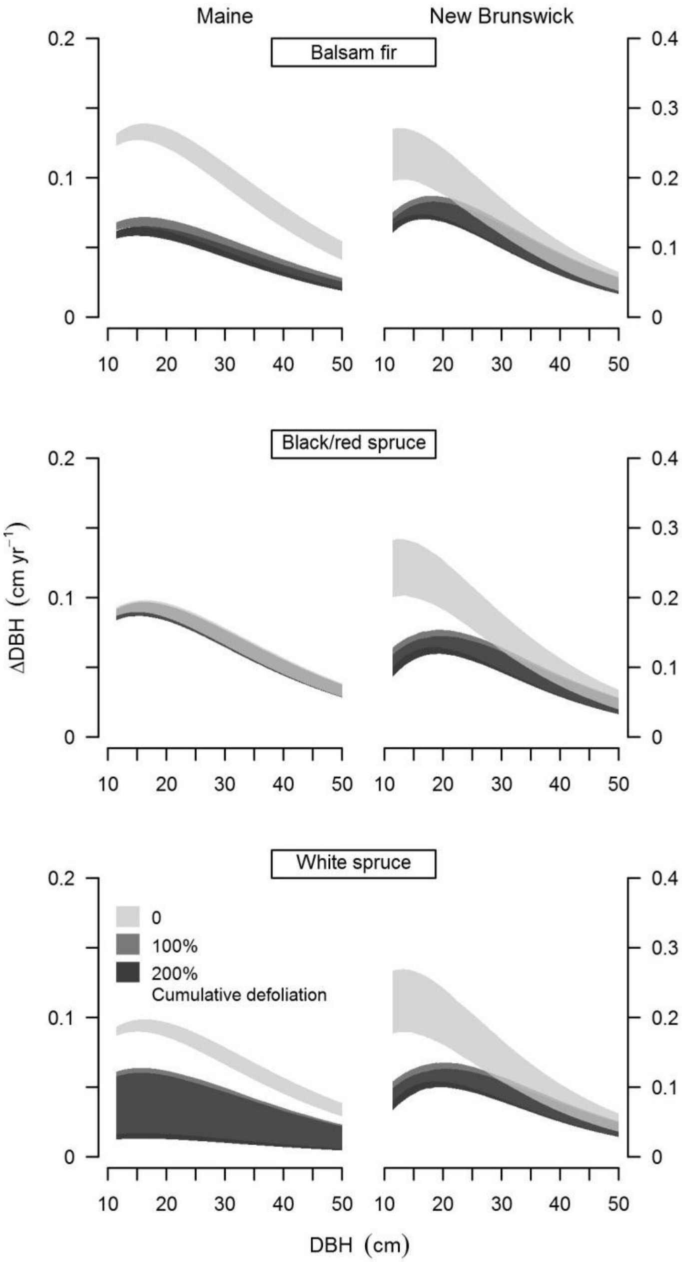

Figure 3.2. Predictions of annual diameter increment (ΔDBH; cm yr^{-1}) as a function of initial DBH (cm) under 0, 100% (moderate), and 200% (relatively high) cumulative defoliation with all the other covariates set at their mean values by species for Maine and New Brunswick. Shaded areas represent 95% confidence intervals of these predictions.

3.3.2. Height Increment

The observed mean annual height increments for balsam fir, red/black spruce, and white spruce were 0.07 ± 0.21 (mean ± SD), 0.05 ± 0.15, and 0.06 ± 0.18 m yr^{-1}, respectively, for Maine (Supplemental Materials B.1). The height increment model for Maine explained 26% (40%) of the variation (including random effects) in the data, with mean bias (including random effects) averaging -16.85% (-1.21%). Most parameter estimates were highly significant ($p < 0.0001$) and logical in their direction and magnitude, except the influence of defoliation on white spruce height increment was quite variable (Table 3.2).

Table 3.2. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual height increment model (m yr^{-1}) for Maine. BF, BS, RS, and WS are balsam fir, black spruce, red spruce, and white spruce, respectively; DBH is initial diameter at breast height (cm); HT_{DOM} is dominant height (m); CR is crown ratio; CDEF is cumulative defoliation (%).

Parameter and Fit Statistic	Value	SE	p-value
β1 (DBH·BF)	0.0053	0.0003	< 0.0001
β1 (DBH·BS/RS)	0.0045	0.0003	< 0.0001
β1 (DBH·WS)	0.0037	0.0003	< 0.0001
β2 (DBH)	-0.0514	0.0024	< 0.0001
β3 (HT_{DOM})	0.0171	0.0031	< 0.0001
β4 (log(CDEF+1)/exp(CR)·BF)	-0.0204	0.0150	0.1719
β4 (log(CDEF+1)/exp(CR)·BS/RS)	-0.0638	0.0176	0.0003
β4 (log(CDEF+1)/exp(CR)·WS)	-0.7062	0.3134	0.0242
γ2 (Random effects on β2)		0.0433	
R^2 (Fixed effects)	0.26		
R^2 (Incl. random effects)	0.40		
%Bias (Fixed effects)	-16.85		
%Bias (Incl. random effects)	-1.21		

Height increment exhibited the same pattern as diameter increment over initial DBH, but was rather insensitive to changes in DBH, and remained low regardless of the levels of defoliation (Figure 3.3). Unlike the generally more significant reduction of diameter increment in response to defoliation, such reduction from the already low baseline height increment was minimal at both absolute and relative scales (Figure 3.3). Although improved site productivity (as indicated by dominant height) appeared to improve height increment, this effect was negligible in quantity.

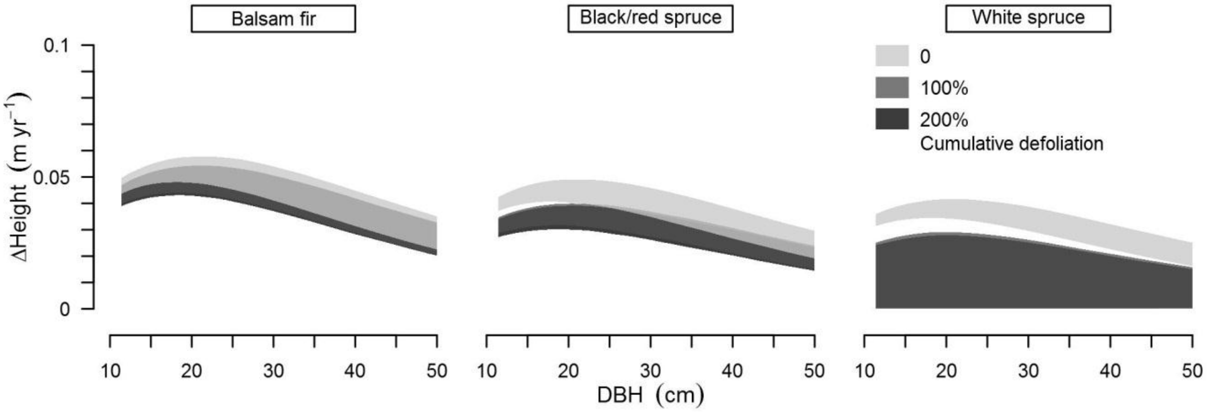

Figure 3.3. Predictions of annual height increment (ΔHeight; m yr^{-1}) as a function of initial DBH (cm) under 0, 100% (moderate), and 200% (relatively high) cumulative defoliation with all the other covariates set at their mean values by species for Maine. Shaded areas represent 95% confidence intervals of these predictions.

3.3.3. Crown Recession

The observed mean annual height to crown base increments for balsam fir, red/black spruce, and white spruce were 0.22 ± 0.69 (mean ± SD), 0.14 ± 0.50, and 0.19 ± 0.59 m yr^{-1}, respectively, for Maine (Supplemental Materials B.1). The crown recession model for Maine explained 37% and 23% of the variation in the data, with percentage bias averaging -7.56% and -25.91% with and without accounting for random effects in the data, respectively (Table 3.3). Most parameter estimates were highly significant ($p < 0.0001$) and logical in their direction and magnitude.

Table 3.3. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual crown recession model (changes in height to crown base; m yr^{-1}) for Maine. BF, BS, RS, and WS are balsam fir, black spruce, red spruce, and white spruce, respectively; DBH is initial diameter at breast height (cm); HT is initial height (m); BAL is basal area of trees larger than the subject tree in DBH (m^2 ha^{-1}); BA and BA_{SW} are basal area and that of softwood trees (m^2 ha^{-1}); CR is crown ratio; CDEF is cumulative defoliation (%).

Parameter and Fit Statistic	**Value**	**SE**	**p-value**
β1 (DBH^2·BF)	-0.0013	< 0.0001	< 0.0001
β1 (DBH^2·BS/RS)	-0.0015	< 0.0001	< 0.0001
β1 (DBH^2·WS)	-0.0016	< 0.0001	< 0.0001
β2 (HT/DBH)	-4.8643	0.0776	< 0.0001
β3 (BAL)	-0.0029	0.0009	0.0017
β4 (BA_{SW}/BA)	-0.0331	0.0040	< 0.0001
β5 (log(CDEF+1)/exp(CR)·BF)	-0.0394	0.0148	0.0079
β5 (log(CDEF+1)/exp(CR)·BS/RS)	-0.4541	0.0159	< 0.0001
β5 (log(CDEF+1)/exp(CR)·WS)	-0.3540	0.1151	0.0021
γ2 (Random effects on β2)		1.3117	
R^2 (Fixed effects)	0.23		
R^2 (Incl. random effects)	0.37		
%Bias (Fixed effects)	-25.91		
%Bias (Incl. random effects)	-7.56		

The crown recession model exhibited a similar behavior as the height increment model over initial diameter, but peaked at larger diameters and showed greater reduction in response to defoliation (Figure 3.4). Specifically, when comparing no and relatively high defoliation (200% cumulative defoliation), predicted mean annual height to crown base increments for balsam fir, red/black spruce, and white spruce decreased from 0.15, 0.19, and 0.20 m yr^{-1} to 0.13, 0.03, and 0.05 m yr^{-1}, respectively, in Maine. In addition, higher height to DBH ratio, BAL, and proportion of softwood trees all reduced the rate of crown recession, while greater crown ratio was related to increased rate of crown recession.

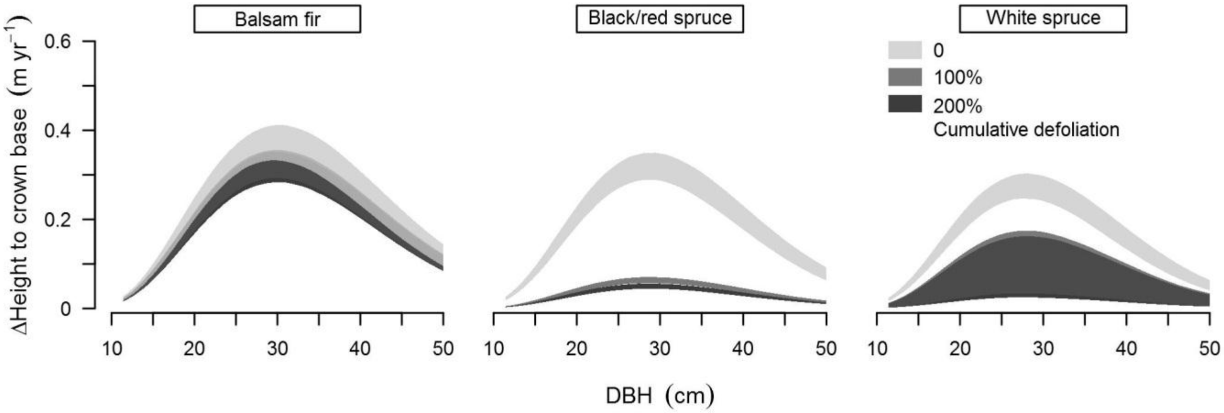

Figure 3.4. Predictions of annual crown recession (ΔHeight to crown base; m yr^{-1}) as a function of initial DBH (cm) under 0, 100% (moderate), and 200% (relatively high) cumulative defoliation with all the other covariates set at their mean values by species for Maine. Shaded areas represent 95% confidence intervals of these predictions.

3.3.4. Mortality

Observed annual mortality rate changed considerably over the duration of the SBW outbreak, and averaged 5.8, 1.3, and 0.4% for balsam fir, red/black spruce, and white spruce, respectively, in Maine, and 2.8, 1.2, and 1.1%, respectively, in New Brunswick (Supplemental Materials B.1). Cumulative mortality rates for balsam fir, red/black spruce, and white spruce were 40.5, 11.3, and 3.3% (over 10 years), respectively, in Maine, and 8.9, 4.9, and 4.7% (over 6 years), respectively, in New Brunswick. The mortality models had maximum classification accuracy of 95% and 99% regardless of the inclusion of random effects, and areas under the receiver operating characteristic curve were 0.76 and 0.65 (0.84 and 0.80 including random effects) for Maine and New Brunswick, respectively. Most parameter estimates were highly significant ($p < 0.0001$) and logical in their direction and magnitude. Parameter estimates were also largely consistent between the two regions, and in agreement with the diameter increment models (Table 3.4).

Table 3.4. Parameter estimates with corresponding standard errors (SE) and p-values, and model fit statistics of the annual mortality rate models by region. BF, BS, RS, and WS are balsam fir, black spruce, red spruce, and white spruce, respectively; DBH is initial diameter at breast height (cm); $\mathrm{MHT}_{\mathrm{SW}}$ is mean height of softwood trees (m); HT is initial height (m); BAL is basal area of trees larger than the subject tree in DBH ($\mathrm{m}^2\ \mathrm{ha}^{-1}$); BA and $\mathrm{BA}_{\mathrm{SW}}$ are basal area and that of softwood trees ($\mathrm{m}^2\ \mathrm{ha}^{-1}$), respectively; $\mathrm{HT}_{\mathrm{DOM}}$ is dominant height (m); CR is crown ratio; CDEF is cumulative defoliation (%).

	Maine (n = 191 277)			**New Brunswick (n = 7 161)**		
Parameter and Fit Statistic	**Value**	**SE**	**p-value**	**Value**	**SE**	**p-value**
β1 (Intercept)	-5.2900	0.2364	< 0.0001	-13.9284	1.1494	< 0.0001
β2 (log(DBH)·BF)	-0.0400	0.0541	0.4601	--	--	--
β2 (log(DBH)·BS/RS)	-0.9416	0.0624	< 0.0001	--	--	--
β2 (log(DBH)·WS)	-0.9899	0.1434	< 0.0001	--	--	--
β3 ($\mathrm{MHT}_{\mathrm{SW}}$)	0.1716	0.0128	< 0.0001	--	--	--
β4 ($\mathrm{HT}/\mathrm{MHT}_{\mathrm{SW}}$)	1.0121	0.0478	< 0.0001	--	--	--
β5 (BAL)	0.0256	0.0014	< 0.0001	--	--	--
β6 ($\exp(\mathrm{BA}_{\mathrm{HW}}/\mathrm{BA})$)	-0.1882	0.0702	0.0073	--	--	--
β6 (HT/DBH)	--	--	--	9.8633	0.5438	< 0.0001
β7 ($\mathrm{HT}_{\mathrm{DOM}}$)	-0.1977	0.0060	< 0.0001	-0.1887	0.0361	< 0.0001
β8 (log(CDEF+1)/exp(CR)·BF)	0.3889	0.0073	< 0.0001	--	--	--
β8 (log(CDEF+1)/exp(CR)·BS/RS)	0.5366	0.0234	< 0.0001	--	--	--
β8 (log(CDEF+1)/exp(CR)·WS)	0.9257	0.0770	< 0.0001	--	--	--
β8 ($\log(\mathrm{CDEF}+1)\cdot\mathrm{HT}/\mathrm{MHT}_{\mathrm{SW}}\cdot\mathrm{BF}$)	--	--	--	0.7026	0.1243	< 0.0001
β8 ($\log(\mathrm{CDEF}+1)\cdot\mathrm{HT}/\mathrm{MHT}_{\mathrm{SW}}\cdot\mathrm{BS/RS}$)	--	--	--	0.3676	0.1502	0.0144
β8 ($\log(\mathrm{CDEF}+1)\cdot\mathrm{HT}/\mathrm{MHT}_{\mathrm{SW}}\cdot\mathrm{WS}$)	--	--	--	0.3174	0.1378	0.0213
γ1 (Random effects on β1)		1.3602			2.5955	

(Table 3.4. continued)

	Maine (n = 191 277)			New Brunswick (n = 7 161)		
Parameter and Fit Statistic	**Value**	**SE**	**p-value**	**Value**	**SE**	**p-value**
Max. classification accuracy (%) (Fixed effects)	95			99		
Max. classification accuracy (%) (Incl. random effects)	95			99		
Area under curve (Fixed effects)	0.76			0.65		
Area under curve (Incl. random effects)	0.84			0.80		

Mortality rates generally remained low over the observed DBH range, and were most strongly influenced by the severity of defoliation, even at the relatively moderate defoliation levels (two age classes of foliage removed) observed in the sample plots (Figure 3.5). Mortality decreased with increased DBH, and this decrease was much sharper in New Brunswick where mortality was mainly observed among small trees. The highest mortality rates were observed and predicted for balsam fir, although mortality rates of white spruce in Maine tended to be as sensitive to these increases in defoliation as balsam fir, which resulted in relatively large amount of variation in their mortality (Figure 3.6). In addition, higher mortality rate was attributed to both larger BAL and trees with advantageous social status (as identified by Reams et al. 1988; indicated by the ratio of tree height to mean tree height in a plot), while better site productivity (indicated by dominant height), higher proportion of hardwood trees (as identified by Reams et al. 1988), and improved tree vigor (indicated by crown ratio) all lowered mortality rates.

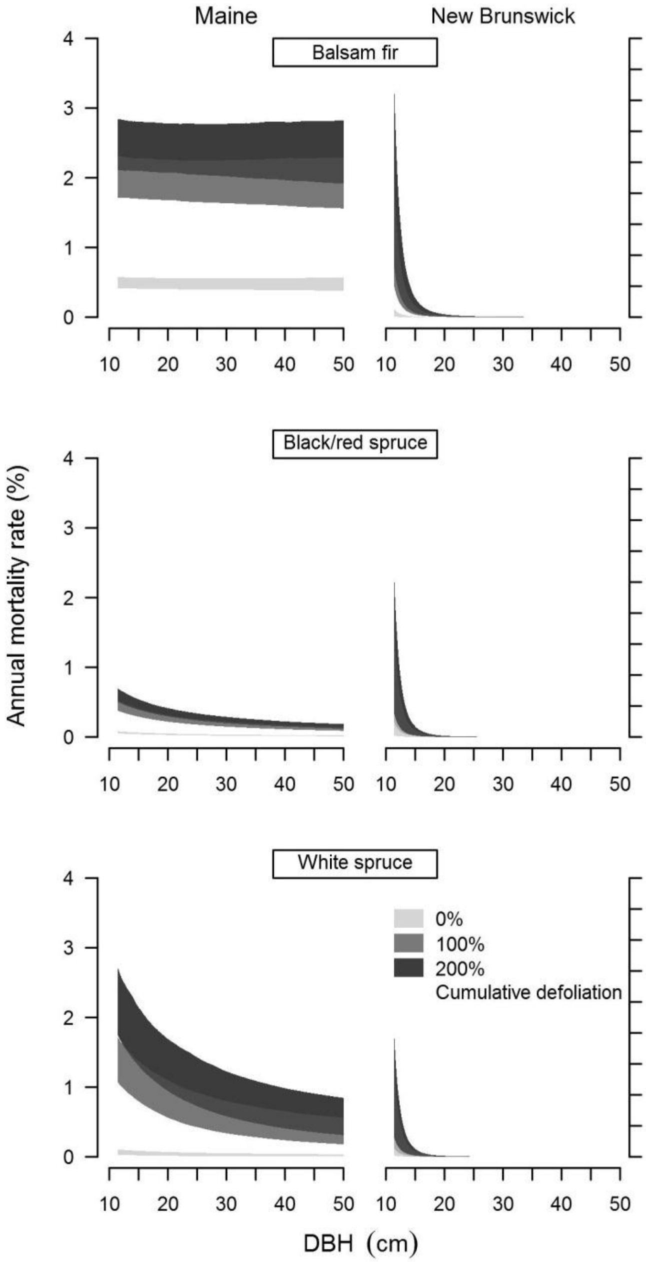

Figure 3.5. Predictions of annual mortality probability (%) as a function of initial DBH (cm) under 0, 100% (moderate), and 200% (relatively high) cumulative defoliation with all the other covariates set at their mean values by species for Maine and New Brunswick. Shaded areas represent 95% confidence intervals of these predictions

3.4. Discussion

Overall, the fit of our models was generally sufficient and on par with expectations from previous growth modeling in the region (e.g. Weiskittel et al. 2011b, Russell et al. 2014). In particular, all of our models had relatively small biases, and were consistent with biological expectations despite the large underlying variation in the data.

Nevertheless, considerable amount of variation remained unexplained by our models. This could be due largely to the inherently high variability in tree growth as well as the large range in stand and site conditions present in our data, particularly with respect to observed defoliation levels. Defoliation is typically variable both temporally and spatially when at low-moderate SBW population levels, but is more uniformly severe at high SBW population levels (Zhao et al. 2014). In addition, sampling issues such as the difficulty in obtaining reliable annual height and height to crown base measurements, the use of variable radius sample plots in New Brunswick, and the degree of training of crews in defoliation assessment might also be potentially influential. Regardless, the data used are extensive, long-term, and representative so the developed models should be relatively robust to these sampling issues and predicted behavior was consistent with expectations.

Generally, it was found that the effects of SBW defoliation on diameter and height increment, crown recession, and mortality were all highly significant, but relatively moderate in magnitude. For example, mean relative diameter growth reduction for balsam fir between no noticeable defoliation and 200% cumulative defoliation (equivalent to removal of two age classes of foliage) was estimated to be 54 and 29% for Maine and New Brunswick, respectively. These values are in the range of the 20-60% reduction reported for years 3-5 of a SBW outbreak by MacLean (1979) and the maximum 50% reduction estimated by Pothier et al. (2005). In contrast, under more severe cumulative defoliation levels of 400-600%, increment reduction was about

80% or more (Ostaff and MacLean 1995). In absolute terms, MacLean (1988) reported balsam fir annual diameter increment ranged from 0.06 to 0.17 cm, while Steinman and MacLean (1994) showed annual diameter increment for balsam fir, black spruce, and white spruce to be 0.10-0.28, 0.10-0.24, and 0.10-0.36 cm, respectively, which all overlap with our predictions (Figure 3.3).

Interestingly, there was relatively little reduction in both observed and predicted height increment due to SBW defoliation. Unfortunately, limited quantitative information on the effect of defoliation on height increment was found from previous studies. Ostaff and MacLean (1989) suggested that severe defoliation resulted in the cessation of height growth as leaders were repeatedly destroyed, while Van Sickle (1987) stated that height growth dropped abruptly under moderate and severe defoliation due to the destroyed terminal buds not producing annual internodes and consequent top-kill affected up to 63% of the Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) trees with defoliation from western spruce budworm. In this analysis, 76% of the observations had no observable height increment and their consequent low predicted values likely confirmed the findings of Van Sickle (1987). In addition, observed and predicted height increment in this analysis were also much lower than those reported by Russell et al. (2014), which suggests the effect of SBW was already implicit in the underlying data. For example, Russell et al. (2014) reported a mean annual height increment for balsam fir, black spruce, red spruce, and white spruce of 0.32, 0.17, 0.25, and 0.28 m yr^{-1}, respectively, while observed and predicted mean values in this analysis never exceeded 0.1 m yr^{-1}.

In this analysis, presence of broken tops was noted and these observations were not included in the analysis so this would be an unlikely reason for the low predicted height increments. When the reductions due to 200% cumulative defoliation (equivalent to removal of two age classes of foliage) in both diameter and height increments for the average sized tree were combined to estimate annual volume increment reduction using a species-specific taper function (Li et al. 2012), values of 28, 16, and 54% were observed for balsam fir, red/black spruce, and white spruce, respectively. This volume increment reduction was obviously influenced more by the reduction in diameter increment rather than height increment. In comparison, MacLean et al. (1996) reported an 83% reduction in annual specific volume increment for balsam fir that sustained about 550% cumulative defoliation over 7 years.

Observed and predicted mean crown recession rates in this study were much lower than those of 0.42, 0.23, 0.31, and 0.27 m yr^{-1} for balsam fir, black spruce, red spruce, and white spruce, respectively, reported by Russell et al. (2014). Our models indicated such a strong effect of defoliation in reducing crown recession that practically halted it for the spruce species. This could be a result of more light penetrating through the defoliated crown and allowing lower branches to remain on trees longer. However, crown recession rates of different species are in the same order (i.e. balsam fir > red/black spruce > white spruce) in these two studies, which means the much higher levels of defoliation of balsam fir compared to the spruce species did not slow crown recession proportionally, but likely indicates that other physiological or environmental factors other than light availability also considerably affected crown recession under the influence of SBW defoliation.

In contrast, some important differences in terms of observed and predicted mortality patterns between this study and previous ones exist. For example, MacLean (1979) reported balsam fir mortality between 1977 and 1978 in Cape Breton Island to be <1-17% by stem number, while a 20% annual mortality rate (and 87% cumulative mortality rate) by volume was reported by MacLean and Ostaff (1989). The cumulative mortality rates of 92-100% and 32-59% by basal area were reported for balsam fir and spruce species, respectively, in Maine (Solomon et al. 2003). However, all of these figures were significantly higher than both observed and predicted values in our study (Supplemental Materials B.1 and Figure 3.5), which is likely explained by differences in defoliation level. Mean cumulative defoliation was 136% and 82% in Maine and New Brunswick, respectively, while that in severe outbreaks was typically 400-600% or higher, equivalent to removal of four to six age classes of foliage. Most of the studies that indicated heavier influences of defoliation were conducted in uncontrolled severe SBW outbreaks either on Cape Breton Island, Nova Scotia, Canada (e.g. MacLean 1979, 1988, MacLean and Ostaff 1989) or in Baxter State Park, Maine (e.g. Osawa et al. 1986, Solomon et al. 2003), and probably reflect the upper boundary of observed mortality rates due to defoliation during a severe outbreak (MacLean 1980). Although the observations in this analysis were conducted after the start of the last major SBW outbreak, they were taken across a larger geographic area and longer temporal period than most of these previous studies.

Our study showed that the examined species responded to defoliation differently in Maine such that greatest diameter growth reductions and higher mortality rates were observed for balsam fir than for those spruce species under the same level of defoliation. However, these species were unlikely to be equally susceptible to defoliation. Hennigar et al. (2008) and Chen et al. (2017b) both indicated that balsam fir sustained higher levels of defoliation than other host species at the same location. Balsam fir and black and red spruce were significantly more susceptible than white spruce in Maine such that the latter species was unlikely to experience high levels of defoliation (Supplemental Materials B.1). This finding is partially contrary to what was observed in New Brunswick and previous studies that have suggested that white spruce was more susceptible than black and red spruce (e.g. MacLean and Erdle 1986, Hennigar et al. 2008). Interestingly, all of our estimated model parameters for white spruce in this analysis had larger amount of variation, which may indicate less representative samples from both regions.

Defoliation also likely altered the relationship between competition and growth such that relative growth rates declined with decreased social status (Perry 1985). Specifically, improved tree social status, measured as the ratio between a tree's height and the mean height of softwood trees in a plot, was related to decreased diameter increment and increased mortality when the other factors were held constant. This finding agrees with Turner (1952) that mortality generally increased with the relative height of balsam fir and Reams et al. (1988) that suppressed trees were more likely to survive, which could be the result of lower energy reserve, reduced wind-firmness, and higher crown exposure to SBW of these larger trees (Mott 1963). Although some studies suggested that understory trees were extremely vulnerable to defoliation (e.g. Irland et al. 1988), it was rather difficult to relate this to either the effect of defoliation or the generally low vigor of these trees.

It had long been observed that SBW host species received protection from defoliation by hardwood trees in stands and forests due to increased dispersal and migration losses of SBW (Mott 1963; Baskerville 1975). In this study, a similar potential effect was noted as diameter increment increased (i.e. was less reduced compared to average stand conditions) and mortality rate decreased (i.e. was less increased compared to average stand conditions) in stands with higher hardwood content under the influence of defoliation (Tables 3.1 and 3.4). This effect on decreased mortality rate has also been reported by Turner (1952) and Reams et al. (1988), while Su et al. (1996) showed that defoliation of balsam fir significantly decreased with increases in hardwood content, which obviously would result in less reduced tree growth.

Differences in mortality rate were observed between Maine and New Brunswick, but these differences did not follow the same pattern across species. In general, mortality rates among trees of different sizes were less distinctive in Maine, but much higher among smaller trees in New Brunswick. Mortality of balsam fir was most sensitive to defoliation in both regions, while red/black spruce was least sensitive to defoliation both in terms of mortality and diameter increment in Maine. The high variation in white spruce's response to defoliation in terms of mortality as well as diameter and height increment, and crown recession was likely an effect of extrapolation of a less representative sample. Considering balsam fir, on average, experienced higher level of defoliation than the other subject species, it indicated the dominant effect of defoliation on host tree mortality during a SBW outbreak. In addition, higher levels of defoliation of balsam fir and red/black spruce in Maine could be a cause for their much lower diameter growth when compared to New Brunswick. Other factors such as management history, age, composition, and productivity of forests, and the fact that data were collected in New Brunswick more towards the end of the SBW outbreak could also have contributed to these regional differences.

In each of our models, considerable variation was accounted for by random effects among sample plots. Our previous stand-level analysis (Chen et al. 2017b) indicated that these random effects likely reflected spatio-temporal autocorrelation in individual tree growth and mortality as well as in the dynamics of SBW outbreak. The fact that models constructed for New Brunswick (where stratification was applied in the sampling process) tend to explain relatively large amount of variation of the data with the inclusion of fewer predictors likely confirms such autocorrelation. However, preliminary analysis indicated that the inclusion of a spatial or temporal autocorrelation error structure did not significantly improve model fit. Modeling spatial autocorrelation would require a denser sample plot network over a broad area, while addressing temporal autocorrelation would require data of longer time series than most SBW outbreaks last. Despite these limitations, the developed equations in this analysis represent one of the most comprehensive assessments of the effects of SBW individual tree growth and mortality, but their performance will need to be assessed during the next SBW outbreak to evaluate their representativeness.

CHAPTER 4

MODELLING VARIATION AND TEMPORAL DYNAMICS OF INDIVIDUAL TREE DEFOLIATION CAUSED BY SPRUCE BUDWORM IN MAINE, US AND NEW BRUNSWICK, CANADA[1]

4.1. Introduction

Insect defoliation reduces the growth and survival of trees. Variability in these effects on trees has been defined as trees' vulnerability to defoliation by Mott (1963) and has been rather intensively studied for a variety of forest insect defoliators (e.g., Muzika and Liebhold 1999, Anstey et al. 2002, Chen et al. 2017a). In contrast, trees vary in their capacity in supporting insect defoliator population, i.e., trees tend to be defoliated to various levels depending on a number of possible factors like their species, size, and crown position. This variation in defoliation has been defined as trees' susceptibility to defoliation caused by a defoliator (Mott 1963). Although the damaging effects of defoliation are the result of both the vulnerability and susceptibility of trees, these effects are often evaluated at defoliation levels predetermined by investigators (scenarios; e.g., Pothier et al. 2005, Hennigar et al. 2013) such that the variation in defoliation has been largely ignored.

Overlooking the variation in defoliation is especially the case for the defoliation of spruce-fir (*Picea-Abies*) forests caused by spruce budworm (SBW; *Choristoneura fumiferana* (Clem.)), which is the primary forest defoliator in North America. SBW defoliation has affected over 58 million ha of forests during its last major outbreak in the 1970s and 1980s (Blais 1983, USDA Forest Service 2009), and frequently shifted between conditions of low to almost complete defoliation over large temporal and spatial extents of outbreaks (Irland et al. 1988). Variation in SBW defoliation has long been observed among trees and over time (e.g., MacLean and Lidstone

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[1] This chapter previously appeared as an article as follows: Chen, C., Weiskittel, A., Bataineh, M., and MacLean, D.A. 2018. Modelling variation and temporal dynamics of individual tree defoliation caused by spruce budworm in Maine, US and New Brunswick, Canada. Forestry 92: 133-145.

1982, Gray et al. 2000, Doran et al. 2017). While many entomological studies have implicitly investigated this variation from the perspective of SBW population dynamics (e.g., birth and death, immigration and emigration, and SBW and host relationship; Greenbank 1963a, Royama 1984, Nealis and Régnière 2004), patterns of this variation has been little examined or modelled for direct use in forest management, especially in the application of forest growth and yield models. Nevertheless, a few studies have looked into this variation at a relatively coarse scale of forest stands. For example, Alfaro et al. (2001) found old and less dense stands were more susceptible to SBW defoliation, while Hennigar et al. (2008) quantified defoliation of each spruce (*Picea* spp.) species relative to observed mean defoliation of balsam fir (*Abies balsamea* L.) in the same stand, where red spruce (*Picea rubens* Sarg.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss) and balsam fir were all present.

However, the coarseness of analytical scales of defoliation may have limited our understanding of the variation in SBW defoliation. While tree-level models have been considered the new standard for modelling forest growth and survival (e.g., Crecente-Campo et al. 2010, Weiskittel et al. 2011a), variation in SBW defoliation has been predominantly evaluated at stand-level (e.g., Irland et al. 1988, Alfaro et al. 2001, Hennigar et al. 2008), which is potentially problematic in distinguishing the effects of various factors on susceptibility. For example, a pure stand being more susceptible may be attributed to either the susceptibility of the species or the lack of diversity of the stand. Likewise, susceptibility of mixed stands may also be affected by a variety of specific, compositional, and structural factors, which could all be evaluated as the possible influence of stand species composition. Therefore, the evaluation of susceptibility to SBW defoliation would benefit significantly from a cross-scale approach, which would allow potential effects to be evaluated at suitable scales (e.g., specific effects may be better assessed at tree-level to separate structural and compositional effects of stands, while diversity can be analysed at larger scales) by utilizing a variety of tree-, stand-, and site-level characteristics.

An important potential application of this cross-scale approach, which utilizes information of forest at various scales, is to replace costly and time-consuming individual tree defoliation measurements with predictions based on defoliation measured through remote sensing at relatively large spatial scales. Measurements of SBW defoliation have been relied mainly on four methods: 1) egg-mass counting (Simmons 1974), 2) moth trapping (Irland et al. 1988), 3) on-site visual examination of defoliation (Solomon and Brann 1992), and 4) aerial sketch-mapping of defoliation (visual estimation of defoliation by an observer in an airplane; MacLean and MacKinnon 1996). While aerial sketch-mapping can be used to measure defoliation over large areas, it requires observers to make large area assessments in a limited time frame. It is also too coarse to be used to evaluate the variation in defoliation at a meaningful scale in forest management (e.g., a single defoliation category has been assigned to areas from several km^2 to tens of thousands km^2, within which defoliation levels as well as forest conditions and types varied greatly; Hennigar et al. 2013). In addition, the first three methods could be costly and time-consuming depending on sample size, and require conversion of indirect measurements of defoliation as well as spatial statistical techniques to infer defoliation over large areas. As forest measurements increasingly rely on remote sensing, SBW defoliation can potentially be measured at large spatial scales (e.g., at stand-level) using aerial or satellite imagery at a resolution of tens of meters or coarser (e.g., Rahimzadeh-Bajgiran et al. 2018). Consequently, it is desirable to create cross-scale models that are able to leverage these coarse observations of defoliation, while providing detailed defoliation predictions for individual trees where the effects of defoliation on the growth and survival of trees actually occur.

Our evaluation of the variation in individual tree defoliation was supported by over 47 000 individual tree observations of SBW defoliation from an extensive network of 560 permanent sample plots (PSP), which covered a longitudinal range of ~ 490 km and a latitudinal range of ~ 340 km, as well as 10 years of the last SBW outbreak in the 1970s-1980s in Maine and New Brunswick. These data comprised a wide range of forest conditions and defoliation observations (although mainly in relatively low levels of < 30% annually; Chen et al. 2017b) accompanied by detailed tree measurements, from which a variety of tree- and stand-level characteristics were derived and evaluated for their potential effects on individual tree defoliation dynamics.

While considering the effects of tree-, stand-, and site-level characteristics on SBW defoliation, the primary relationship that our models evaluated was between individual tree- and stand-level defoliation, which has the potential to be more efficiently measured through remote sensing (e.g., Rahimzadeh-Bajgiran et al. 2018). Regardless of measurement method, stand-level defoliation is the mean of individual tree defoliation of trees within a stand (weighted by their crown sizes). However, this exact measure of stand-level defoliation cannot be obtained through the inherently coarse aerial sketch-mapping, which is the only method that has been applied to measure SBW defoliation over large areas. For example, aerial sketch-mapping indicated defoliation of whole northern Maine to be 30%-70% in 1975 and 1976 (Hennigar et al. 2013), while stand-level defoliation calculated from on-site measurements of individual tree defoliation were actually out of this broad range in 88% of the cases (Chen et al. 2017b). In addition, future remote sensing measurements of stand-level defoliation likely are based on a trained relationship between this calculated exact stand-level defoliation and optical remote sensing signals of aerial or satellite imagery (e.g. Rahimzadeh-Bajgiran et al. 2018). Consequently, stand-level defoliation was obtained as the mean of individual tree defoliation observations (weighted by volumes as a surrogate of crown sizes, which were not measured) in this study. In this way, the underlining relationship between individual tree- and stand-level defoliation was evaluated without losing generality due to measurement errors inherent in remote sensing signals and errors in predicting stand-level defoliation from these signals.

Chen et al. (2017b) showed that there was a large variation in observed SBW defoliation among a number of previous studies. Therefore, it is less intuitive to interpret these observations of defoliation from various studies as repeatable random samples generated by a set of fixed but unknown parameters. Instead, these parameters may be considered random and distributed over large ranges, which were consequently related to the significant spatial and temporal variation in observed SBW defoliation. This motivated this study to be the first to analyse SBW defoliation dynamics using a Bayesian method, which offers several key advantages. First, the results from this study have the potential of providing highly informative priors to similar studies. Second, these results may also be improved with the inclusion of increasingly available data. Third, this method will be able to better represent the observed variation in defoliation and partition it to the appropriate hierarchical levels.

Our specific research objectives were to: 1) assess the relationship between individual tree defoliation and stand-level defoliation across multiple SBW host species; 2) evaluate the effects and relative importance of various tree-, stand-, and site-level factors on individual tree defoliation; 3) model the temporal dynamics of individual tree defoliation based on its initial observation; and 4) compare and evaluate the determined relationships across Maine and New Brunswick to better verify the robustness and consistency of our findings. Despite some previous studies that have emphasized the effects of stand structure and composition on the susceptibility to defoliation (e.g. MacLean 1979, Colford-Gilks et al. 2012), we expect these effects to be of much smaller magnitudes compared with differences among SBW host species' susceptibility to SBW defoliation. Moreover, we expect the temporal development of SBW defoliation to follow similar trajectories regardless of initial differences in tree-, stand-, and site-level factors.

4.2. Methods

4.2.1. Study Area

The combined study area (44°56'-48°00' N, 64°28'-70°44' W) in Maine and New Brunswick mainly belongs to the temperate broadleaf mixed forest biome. The most common forest types in Maine include maple-beech-birch (*Acer-Fagus-Betula*) of 2.9 million ha and spruce-fir of 2.4 million ha in 2003 (McWilliams et al. 2005). Growing stock of SBW's major hosts of balsam fir, red spruce, black spruce, and white spruce was 117, 146, 14, and 17 million m^3, respectively, in 1982, and 65, 100, 15, and 17 million m^3, respectively, in 2003 (McWilliams et al. 2005). New Brunswick has 2.5, 1.8, and 1.4 million ha of softwood, mixedwood, and hardwood forests, respectively, in 2001 (Power and Gillis 2006). Growing stock of balsam fir and spruce was 118 and 154 million m^3, respectively, in 1981, and 91 and 174 million m^3, respectively, in 2001 (Bonnor 1982, Power and Gillis 2006).

Soils in Maine and New Brunswick are generally infertile, acidic, and low in permeability (Ferwerda et al. 1997; Rees et al. 2005). Maine has a humid continental climate with warm, humid summers, and cold, snowy winters. Annual precipitation varies from 909 to 1 441 mm and is distributed evenly year-round. Climate in New Brunswick is similar to that of Maine with annual precipitation ranging from 889 to 1 143 mm, evenly distributed through the year. Elevation of the study areas in Maine and New Brunswick ranged from 41-691 m and 0-578 m, respectively. These two areas have generally similar SBW outbreak histories and both experienced a relatively severe one in the 1970s-1980s.

4.2.2. Data

The data used in this study came from the University of Maine Cooperative Forestry Research Unit Growth Impact Study data collected in northern Maine, US (Solomon and Brann 1992) and Canadian Forest Service permanent sample plots data collected in New Brunswick, Canada (MacLean and Erdle 1986). There are two major differences between the two datasets:

1) Species composition. Balsam fir, red spruce, black spruce, white spruce, and hardwoods accounted for 36%, 24%, 2%, 3%, and 18% of all trees, respectively, in Maine, and 32%, 23%, 11%, 9%, and 14% of all trees, respectively, in New Brunswick at the offset of these data.

2) Stage of the SBW outbreak. The Maine data covered most of the temporal extent of the outbreak in the 1970s-1980s, while New Brunswick data were at the declining stage of this outbreak.

4.2.2.1. Growth Impact Study of Maine

The Growth Impact Study was initiated in 1975 (after SBW activity reached epidemic level in 1974) as a cooperative effort among federal and state forest agencies, as well as private forestry companies to document the impact of SBW on growth and mortality of the Maine forest. Data were collected at 424 ~ 0.02 ha circular plots including 8 762 trees ≥ 11.4 cm in diameter at breast height (DBH) throughout northern Maine during 1975-1985. The data included annual records of species, DBH, crown position, cause of death, total height, crown length, and degree of defoliation. Each year during the study period, current-year and previous-years foliage on each host tree within the plot were visually examined for the degree of defoliation, and categorized separately into one of five (before 1982; 0, 1-5%, 6-20%, 21-50%, and 51-100%) or eleven classes (after 1982; 0-10%, 11-20%, 21-30%, 31-40%, 41-50%, 51-60%, 61-70%, 71-80%, 81-90%, 91-99%, and 100%) of defoliation. In addition, aerial spraying of insecticide has been applied to a part of these plots during 1970-1974. More detailed descriptions of the data are provided in Chen et al. (2017a, 2017b).

4.2.2.2. Permanent Sample Plots of New Brunswick

Approximately 1 500 random PSPs were established between 1976-1979 as part of the New Brunswick Department of Forests, Mines, and Energy Forest Inventory. Of these plots, 136 were selected for SBW related studies based on stratification by species, maturity, and degree of insecticide use for protection. Each PSP consisted of three permanent prism points (basal area factor = 2 m^2 ha^{-1}) located 40 m apart where species, DBH, crown class, year of death, initial height, and degree of defoliation of each tree were recorded. The above data were collected during 1976-1993, with DBH initially measured between 1976 and 1979 and remeasured in 1980, 1983, 1985, 1988, and 1991. Current-year and total defoliation (defoliation on all age classes of foliage) were both measured annually during 1984-1993, while height was measured once during 1976-1979. For all of the 6 316 sample trees in the PSP data set, only the 5 503 trees compatible in size with the Growth Impact Study dataset (i.e. DBH $\geq$ 11.4 cm) were included in this study. Both current-year and total defoliation in the New Brunswick PSPs was estimated for each host tree each year by scanning the crowns with binoculars. The results of both types of defoliation were separately put into seven percentage classes of 0-10%, 11-20%, 21-40%, 41-60%, 61-80%, 81-99%, and 100%. Again, more detailed descriptions of the data are provided in Chen et al. (2017a, 2017b).

4.2.2.3. Data Compilation

Since SBW defoliation primarily affects current-year foliage (Irland et al. 1988), response variable of individual tree defoliation was taken as the midpoints of current-year defoliation observations, which averaged 28% and 22% in Maine and New Brunswick, respectively. Stand-level defoliation was calculated as the mean of individual tree defoliation of trees within a plot weighted by their volumes (Chen et al. 2017b), which averaged 19% and 16% in Maine and New Brunswick, respectively. The SBW host species analysed in this study were balsam fir as well as red, black, and white spruce. Since natural hybridization between red and black spruce may have caused identification problems during the data collection (Gordon 1976, Bobola et al. 1992), and the sample size of black spruce in Maine was relatively small, red and black spruce were combined into one species group in this study. Temporal development of individual tree defoliation (defoliation in future years) was analysed only for trees with more than two annual observations of defoliation to allow a little flexibility in model set-up. Also, because of the generally much shorter time series of defoliation observations in New Brunswick, this analysis for temporal development of defoliation was not applied.

As shown in Chen et al. (2017a, 2017b), a variety of tree-, stand-, and site-level characteristics derived from the data were evaluated for their potential effects on individual tree defoliation. These characteristics included the following: 1) SBW host species (balsam fir, red/black spruce, and white spruce); 2) host species composition represented by the abundance of each of these species in each plot; 3) proportion of non-host trees in each plot; 4) individual tree size attributes including DBH, height, crown ratio, and various transformations of these variables; and 5) measures of competition and tree social status such as basal area of larger trees and the ratio between height and mean height of trees in each plot. While some previous studies considered topography an important factor affecting SBW defoliation (e.g., Osawa et al. 1986, Bouchard and Auger 2014), preliminary analysis found no noticeable relationship between common topographic attributes (e.g. elevation, slope, aspect) and SBW defoliation in the data (Figure 4.1). Similarly, there was no clear relationship between insecticide spraying and SBW defoliation (Figure 4.1; Chen et al. 2017b). Consequently, these attributes were not included in our models. In addition, attributes of site potential productivity were also not considered since they were metrics derived from other stand and site characteristics. A summary of these attributes is presented in Supplemental Materials C.1.

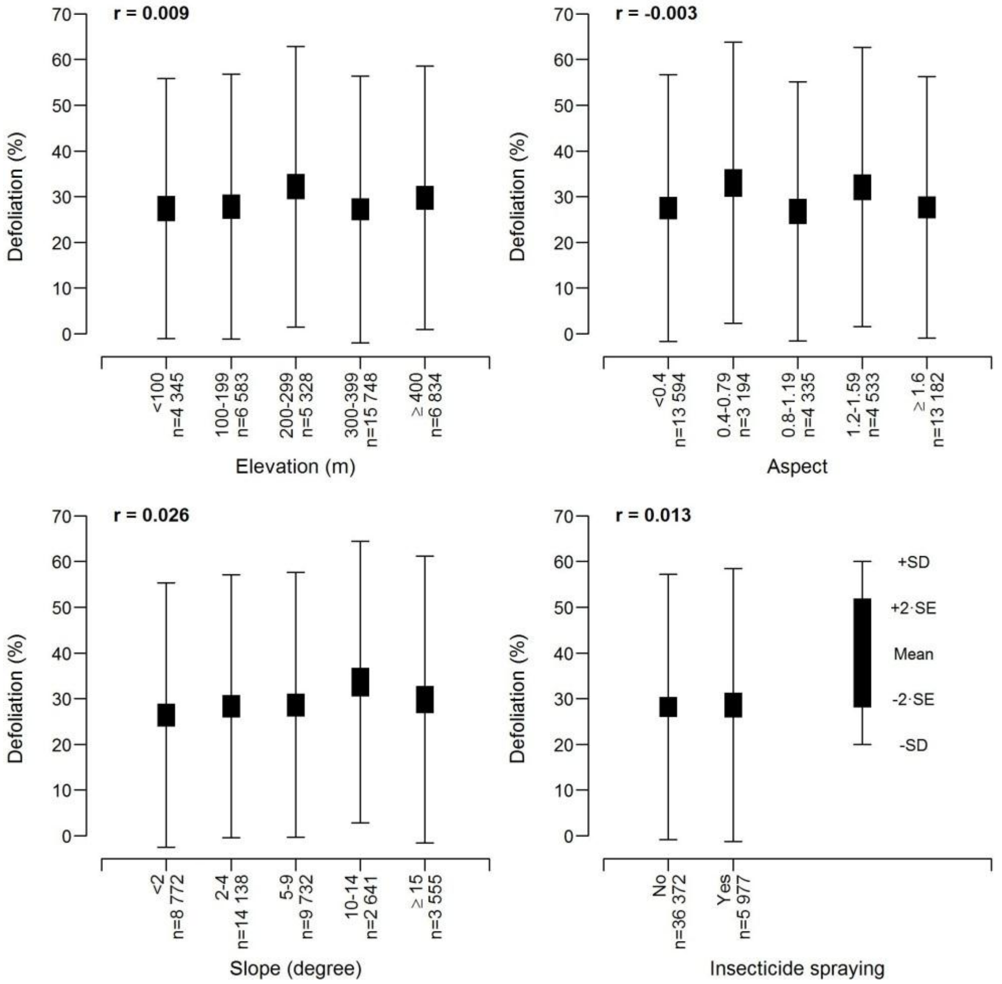

Figure 4.1. Relationships between individual tree defoliation and topographic as well as insecticide spraying attributes, where aspect is computed as cos(45º - aspect in degree) + 1, and r is the correlation coefficient.

4.2.3. Statistical Analysis

Individual tree defoliation and its temporal development were analysed using Bayesian models based on a Markov chain Monte Carlo (MCMC) technique. All of these analyses were conducted in R v3.2.2 (R Core Team 2015). Model selection (of suitable model formulations and explanatory variables) was based on a combined consideration of biological interpretability and

Akaike Information Criterion (AIC). The selected models are described in more detail below. Additionally, coefficient of determination (R^2; defined as 1 - residual sum of squares/total sum of squares) and mean bias (predicted - observed) were also calculated and reported.

4.2.3.1. Individual Tree Defoliation

Distributions of observed individual tree and stand-level defoliation showed a relatively close resemblance, and were both bounded and skewed (Figure 4.2). Therefore, a beta distribution, which is bounded and flexible in skewness, was a suitable option to summarize these data. Therefore, by assuming a multivariate normal prior distribution on β (parameter on the mean of individual tree defoliation; with mean μ and variance-covariance Σ) and a uniform prior distribution on ϕ (parameter on the precision of individual tree defoliation), the posterior distribution of these parameters, $\pi(\beta, \phi | y)$, was expressed as follows:

$$\pi(\beta, \phi|y) \propto Beta\,(a, b) \cdot N(\mu, \Sigma)$$

$$\propto \prod_i \frac{\Gamma(a_i + b_i) y_i^{a_i - 1} (1 - y_i)^{b_i - 1}}{\Gamma(a_i)\Gamma(b_i)} \cdot \frac{e^{-1/2(\beta-\mu)'\Sigma^{-1}(\beta-\mu)}}{\sqrt{|\Sigma|}} \qquad (1)$$

where $a_i = \beta X_i \cdot \phi$; $b_i = (1 - \beta X_i) \cdot \phi$; y is the response variable of individual tree defoliation (%) transformed to a proportion of (0, 1); and X are the covariates.

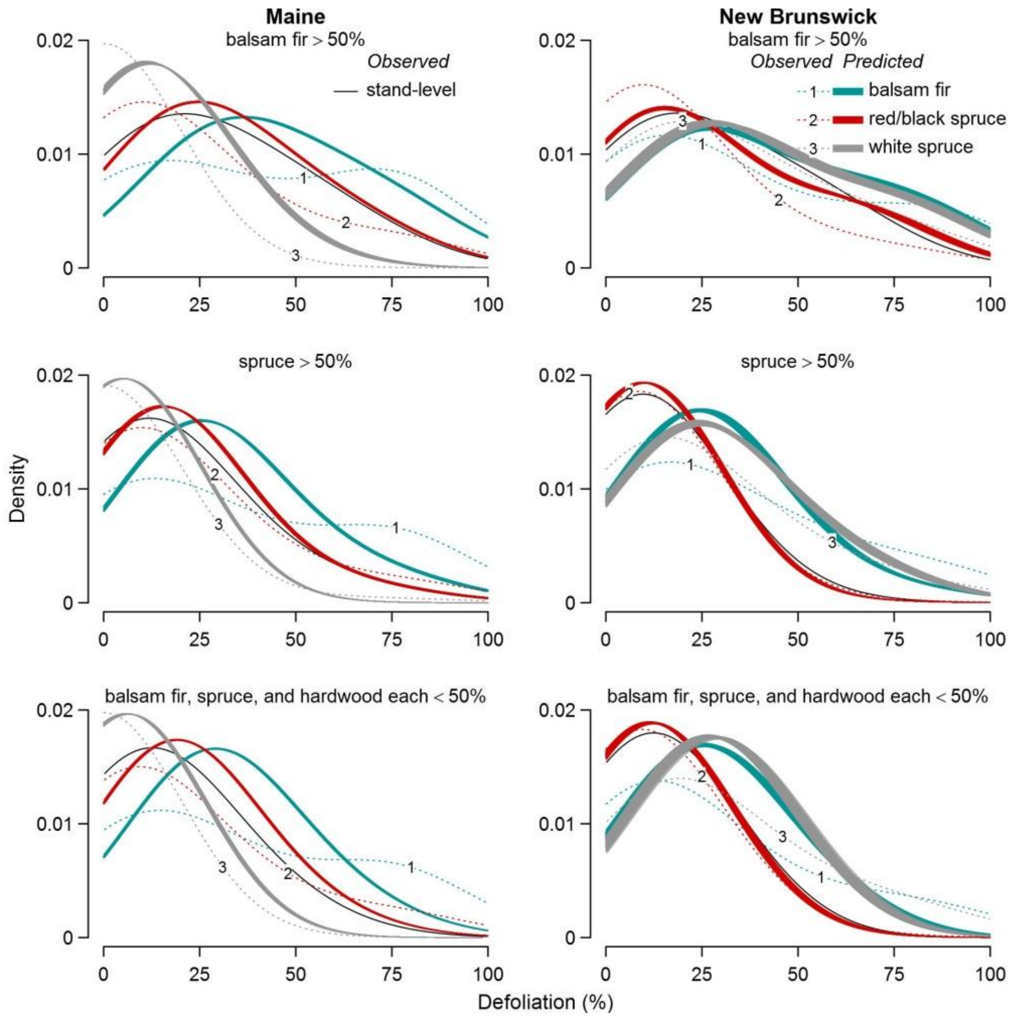

Figure 4.2. Distributions of observed individual tree and stand-level defoliation, as well as ranges of distributions of individual tree defoliation predictions by stand type and region.

The computation of the above posterior distribution was based on a MCMC technique, which allowed us to test different options of prior distributions, e.g., flat priors for both β and ϕ as well as the one selected for this analysis shown above, without being limited to special forms of prior distribution like conjugate priors that yield analytical forms of posteriors. Specifically, this computation was based on a random walk Metropolis-Hastings algorithm in the following form:

$$(\upbeta, \upphi)^{\mathrm{n}+1} = \begin{cases} (\upbeta, \upphi)^{\mathrm{n}} + \mathrm{Uniform}(-1,1) \cdot \mathrm{s} \\ \text{with probability} \min\left\{1, \dfrac{\uppi((\upbeta, \upphi)^{\mathrm{n}} + \mathrm{Uniform}(-1,1) \cdot \mathrm{s}|\mathrm{y})}{\uppi((\upbeta, \upphi)^{\mathrm{n}}|\mathrm{y})}\right\} \\ (\upbeta, \upphi)^{\mathrm{n}} \ \ \text{otherwise} \end{cases} \tag{2}$$

where $Uniform(-1,1) \cdot s$ is the random perturbation at iteration *n*, and *s* is a scale constant chosen to control the behavior of convergence (i.e., searching the support with a relatively small or large step size; set to be 1/100 - 1/10 of the starting values of different parameters).

Starting values of the above computation were randomly taken from the distributions of the parameter estimates of a linear model of the logit of the same response variable. A chain of 2 500 iterations of the simulation was used to generate posterior samples, and this procedure was repeated five times to verify the convergence of these chains, for each of the two study regions. The last 1 000 iterations in each of these five chains were pooled together to summarize *β* (Table 4.1).

Table 4.1. Model parameter estimates and 95% credible intervals for individual tree defoliation (Equation 3).

Parameter	**Mean (95% credible interval)**	
	Maine	**New Brunswick**
β_1 (Intercept)	-2.2831 (-2.3048, -2.2570)	-2.7603 (-2.8270, -2.7006)
β_2 (Balsam fir · DEF_P)	0.6888 (0.6777, 0.7019)	0.8592 (0.8044, 0.9114)
β_2 (DEF_P)	0.0512 (0.0505, 0.0518)	0.0586 (0.0573, 0.0598)
β_2 (White spruce · DEF_P)	-1.2676 (-1.4087, -1.2115)	0.6858 (0.6187, 0.7590)
β_3 (ABD_{BF})	-0.0080 (-0.0087, -0.0076)	-0.0035 (-0.0040, -0.0030)
β_3 (ABD_{RS})	-0.0043 (-0.0049, -0.0038)	-0.0009 (-0.0014, -0.0006)
β_3 (ABD_{WS})	-0.0048 (-0.0058, -0.0040)	-0.0029 (-0.0036, -0.0023)
β_4 (BA_{HW}/BA)	0.7845 (0.7219, 0.8403)	0.2337 (0.0882, 0.3542)

DEF_P is stand-level defoliation (%); *ABD* is species abundance in a plot; *BF, RS, and WS* are balsam fir, red/black spruce, and white spruce, respectively; *BA* and BA_{HW} are basal area and that of non-host (mainly hardwood) trees in a plot (m^2 ha^{-1}), respectively.

When AIC of models with various covariates *X* was compared, it indicated that SBW host species (*SPP*; an indicator variable; including balsam fir, red/black spruce, and white spruce) was the single most important predictor of individual tree defoliation for a given level of stand defoliation (DEF_P; %), while all the other examined tree-, stand-, and site-level characteristics did not have as much influence individually or even in combination (Table 4.2). Consequently, βX took the following form:

$$\beta X = \beta_1 + \beta_2 \cdot DEF_P \cdot SPP + \beta_3 \cdot ABD + \beta_4 \cdot BA_{HW}/BA \qquad (3)$$

where *ABD* is a metric reflecting both relative and absolute abundance of SBW host species at a location calculated as $(z_i - \overline{z}) \cdot \overline{z}$, in which z_i is the number of non-host or host species *i*, and $\overline{z}$ is the mean of z_i; *BA* and BA_{HW} are total basal area (m^2 ha^{-1}) and that of non-host (mainly hardwood) trees in a plot (m^2 ha^{-1}), respectively. BA_{HW}/BA worked as a limiting factor of stand-level defoliation (i.e., stand-level defoliation cannot exceed 100% - non-host%).

Table 4.2. Akaike Information Criterion (AIC) and changes in AIC (ΔAIC) in model selection for individual tree defoliation (Equation [3]) and its temporal development (Equation 4).

Model	**AIC**	**ΔAIC**	**AIC**	**ΔAIC**
Equation (3)	*Maine (n = 42 349)*		*New Brunswick (n = 5 519)*	
Null	14904	--	241	--
DEF_P	-10614	-25518	-4151	-4392
DEF_P, SPP	-18711	-8097	-4868	-717
DEF_P, SPP, ABD	-22180	-3469	-5396	-528
DEF_P, SPP, ABD, BA_{HW}/BA	-22634	-454	-5411	-15
DEF_P, SPP, ABD, BA_{HW}/BA, DBH, HT, HT/MHT_{SW}, BAL, CR*	-23181	-547	-5428	-17
Equation (4)	*Balsam fir (n = 21 368)*		*Red/black spruce (n = 17 547)*	
t	9587	--	-1643	--
t, DEF_I, CR	9299	-288	-2047	-404
t, DEF_I, CR, ABD, BA_{HW}/BA, DBH, HT/MHT_{SW}, BAL	9178	-121	-1927	+120

* For New Brunswick, HT and MHT_{SW} were initial values measured at the beginning of the study, and CR was not available.

DEF_P is stand-level defoliation (%); DEF_I is initial (first year) defoliation (%); SPP is species (balsam fir, red/black spruce, and white spruce); BA and BA_{HW} are basal area and that of non-host (mainly hardwood) trees at a location (m^2 ha^{-1}), respectively; ABD is species abundance at a location; DBH is diameter at breast height (cm); HT is height (m); MHT_{SW} is mean height of softwood trees at a location (m); BAL is basal area of trees larger than the subject tree in DBH at a location (m^2 ha^{-1}); CR is crown ratio; and t is time (year).

4.2.3.2. Temporal Development of Individual Tree Defoliation

A two-step approach was used to model the temporal development of balsam fir and red/black spruce individual tree defoliation in Maine (white spruce was not modeled due to insufficient observations of defoliation over time). First, a combination of a function similar to that proposed by Ratkowsky et al. (1983) and a Ricker function was used to model the hump-shaped temporal trends exhibited in individual tree defoliation y (Figure 4.3). The Ricker function has been considered efficient in depicting density-dependent population growth such as in the case of SBW (Bolker 2008), while the former function supplemented it to capture the sudden collapse of SBW population hence defoliation that has been observed (Irland et al. 1988).

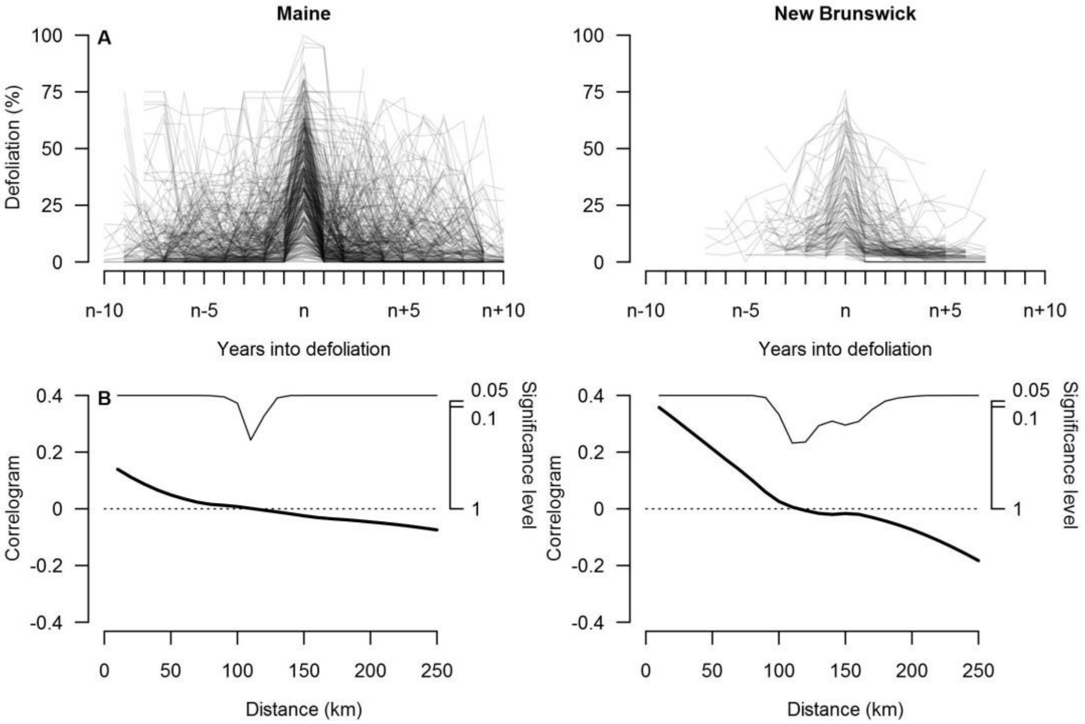

Figure 4.3. A) Temporal development of stand-level defoliation, by region, where each line represents one sample plot and n is the year that defoliation peaked at this plot; B) Spatial autocorrelations and their significance levels of stand-level defoliation, which turns negative at distances over 120 km in both regions.

Initial (first year) defoliation (DEF_I; % transformed to a proportion of (0, 1)) and crown ratio (CR) were found to have greater influence on the temporal development of individual tree defoliation, while it appeared to be invariant to a variety of tree-, stand-, and site-level factors (Table 4.2). Consequently, this temporal development was modeled as follows:

$$y = t \cdot \left(1 - e^{\gamma_1 \cdot (t - \gamma_2)}\right) + \gamma_3 \cdot t \cdot e^{(\gamma_4 \cdot DEF_I + \gamma_5 \cdot CR) \cdot t} + \varepsilon \qquad (4)$$

where t is time (year); and ε is the error. Parameters γ_1 - γ_5 were estimated for each of the two species (group) using the same Bayesian model and settings described in the previous section, except that starting values of the computation were randomly taken from the distributions of the parameter estimates of a nonlinear least squares model for the same response variable. Second, 2 847 and 2 070 time series errors ε of balsam fir and red/black spruce, respectively, from Equation (4) were each fitted with a single autoregressive moving average (ARMA) model. Selection of these two ARMA models was based on maximum likelihood and by comparing various candidate models' theoretical autocorrelations and partial autocorrelations to the observed ones. Consequently, a first order ARMA model in the following form was applied to each of the species (group):

$$\varepsilon_t = \delta + \omega_t + \varphi \cdot (\varepsilon_{t-1} - \delta) + \theta \cdot \omega_{t-1} \tag{5}$$

where $\omega_t = \varepsilon_t - \hat{\varepsilon}_t$. Parameters δ (mean of ε), φ, and ϑ were estimated using the same Bayesian model and settings described in the previous section, except that uniform priors were assigned to these parameters, and starting values of the computation were taken from the parameter estimates of a linear least squares model for the same response variable.

4.3. Results

4.3.1. Individual Tree Defoliation

A total of 21 987, 18 422, and 1 940 observations of balsam fir, red/black spruce, and white spruce, respectively, from Maine, and 2 336, 2 523, and 660 observations, respectively, from New Brunswick were available in the analysis of individual tree defoliation. Our models had R^2 of 0.78 and 0.80 and mean biases (predicted - observed) of +1.32% and +1.48% for Maine and New Brunswick, respectively. All parameter involved in these models converged distinctively and significantly from zero, and were consistent in their direction and magnitude, except individual tree defoliation of white spruce relative to that of red/black spruce was in opposite directions between the two regions (Table 4.1).

For a given stand-level defoliation, individual tree defoliation was predominantly influenced by species (Table 4.2). Specifically, at 25% stand-level defoliation (with all the other covariates at their means), individual tree defoliation of balsam fir, red/black spruce, and white spruce were predicted to be 42%, 26%, and 9%, respectively, in Maine, and 41%, 22%, and 37%, respectively, in New Brunswick. The orders of individual tree defoliation of the species indicated above (i.e., balsam fir > red/black spruce > white spruce in Maine and balsam fir > white spruce > red/black spruce in New Brunswick) remain the same over the complete range of stand-level defoliation (Figure 4.4).

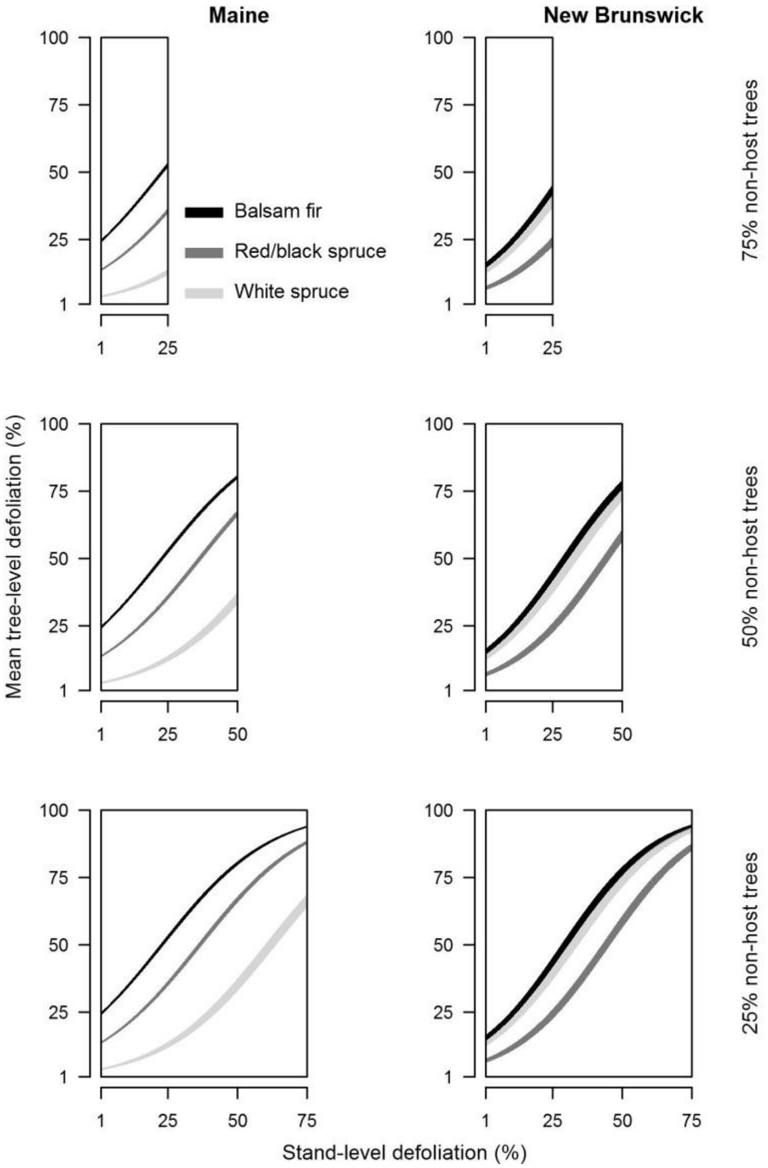

Figure 4.4. Predicted individual tree defoliation (%) with 95% credible intervals as a function of stand-level defoliation (%; with all the other covariates at their means) by percentages of non-host trees in a location and region.

Additionally, host abundance had a secondary role in individual tree defoliation such that it was lower in pure stands than in mixed stands. Specifically, a 10% increase in the numbers of balsam fir, red/black spruce, and white spruce from their means at a location would reduce their defoliation by 0.71%, 0.24%, and 0.01%, respectively, in Maine, and by 0.64%, 0.08%, and 0.14%, respectively, in New Brunswick (with all the other covariates at their means). Meanwhile, a variety of other common tree-, stand-, and site-level characteristics tested in this study were found to have negligible effects on individual tree defoliation (Figure 4.1, Table 4.2). Observed correlations between these characteristics and individual tree defoliation also confirmed this finding (Figure 4.1, Supplemental Materials C.2).

4.3.2. Temporal Development of Individual Tree Defoliation

A total of 2 847 and 2 070 time series with more than two annual observations of balsam fir and red/black spruce defoliation, respectively, were available for this analysis. The models for the temporal trends in defoliation alone had R^2 of 0.59 and 0.44 and mean biases (predicted - observed) of +1.97% and -0.30% for balsam fir and red/black spruce, respectively. When combined with the ARMA models, R^2 was 0.63 and 0.53 and mean biases (predicted - observed) were +0.63% and +0.24% for balsam fir and red/black spruce, respectively. All parameter estimates converged distinctively and significantly from zero (Table 4.3).

Table 4.3. Model parameter estimates and 95% credible intervals for the temporal development of individual tree defoliation by species.

Parameter	**Mean (95% credible interval)**	
	Balsam fir	**Red/black spruce**
	Equation [4]	
γ_1	-0.018 (-0.017, -0.018)	-0.004 (-0.004, -0.005)
γ_2	11.96 (11.86, 12.06)	18.16 (17.74, 18.56)
γ_3	-0.044 (-0.046, -0.042)	-0.022 (-0.025, -0.020)
γ_4	-0.001 (-0.001, -0.001)	-0.004 (-0.004, -0.003)
γ_5	-0.297 (-0.316, -0.273)	-0.087 (-0.102, -0.076)
	Equation [5]	
δ	-0.072 (-0.113, -0.051)	-0.877 (-1.378, -0.482)
θ_1	0.295 (0.281, 0.315)	0.564 (0.542, 0.583)
θ_2	0.018 (0.007, 0.025)	-0.150 (-0.166, -0.127)

A large amount of variation existed in the temporal development of individual tree defoliation (Figure 4.3), and it appeared to be invariant to the common tree-, stand-, and site-level characteristics in that defoliation developed through similar trajectories regardless of these characteristics and initial defoliation (SBW population). Specifically, individual- tree defoliation reached peak levels of approximately 40% and 25% for balsam fir and red/black spruce, respectively, and subsequently declined to zero in 12-13 years and 18-19 years for balsam fir and red/black spruce, respectively. In addition, crown ratio was found to be most influential among the aforementioned characteristics, even though greater crown ratio only led to a slightly longer duration and higher levels of defoliation (Figure 4.5).

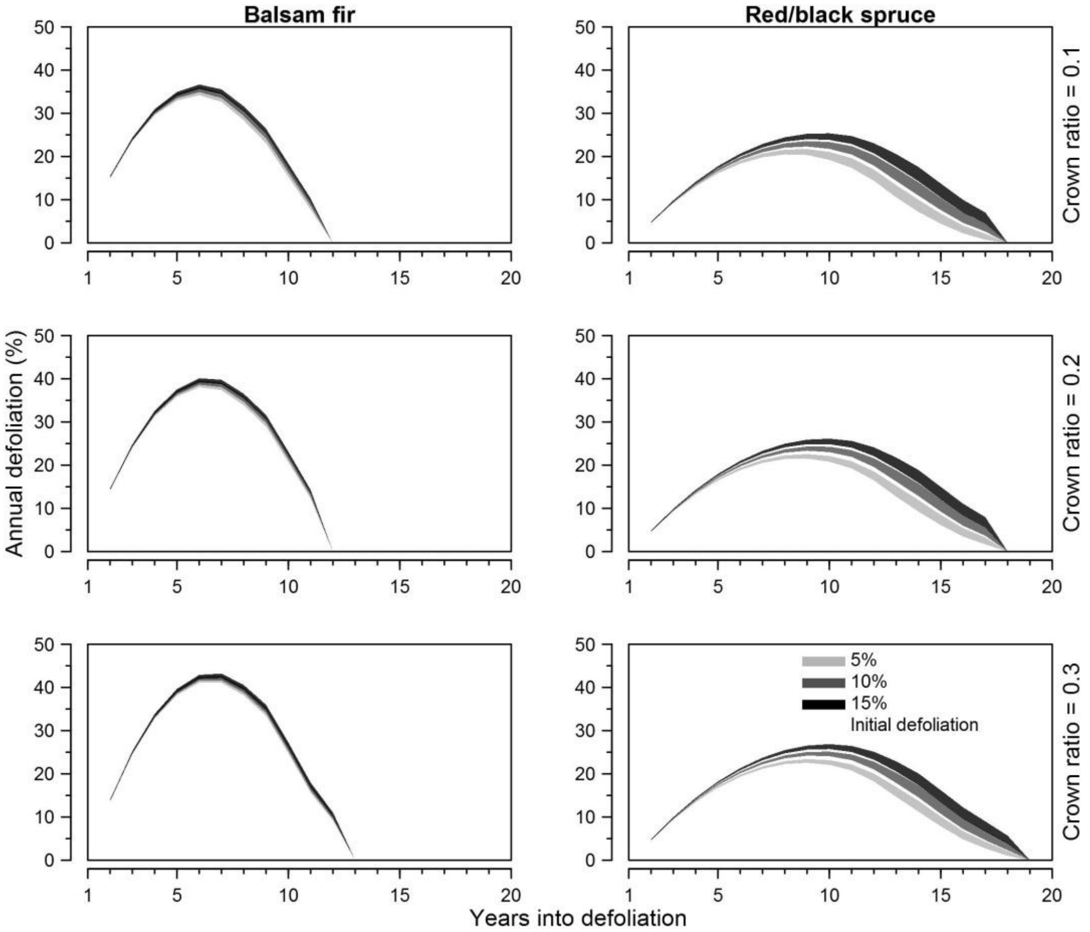

Figure 4.5. Temporal development of individual tree defoliation (%) with 95% credible intervals as a function of time (year) at three levels of initial (first year) defoliation (%) by species and crown ratio.

4.4. Discussion

Despite the variation in SBW defoliation being previously discussed from an implicit entomological perspective of SBW population dynamics (e.g., birth and death, immigration and emigration, and SBW and host relationship; Greenbank 1963a, Royama 1984, Nealis and Régnière 2004) as well as a forest ecology perspective on specific tree and stand characteristics (e.g., species, pure vs. mixed stands, hardwood contents in stands, and stand age; Greenbank 1963b, Seymour 1980, Alfaro et al. 2001, Colford-Gilks et al. 2012), there was a lack of systematic and quantitative evaluations of trees' susceptibility to SBW defoliation. One exemption is Hennigar et al. (2008) who quantified defoliation of each spruce species relative to observed mean defoliation of balsam fir in the same stand. In comparison, our study has significantly advanced our current understanding in trees' susceptibility to SBW defoliation in several aspects.

First, the above literature in forestry has primarily focused on the variation in SBW defoliation at stand-level. Consequently, comparisons of this variation among species were based on aggregations of trees of various species, while whether this variation was also due to differences among trees (e.g., DBH, height, crown ratio, crown position), degree of tree-level competition, and/or their locations (hence site characteristics like elevation, aspect, and slope) were largely left unresolved. In contrast, our study has performed a rather comprehensive evaluation of the effects of a variety of tree-, stand-, and site-level characteristics on the variation and temporal dynamics in SBW defoliation, which were found to be predominantly dependent on species, while all the other examined tree-, stand-, and site-level characteristics had more limited influences individually or even in combination (Table 4.2), which has important implications for future analyses on the topic.

In addition, the current literature has generally relied on on-site measurements of defoliation to evaluate the variation in SBW defoliation. For example, Hennigar et al. (2008) used mean defoliation of balsam fir as a predictor of the defoliation of spruce species in the same stand. On-site measurements of defoliation, even for only one species (e.g., balsam fir as mentioned above), could be costly and time-consuming, which may consequently hinder the application of the findings to predict defoliation. In comparison, our study has developed an approach to predict individual tree defoliation using stand-level measurements of defoliation, which can potentially be obtained through remote sensing (e.g., aerial or satellite imagery; Rahimzadeh-

Bajgiran et al. 2018). This approach could open up an opportunity of more timely and efficient monitoring of the frequently shifting SBW defoliation over large areas during outbreaks.

Finally, limited data in previous studies may have restricted their general applicability. For example, Nealis and Régnière (2004) was based on data from one balsam fir-spruce-trembling aspen (*Populus tremuloides* Michx.) mixed stand; Hennigar et al. (2008) only considered stands where red, black, and white spruce, as well as balsam fir were all present; and Colford-Gilks et al. (2012) was limited to balsam fir and spruce mixedwood stands. To our knowledge, much of the previous literature on this topic has relied on data from eastern Canada. Contrarily, our data comprised a wide range of forest conditions and types including Maine, and likely better represent the general variation in SBW defoliation, which affects broad areas and forest types in North America. As a result, our data helped to show that SBW defoliation was lower in pure than mixed stands of the host species (i.e., red, black, and white spruce, as well as balsam fir), which indicates that monoculture of any of the host species likely results in less SBW defoliation of this species than in mixed stands with other host species.

The relationship between individual tree defoliation of various host species and stand-level defoliation was nonlinear (Figure 4.4), which indicates that these species' susceptibility varied with SBW defoliation pressure (SBW population). However, the orders of these species' susceptibility remained unchanged, but differed between the two regions. Specifically, this order of susceptibility was balsam fir > white spruce > red/black spruce in New Brunswick, which matched that reported by Hennigar et al. (2008) who used data from the same source from New Brunswick as our analysis. In Maine, this order was slightly different and indicated that balsam fir > red/black spruce > white spruce, which agreed with some professional opinions gathered in Irland et al. (1988) such that white spruce was less susceptible to SBW defoliation than red spruce. Balsam fir was found to be more susceptible than red/black spruce in both regions, where both species (group) were abundant in regard to their distributions in space and in the range of defoliation pressure. Consequently, their order in susceptibility found in this analysis was likely representative. Contrarily, white spruce was much less common, and its gradients of distribution in our data such that more observations were obtained from areas of higher defoliation pressure in New Brunswick (i.e. its north) and areas of lower defoliation pressure in Maine (i.e. its southeast), likely played a role in the regional discrepancy in its susceptibility (Supplemental Materials C.1). As a result, the predicted defoliation of white spruce was more likely a function of extrapolation of these unbalanced samples, which resulted in overestimation and underestimation of its susceptibility in New Brunswick and Maine, respectively. Although the results clearly indicated that white spruce is less susceptible than balsam fir, its susceptibility relative to red/black spruce needs to be more thoroughly investigated using more comprehensive and balanced data.

In general, it has been considered that insect pest populations are lower in diversified forest stands. For example, Jactel et al. (2005) reviewed 54 studies on the response of insect damage or abundance to pure vs. mixed forest stand, and found this damage or abundance was significantly greater in pure forest stands. However, they also noted that stands infested by polyphagous insects were exceptions to their findings. Similarly, Vehvilainen et al. (2007), which applied a meta-analysis to seven long-term forest diversity experiments, also concluded that whether forest diversity increased or reduced insect herbivore abundance was largely species specific. SBW preferably feeds on the buds of a range of coniferous trees (mainly the species presented in this study). Since these host species' buds break at different times, which are 10-14 days later for red/black spruce than for balsam fir and white spruce (Greenbank 1963b, Irland et al. 1988), such differences in phenology likely lead to the provision of alternative sources of preferred food to SBW for an extended period in mixed-species stands, and consequently result in increases in SBW population (i.e., more survival of SBW) and defoliation of its hosts. Our preliminary analysis also indicated that individual tree defoliation was negatively correlated with the proportion of hardwood in plots, which has long been observed (Mott 1963, Baskerville 1975). However, the effects of hardwood in reducing defoliation as well as in increasing the variation in defoliation were both at a minimal magnitude, which may be related to the generally low hardwood contents in our plots.

Despite the high variation observed in the temporal development of defoliation (Figure 4.3), a relatively large amount of this variation was explained by our models. More importantly, our models showed comparable trajectories of the temporal development of defoliation between SBW's major hosts of balsam fir and red/black spruce in addition to their distinctive differences in magnitude. Specifically, defoliation of both species seemed to have developed towards their respective converged trajectories, despite differences in initial defoliation, stand and site conditions, and geographical locations, which resembled the movement towards an equilibrium of SBW defoliation during its epidemic (Pureswaran et al. 2016). In addition, there tended to be sudden surges in defoliation over time in our data (Figure 4.3), which was short-lived (mostly one year) and occurred at various times at different locations. It was difficult for our models to capture these sudden surges, which appeared to be stochastic oscillations towards equilibria and unlikely to be explained by the birth and death process in SBW population dynamics without resorting to immigration and emigration. While Royama (1984) suggested a synchrony between SBW populations during an outbreak, it was not observed in this study, especially considering that spatial autocorrelation in defoliation were actually negative at distances over 120 km in both Maine and New Brunswick (Figure 4.3). Therefore, SBW populations are likely synchronized over large spatio-temporal scales, while oscillating significantly at small scales. Our results also indicated that an outbreak would likely last much longer (~ 15 years) than the 10-year observation period currently available in our data.

Considering our sample size, the Bayesian models developed in this study generated parameter estimates very close to those from frequentist methods as expected. However, two valuable advantages of these Bayesian models remained. First, our observations of a wide range of SBW defoliation were concentrated in relatively low levels that have been largely overlooked in previous studies as outlined by Chen et al. (2017b). Therefore, the posterior distribution of individual tree defoliation generated in this study would likely improve our existing knowledge either as input to similar studies or when combined with additional data. Second, MCMC simulations were conveniently applied in our Bayesian models, and helped prevent potentially misleading estimations in an obvious multi-modal situation (Equation 4), which is fairly common in nonlinear modeling and often challenging for frequentist methods to adequately handle.

A variety of factors showed comparable effects on individual tree defoliation between Maine and New Brunswick despite their differences in sampling procedure, past defoliation and management histories, and forest composition. This likely indicates the overall validity of this variety of factors' effects on individual tree defoliation found in our analysis over a rather wide range of forest and defoliation conditions. Nevertheless, inconsistency in sampling procedures may hinder the utilization of data from various sources such as the gradients in our samples may have caused regional discrepancy in white spruce' susceptibility. Future studies of SBW defoliation will benefit from more balanced and comprehensive samples over space and the range of defoliation, not only in terms of species composition, but other relevant factors like management history and stand structure. Overall, the results of this analysis highlight the distinctive spatial and temporal patterns present in regional SBW defoliation data as well as provide a flexible modeling framework for extension to other forms of defoliation.

CHAPTER 5

REFINING THE FOREST VEGETATION SIMULATOR FOR PROJECTING THE EFFECTS OF SPRUCE BUDWORM DEFOLIATION IN THE ACADIAN REGION OF NORTH AMERICA[1]

5.1. Introduction

The Forest Vegetation Simulator (FVS) is a distance-independent, individual-tree forest growth model widely used in the United States and parts of Canada by government agencies, industry, educational institutions, and private landowners to support forest management decision making (Dixon 2002). FVS was developed to predict stand dynamics and development in response to various management alternatives and disturbance-causing agents. Specifically, FVS has incorporated the effects of a number of insect and pathogen agents including root diseases (*Heterobasidion annosum* (Fr.) Bref., *Armillaria ostoyae* (Romag.) Herink, and *Phellinus weirii* (Murrill) R. L. Gilbertson), white pine blister rust (*Cronartium ribicola* Fisch.), bark beetles (*Dendroctonus* spp.), and Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) on forest stand dynamics through its more than a dozen extensions (Crookston and Dixon 2005). Spruce budworm (SBW; *Choristoneura fumiferana* (Clem.)) is the most influential insect disturbance agent in the spruce-fir (*Picea-Abies*) forests in North America. Periodic SBW outbreaks of every 30-60 years have occurred for hundreds of years and caused tens of millions m^3 of tree mortality in both the 1910s and 1970s-1980s outbreaks in Maine alone (Royama 1984, Irland et al. 1988, Fraver et al. 2007). Since SBW outbreaks result in great uncertainty in future wood supply and forest conditions in this region, it is important for forest growth models to account for the potential effects of SBW defoliation on forest development and provide information for forest management and protection planning. Although FVS is widely used in

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[1] This chapter previously appeared as an article as follows: Chen, C., Weiskittel, A., Bataineh, M., and MacLean, D.A. 2018. Refining the Forest Vegetation Simulator for projecting the effects of spruce budworm defoliation in the Acadian Region of North America. Forestry Chronicle 94: 240-253.

eastern North America, it currently does not have an extension with the capacity to account for effects of SBW defoliation.

An exception is the work by Hennigar et al. (2011, 2013a), who developed multipliers that simulate the effects of SBW defoliation on tree growth and survival that can be used in FVS through its keywords (Dixon 2002). These multipliers were converted from parameters used in STAMAN, a stand growth model used in the Spruce Budworm Decision Support System from Canada (SBW-DSS; Vanguard Forest Management Services Ltd. 1993, MacLean 1996, MacLean et al. 2001). However, it is potentially problematic to use the STAMAN modifiers in FVS for two reasons: 1) STAMAN applies annual defoliation levels predetermined for five-year periods for each species within simulated plots (MacLean et al 2001, Hennigar et al. 2013b), which cannot represent highly variable SBW defoliation at the tree level within plots over time (Baskerville and MacLean 1979; Chen et al. In press) and 2) STAMAN modifiers were calibrated using historically severe defoliation data from New Brunswick, Canada (MacLean et al. 2001), which differed significantly with the relatively low-level defoliation patterns observed in Maine during the last outbreak in the 1970s-1980s (Chen et al. 2017a). Since the STAMAN modifiers were customized for use in FVS and outside their original geographical range (Hennigar et al. 2013a), SBW modifiers specifically designed for FVS may potentially be superior.

The Acadian variant of FVS (FVS-ACD; Weiskittel et al. 2017) is one of the latest developments among the geographically specific variants of FVS. It offers flexibility of accounting for the specific effects of management activities and disturbance agents on individual trees at an annual resolution, and represents forests in the Acadian region where SBW is endemic (Weiskittel et al. 2017). The inputs required to run FVS-ACD are typical for tree-level growth models and include species, diameter at breast height (DBH), height and crown ratio of each tree (if available), an expansion factor to estimate per unit area (e.g., ha) values of individual tree attributes (e.g., basal area and volume), a threshold DBH of ingrowth, and climate site index (Weiskittel et al. 2017) of each stand. Projections of stand development by FVS-ACD are based on predictions of changes in the dimensions of each tree from each stand, as well as mortality, ingrowth, and their interactions. The specific variables representing these dimensions are DBH, height, and height to crown base (hence crown ratio), of which the increments are predicted recursively at each time step (every year in this study) based on their updated current states, as well as metrics of competition (arithmetically aggregated from the updated dimensions of living trees) and potential productivity (represented by climate site index; held constant from its initial inputs). Meanwhile, individual tree mortality is predicted by the same categories of variables above, while ingrowth is predicted at the stand level by metrics of competition, species composition, and potential productivity (Li et al. 2011). Consequently, interactions among growth, mortality, and ingrowth are reflected in the updated list of trees and their dimensions at each annual time step.

For this analysis, we propose annualized modifiers that adjust annual predictions of each of the components (DBH, height, and height to crown base increments, as well as mortality and ingrowth) of FVS-ACD to account for effects of SBW defoliation. In this case, a modifier with the value zero indicates a complete cessation in the change of a component, while a value of one shows nonexistence of an effect of SBW defoliation. Similarly, a value greater than one represents a magnifying effect of SBW defoliation (e.g., tree mortality). Chen et al. (2017a, 2017b) found that even low levels of SBW defoliation had significant effects on the above components of FVS-ACD, which were primarily dependent on species and less affected by common stand and site factors. Considering FVS-ACD already has a rather comprehensive evaluation of stand and site factors in its component equations, our proposed modifiers were formulated as functions of only defoliation and species. However, additional covariates significantly reduced errors in predicted mortality and height to crown base, and were included in modifiers for these two components of FVS-ACD.

SBW defoliation primarily affects current-year foliage and has cumulative effects on tree growth and mortality (Blais 1958, MacLean 1980, Irland et al. 1988). Therefore, cumulative sums of the defoliation of current-year foliage (cumulative defoliation) were used as the metric of defoliation in our modifiers. Cumulative defoliation was predicted for each tree in each year of a predicted defoliation duration using an equation developed by Chen et al. (In press; described in detail below), who found SBW defoliation tends to converge to similar temporal trajectories for each species despite considerable differences in tree, stand, and site factors. When this duration of predicted defoliation of a tree is over, values of our modifiers will automatically be reduced to one (i.e., defoliation no longer have effects on growth and mortality). In addition, cumulative defoliation can also be set to a series of predetermined values over an assumed period to reflect potential defoliation scenarios like that in Hennigar et al. (2013a), although it is unlikely that defoliation would repeat such a fixed temporal pattern over the range of conditions of Acadian forests (e.g., Zhao et al. 2014), which are also undergoing constant changes. A parametric model like the one proposed by Chen et al. (In press) is flexible enough to be recalibrated to reflect these changing forest conditions and defoliation dynamics with future available data.

Parameter estimations in the proposed modifiers were supported by individual tree defoliation data collected at annual intervals from an extensive network of 375 permanent sample plots that covered > 40 000 km^2 and 10 years of the last outbreak in the 1970s-1980s in Maine. These data comprised a wide range of forest conditions and cumulative defoliation observations, especially at relatively low levels (< 300%) compared to severe defoliation observations from Canada (Chen et al. 2017a). Consequently, these data provided an opportunity to evaluate whether modifiers calibrated using severe defoliation data from Canada (Erdle and MacLean

1999, Hennigar et al. 2011, 2013a) sufficiently represent forest responses to SBW defoliation across the Acadian region, and whether our proposed modifiers significantly improved the ability of FVS-ACD to account for effects of SBW defoliation. This evaluation was performed by applying both types of modifiers to the above data from Maine and data collected in New Brunswick during the same SBW outbreak.

Our specific objectives for this study were to 1) develop annualized modifiers for the components (DBH, height, and height to crown base increments, as well as mortality and ingrowth) of FVS-ACD to account for effects of SBW defoliation; 2) evaluate the performance of FVS-ACD refined by these modifiers and by those from STAMAN against observed forest development in Maine and New Brunswick during the last SBW outbreak; and 3) conduct long-term simulations across contrasting stand types in terms of percentage of susceptible trees (balsam fir (*Abies balsamea* L.), red spruce (*Picea rubens* Sarg.), black spruce (*Picea mariana* (Mill.) B.S.P.), and white spruce (*Picea glauca* (Moench) Voss)), initial volume, and peak defoliation of stands using this refined version of FVS-ACD. It was expected that differences in peak defoliation would have negligible influence on stand development as Chen et al. (In press) found SBW defoliation tends to converge to similar temporal trajectories for each species (differences in cumulative defoliation of trees reduces significantly as years of defoliation increases).

5.2. Material and Methods

5.2.1. Study Area

The combined study area (44°56'-48°00' N, 64°28'-70°44' W) in Maine and New Brunswick is in a transition zone from the temperate hardwood forest to the boreal softwood forest, and is primarily composed of spruce-fir forests. Soils in Maine and New Brunswick are generally infertile, acidic, and low in permeability (Ferwerda et al. 1997, Rees et al. 2005). Maine has a humid continental climate with warm, humid summers, and cold, snowy winters. Annual precipitation varies from 909 to 1 441 mm and is distributed evenly year-round. Climate in New Brunswick is similar to that of Maine with annual precipitation ranging from 889 to 1 143 mm, evenly distributed through the year. Elevation of the study areas in Maine and New Brunswick ranged from 41-691 m and 0-578 m, respectively. Periodic SBW outbreaks every 30-60 years have occurred for hundreds of years in this area (Fraver et al. 2007), while the last outbreak was mostly in the 1970s-1980s.

5.2.2. Data

The modifiers were developed on data collected in Maine, United States by the University of Maine Cooperative Forestry Research Unit Growth Impact Study (Solomon and Brann 1992), while the evaluation of these modifiers was performed using the above data and Canadian Forest Service permanent sample plots (PSP) data collected in New Brunswick, Canada (MacLean and Erdle 1986, Erdle and MacLean 1999). There are two major differences between the two datasets: 1) species composition, with balsam fir, red spruce, black spruce, white spruce, and hardwoods accounting for 36, 24, 2, 3, and 18 percent of all trees, respectively, in Maine, versus 32, 23, 11, 9, and 14 percent of all trees, respectively, in New Brunswick at the beginning of these data and 2) stage of the SBW outbreak, with the Maine data covering most of the temporal extent of the outbreak, while New Brunswick data were at the declining stage of the outbreak. Each of the two datasets is summarized in Table 5.1 and described in detail below.

Table 5.1. List of species and their number, mean diameter at breast height (DBH; cm), and mean height (m) in 1975 in Maine and in 1985 in New Brunswick, as well as mean annual defoliation (%) and its distribution of the susceptible species (balsam fir, as well as red, black, and white spruce) in 1975-1985 in Maine and in 1985-1991 in New Brunswick.

	Maine							**New Brunswick**					
Species	**Number**	**DBH (cm)**	**Height (m)**	**Annual defoliation (%)***				**Number**	**DBH (cm)**	**Annual defoliation (%)***			
				Mean	*Number of observations*					*Mean*	*Number of observations*		
					< 10	*10-30*	*> 30*				*< 10*	*10-30*	*> 30*
American beech	105	20	14.5	--	--	--	--	16	20	--	--	--	--
Aspen	151	22	19.0	--	--	--	--	5	25	--	--	--	--
Balsam fir	2 645	17	14.7	37	3 480	4 992	12 936	1 190	19	26	3 852	2 433	2 045
Black spruce	163	17	13.1	13	1 092	419	311	467	19	8	2 521	712	36
Eastern hemlock	209	22	13.6	--	--	--	--	25	34	--	--	--	--
Paper birch	241	20	16.3	--	--	--	--	109	23	--	--	--	--
Red maple	436	19	15.7	--	--	--	--	193	21	--	--	--	--
Red spruce	1 699	19	14.6	19	7 507	5 627	4 769	812	23	10	4 070	1 482	132
Sugar maple	86	26	16.6	--	--	--	--	50	29	--	--	--	--
White cedar	724	21	11.8	--	--	--	--	183	28	--	--	--	--
White pine	58	24	15.7	--	--	--	--	39	38	--	--	--	--
White spruce	180	21	14.8	1	1 973	17	49	333	23	22	1 052	829	450
Yellow birch	151	23	15.4	--	--	--	--	91	29	--	--	--	--
Other hardwood	100	19	13.3	--	--	--	--	8	16	--	--	--	--
Other softwood	34	22	16.5	--	--	--	--	120	24	--	--	--	--

* For each tree, minimum annual defoliation was 0% and 5% in Maine and New Brunswick, respectively, according to different protocols of measurements.

5.2.2.1. Growth Impact Study of Maine

The Growth Impact Study was initiated in 1975 (after SBW activity reached epidemic level in 1974) as a cooperative effort among federal and state forest agencies, as well as private forestry companies to document the impact of SBW on growth and mortality of the Maine forest. Data were collected at 424 ~0.02 ha circular plots including 8 762 trees ≥ 11.4 cm in DBH throughout northern Maine during 1975-1985. Specifically, 7 798 trees from 375 of these plots with known coordinates (hence climate site indices can be derived) were used in this study. The data included annual records of species, DBH, cause of death, total height, crown length, and degree of defoliation. The exact locations of 49 plots were not able to be determined and were dropped from this analysis.

Each year during the study period, current-year and previous-years foliage on each host tree within each plot were visually examined for the degree of defoliation, and categorized separately into one of five (before 1982; 0, 1-5, 6-20, 21-50, and 51-100 percent) or eleven classes (after 1982; 0-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, 91-99, and 100 percent) of defoliation. Observed annual defoliation of current-year foliage (mean ± SD) of balsam fir, red spruce, black spruce, and white spruce were 37 ± 31%, 19 ± 23%, 13 ± 20%, and 1 ± 8%, respectively.

5.2.2.2. Permanent Sample Plots of New Brunswick

Approximately 1 500 random PSPs were established between 1976-1979 as part of the New Brunswick Department of Forests, Mines, and Energy Forest Inventory. Of these plots, 136 were selected for SBW related studies based on stratification by species, maturity, and degree of insecticide use for protection. Each PSP consisted of three permanent prism points (basal area factor = 2 m^2 ha^{-1}) located 40 m apart where species, DBH, year of death, initial height, and degree of defoliation of each tree were measured intermittently during 1976-1993 (Chen et al

2017a). Specifically, DBH measurements of 3 641 trees compatible in size with the Growth Impact Study dataset (i.e. DBH ≥ 11.4 cm) in 1985, 1988, and 1991, as well as measurements of annual defoliation of current-year foliage during this period from 103 plots with known coordinates (hence climate site indices can be derived) were used in this study. Defoliation of current-year foliage in the New Brunswick PSPs was estimated for each host tree every year by scanning the crowns with binoculars. The results were put into seven percentage classes of 0-10, 11-20, 21-40, 41-60, 61-80, 81-99, and 100 percent. Observed annual defoliation of current-year foliage (mean ± SD) of balsam fir, red spruce, black spruce, and white spruce were 24 ± 27, 10 ± 10, 8 ± 8, and 19 ± 22 percent, respectively.

5.2.2.3. Data Compilation

Midpoints of the defoliation classes were used to calculate cumulative defoliation, which was an input to all of the modifiers. Since height was only measured once during 1976-1979 in New Brunswick, a mixed-effects model outlined by Robinson and Wykoff (2004) was applied to assess the relationship between height and DBH as well as species in this period. Subsequently, this relationship was used to impute height in 1985, which was an input to initiate the projections by FVS-ACD. Similarly, initial crown ratio (in 1985) was set to 0.2 (its approximate mean value in Maine) in New Brunswick since its measurements were also not available.

5.2.3. SBW Modifiers of FVS-ACD

There are various strategies for developing modifiers to be used in growth and yield models with contrasting advantages and disadvantages (e.g. Weiskittel et al. 2011a). In an ideal scenario, the base condition is first modeled and then direct effects are captured in the modifier using the same data (e.g. Kuehne et al. 2016). Unfortunately, this strategy was not possible in this analysis since the available data were after the start of the SBW outbreak in the region and there were relatively few observations that were not defoliated. Instead, the base equations from FVS-ACD, which have been extensively evaluated and show limited bias across a range of conditions, were used to determine expected trends under no defoliation. Consequently, annualized SBW modifiers were developed and used to adjust each component of FVS-ACD in the following way:

$$[1]\ Adjusted\ FVS\text{-}ACD\ component = FVS\text{-}ACD\ component \times modifier$$

Specifically, modifiers for DBH increment (ΔDBH; cm yr^{-1}) and height increment (ΔHT; m yr^{-1}) are in the form of Equation [2], modifier for height to crown base (*HCB*; m) is in the form of Equation [3], modifier for mortality (*MORT*; probability in the form of a 0-1 ratio) is in the form of Equation [4], and modifiers for ingrowth (*IPH*; trees ha^{-1}) and ingrowth proportion of each susceptible species (balsam fir, red, black, and white spruce; IPH_{prop}) are in the form of Equation [5].

$$[2]\ exp\left(b1_{spp} \cdot CDEF\right)$$

$$[3]\ exp\left(b2_{spp} \cdot CDEF + b3_{spp} \cdot CR\right)$$

$$[4]\ b4 + b5 \cdot BAL_{mod} + b6 \cdot {pBAL_{SW}}^{0.5} + b7 \cdot CR + b8 \cdot log(CSI) + b9_{spp} \cdot CDEF$$

$$[5]\ b10 \cdot CDEF + b11$$

In these modifiers, BAL_{mod} is a modified metric of basal area of trees larger than the subject tree in DBH (*BAL*; m^2 ha^{-1}) computed as $(BAL \cdot topht)/(100 \cdot BA \cdot tph^{-0.5})$, in which *topht* is top height (height of the tallest tree; m), *tph* is trees ha^{-1}; and *BA* is basal area (m^2 ha^{-1}); $pBAL_{SW}$ is the proportion of *BAL* of softwood; *CR* is crown ratio; *CSI* is climate site index (m); *CDEF* is cumulative defoliation (%); and *b1-b11* are parameters.

Although two modifiers may share the same form (e.g., Equation [2] for ΔDBH and ΔHT), separate sets of parameters were estimated for each modifier. The *spp* subscripts indicate species-specific parameters (Table 5.2). These parameters were estimated using the Maine data and a recursive annualization technique proposed by Weiskittel et al. (2007). Modifier for *HCB*

(Equation [3]) was limited by recursively calculated crown ratio since *HCB* was predicted using an allometric equation instead of from its increment.

Table 5.2. Parameter estimates of the modifiers developed in this study.

Parameter		Species	Value	SE	p-value
$b1_{spp}$	ΔDBH	balsam fir	-0.0116	0.0001	< 0.0001
		black spruce	-0.0237	0.0022	< 0.0001
		red spruce	-0.0213	0.0003	< 0.0001
		white spruce	-0.1360	0.0064	< 0.0001
	ΔHT	balsam fir	-0.0155	0.0002	< 0.0001
		black spruce	-0.1373	0.0088	< 0.0001
		red spruce	-0.2908	0.0040	< 0.0001
		white spruce	-0.6066	0.0388	< 0.0001
$b2_{spp}$	HCB	balsam fir	0.0075	< 0.0001	< 0.0001
		black spruce	0.0074	0.0003	< 0.0001
		red spruce	0.0069	< 0.0001	< 0.0001
		white spruce	0.0099	0.0003	< 0.0001
$b3_{spp}$		balsam fir	-0.9296	0.0113	< 0.0001
		black spruce	-0.6275	0.0386	< 0.0001
		red spruce	-0.6308	0.0115	< 0.0001
		white spruce	-0.6547	0.0361	< 0.0001
$b4$	$MORT$		0.5232	0.0229	< 0.0001
$b5$			0.0106	0.0006	< 0.0001
$b6$			0.0498	0.0048	< 0.0001
$b7$			-0.1243	0.0046	< 0.0001
$b8$			-0.1994	0.0082	< 0.0001
$b9_{spp}$		balsam fir	0.0022	< 0.0001	< 0.0001
		black spruce	0.0078	0.0007	< 0.0001
		red spruce	0.0016	0.0001	< 0.0001
		white spruce	0.0169	0.0011	< 0.0001
$b10$	IPH		-0.0012	0.0008	0.1409
	IPH_{prop}		-0.0077	0.0054	0.1550
$b11$	IPH		0.1397	0.0218	< 0.0001
	IPH_{prop}		1.2459	0.1268	< 0.0001

ΔDBH is diameter at breast height increment (cm yr^{-1}); ΔHT is height increment (m yr^{-1}); *MORT* is mortality (probability in the form of a 0-1 ratio); *HCB* is height to crown base (m); *IPH* is ingrowth (trees ha^{-1} yr^{-1}); IPH_{prop} is proportion of ingrowth of each susceptible species (balsam fir, as well as red, black, and white spruce); and *b1-b11* are parameters, of which the *spp* subscripts indicate species-specific parameters.

Cumulative defoliation was a covariate included in each of the modifiers, and was computed as the sum of annual defoliation of current-year foliage (%), which was predicted for each year of the duration of FVS-ACD projection using a model proposed by Chen et al. (In press) in the following form:

$$[6]\ CDEF = t \cdot \left(1 - e^{\gamma_1 \cdot (t-\gamma_2)}\right) + \gamma_3 \cdot t \cdot e^{(\gamma_4 \cdot DEF_1 + \gamma_5 \cdot CR) \cdot t} + \varepsilon$$

where t is time (year); *DEF* is annual defoliation of current-year foliage (% transformed to 0-1); *CR* is crown ratio; ε is the error; and parameters γ1 - γ5 were estimated for each species. Since Chen et al. (In press) found SBW defoliation tends to converge to similar temporal trajectories for each species despite considerable differences in tree, stand, and site factors, this predicted series of defoliation (annual defoliation in future years) may also be viewed as a most likely scenario of defoliation based on the initially available information (observed first year defoliation and crown ratio).

5.2.4. SBW Modifiers from STAMAN

Hennigar et al. (2013a) converted parameters that account for effects of SBW defoliation in STAMAN for use as modifiers in FVS. Values of these modifiers were predetermined and stored in a lookup table. Specifically, periodic five-year additive modifier values for survival (hence mortality) were categorized by species, DBH class, and defoliation, while periodic five-year multiplicative modifiers for diameter and height increments shared a single set of values determined by defoliation alone. These periodic modifiers were converted to annualized modifiers to be applied in FVS-ACD and compared with our modifiers. Potential influences of SBW defoliation on ingrowth and crown recession were not considered by these modifiers. Besides being calibrated using different data (i.e., STAMAN modifiers were calibrated using defoliation data from New Brunswick; Erdle and MacLean 1999), there are three main differences between the STAMAN modifiers and those we developed for FVS-ACD: 1) values of our modifiers were predicted by Equations [2-5] for each tree in each year, while modifiers from STAMAN are expressed as a function of defoliation level and were extracted from a lookup table (Hennigar et al. 2013a); 2) cumulative defoliation and a modified six-year moving average of defoliation (MacLean et al. 2001) were used in our modifiers and STAMAN modifiers, respectively; and 3) to reduce prediction errors, a tree would be removed from the list of trees (i.e., its expansion factor (per hectare number of trees it represents) would be zero) in our modifiers when its mortality probability exceeded an optimization criterion, which was the mortality probability that maximized the ratio of true positive rate over false positive rate of mortality. Since information about this criterion was not available for the STAMAN modifiers, a portion of a tree would be killed by reducing its expansion factor proportionally by its predicted mortality probability as commonly done in FVS (Dixon 2002).

5.2.5. Output of the Modified FVS-ACD

The final output used to evaluate and compare FVS-ACD that utilized the above two types of modifiers was in the form of stand total volume (m^3 ha^{-1}), which was estimated using a species-specific taper equation developed for the Acadian region (Li et al. 2012, Weiskittel and Li 2012). Predicted species, DBH, and height of each tree in each year were used as input to the taper equation. Individual tree volume was aggregated using expansion factors to calculate stand volume, of which 95% confidence intervals were also presented.

Projections of stand development with and without the influence of SBW defoliation were performed for 40 years from 1975 to 2015 using FVS-ACD with modifiers developed in this study and FVS-ACD alone, respectively. This projection period roughly represents a full cycle of the periodic SBW outbreak (i.e., from the outset of one outbreak to the next one). These projections were conducted for stands with various percentages of susceptible trees (< 50%, 50-75%, and > 75%), initial volume (< 200 m^3 ha^{-1}, 200-300 m^3 ha^{-1}, and > 300 m^3 ha^{-1}), and peak annual defoliation (< 30%, 30-70%, and > 70%). Observed conditions of these stands and SBW defoliation in 1975 were used as starting points of the projections. Standard errors of the predictions of each of the above stand types at each time step were calculated and used to construct the confidence intervals.

5.3. Results

5.3.1. Values of the Two Types of Modifiers

Values of our modifiers as a function of cumulative defoliation of the range of 0-300% are shown in Figure 5.1. Specific values of our modifiers and STAMAN modifiers (which are available for DBH and height increment, as well as mortality) at 50%, 100%, and 200% cumulative defoliation are listed in Table 5.3. In general, our modifiers for DBH and height increments have smaller values than the STAMAN counterparts, which indicate larger growth reductions from our modifiers. Likewise, larger values of our mortality modifier compared to the STAMAN modifier, which indicate no increase in mortality for any species, represent more predicted mortality under the influence of SBW defoliation. Covariates other than those of defoliation were set at their means in this analysis, while the above three levels of cumulative defoliation were assumed to be equally distributed in five years in STAMAN modifiers, i.e., current-year defoliation to be 10%, 20%, and 40%, respectively, in each of the five years.

Table 5.3. Values of our modifiers and STAMAN modifiers at 50%, 100%, and 200% cumulative defoliation with the other covariates at their means.

Modifier		**Species**	**Cumulative defoliation (%)**		
			50	*100*	*200*
Δ*DBH* (cm yr^{-1})	our modifier	*balsam fir*	0.56	0.31	0.10
		red spruce	0.34	0.12	0.01
		black spruce	0.31	0.09	0.01
		white spruce	0.00	0.00	0.00
	STAMAN modifier	*all species*	0.94	0.88	0.75
Δ*HT* (m yr^{-1})	our modifier	*balsam fir*	0.46	0.21	0.05
		red spruce	0.00	0.00	0.00
		black spruce	0.00	0.00	0.00
		white spruce	0.00	0.00	0.00
	STAMAN modifier	*all species*	0.94	0.88	0.75
Mortality (0-1 ratio)	our modifier	*balsam fir*	2.64	4.28	7.57
		red spruce	2.22	3.44	5.88
		black spruce	6.96	12.93	24.86
		white spruce	13.90	26.81	52.61
	STAMAN modifier	*balsam fir*	1.00	1.00	1.00
		red spruce	1.00	1.00	1.00
		black spruce	1.00	1.00	1.00
		white spruce	1.00	1.00	1.00
Height to crown base (m)	our modifier	*balsam fir*	0.50	0.64	1.05
		red spruce	0.65	0.78	1.16
		black spruce	0.67	0.83	1.30
		white spruce	0.66	0.84	1.36
Ingrowth (trees ha^{-1})	our modifier	(*stand level*)	0.08	0.02	0.00
Ingrowth proportion	our modifier	(*stand level*)	0.86	0.48	0.00

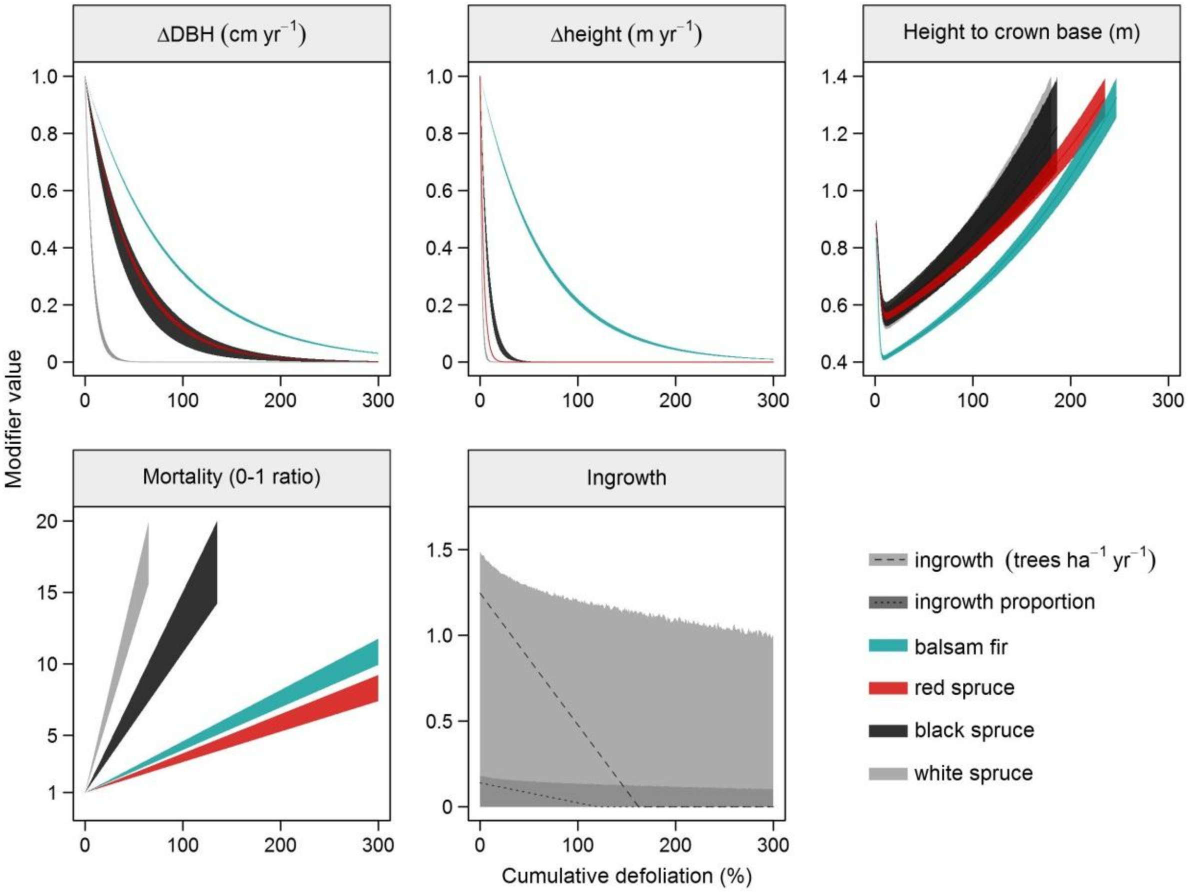

Figure 5.1. Values and their 95% confidence intervals of our modifiers as a function of cumulative defoliation (%) with the other covariates at their means.

5.3.2. Performance of FVS-ACD Using the Two Types of Modifiers

FVS-ACD refined by our modifiers consistently had smaller mean biases (predicted - observed) and root mean squared errors (RMSE) of predicted stand volumes than FVS-ACD refined by STAMAN modifiers and FVS-ACD alone (Table 5.4). Specifically, overall mean bias and RMSE of FVS-ACD refined by our modifiers were 64% and 26% lower, respectively, in Maine and were 79% and 26% lower, respectively, in New Brunswick than those of FVS-ACD refined by STAMAN modifiers. While both mean biases and RMSE appeared to be rather consistent over the range of observed initial stand volume in all three models, they became much higher in FVS-ACD and FVS-ACD refined by STAMAN modifiers over the time period of prediction, although FVS-ACD refined by STAMAN modifiers performed slightly better than FVS-ACD (Figure 5.2). Consequently, stand volumes predicted by FVS-ACD refined by our modifiers were the closest to the observed ones in both regions despite being only developed using the Maine data (Figure 5.3).

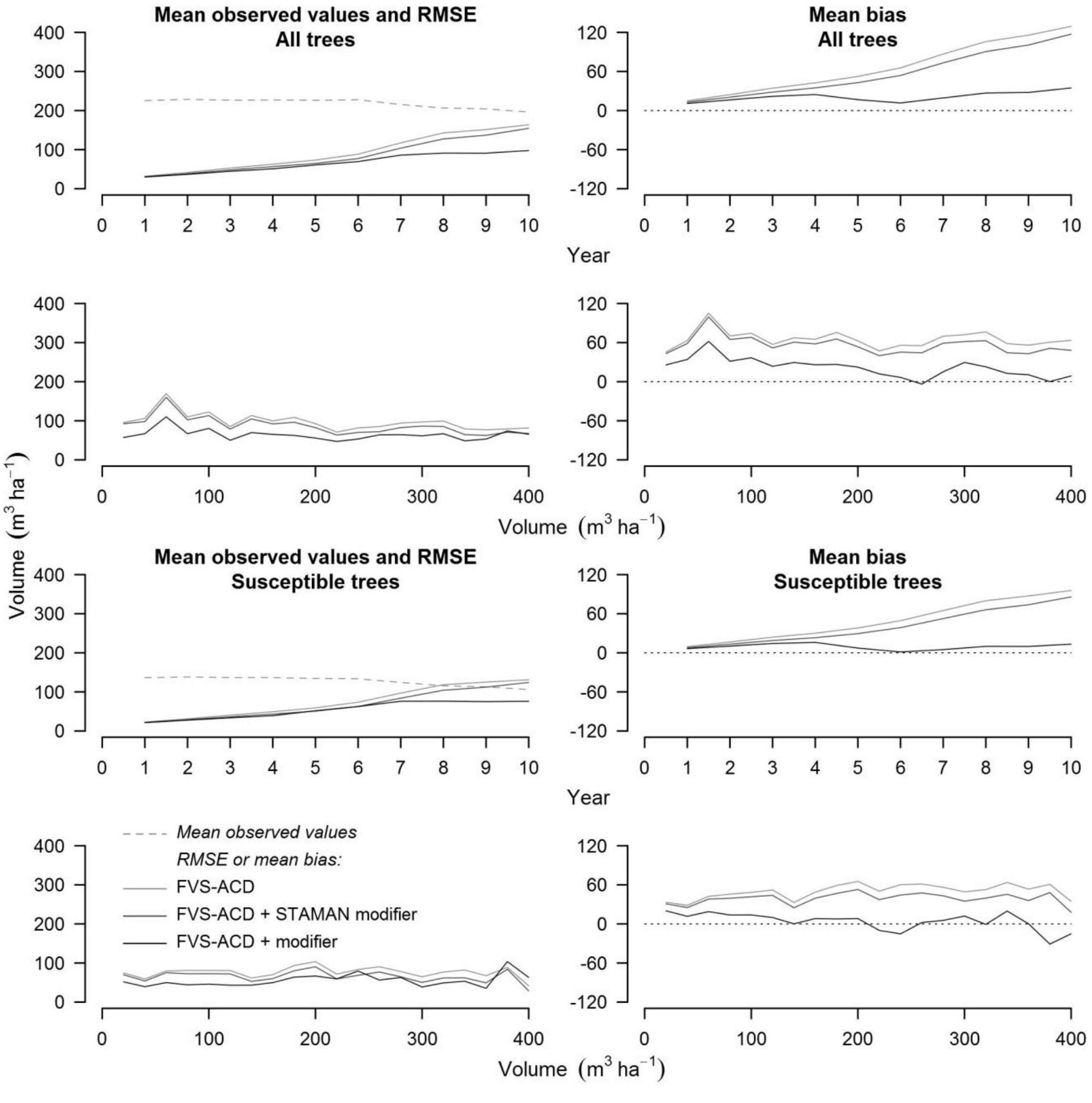

Figure 5.2. Comparisons of root mean squared errors (RMSE) and mean biases (predicted - observed) in predicted stand volume (m^3 ha^{-1}) made by the Forest Vegetation Simulator Acadian variant (FVS-ACD), FVS-ACD refined by our modifiers, and FVS-ACD refined by STAMAN modifier over time and initial volume of stands for the available data in Maine.

Table 5.4. Statistics of the observed stand volume (m^3 ha^{-1}) and its predictions made by Forest Vegetation Simulator Acadian variant (FVS-ACD) refined by our modifiers and STAMAN modifiers, as well as FVS-ACD alone using observed values in 1975 and 1985 in Maine and New Brunswick, respectively, as input.

			Mean (m^3 ha^{-1})		**Mean bias (m^3 ha^{-1})**			**Root mean squared error (m^3 ha^{-1})**		
Maine			*1976*	*1985*	*Overall*	*1976*	*1985*	*Overall*	*1976*	*1985*
	Observed	*all trees*	225	196	--	--	--	--	--	--
		susceptible trees	136	106	--	--	--	--	--	--
	Our modifiers	*all trees*	247	233	+21	+11	+35	70	30	98
		susceptible trees	153	125	+9	+6	+13	58	21	76
	STAMAN modifiers	*all trees*	249	315	+58	+13	+117	94	31	154
		susceptible trees	154	194	+41	+8	+86	75	22	124
	FVS-ACD	*all trees*	251	327	+67	+15	+129	103	32	164
		susceptible trees	156	204	+50	+9	+96	84	23	131
New Brunswick			*1986**	*1991*	*Overall*	*1986**	*1991*	*Overall*	*1986**	*1991*
	Observed	*all trees*	182	179	--	--	--	--	--	--
		susceptible trees	139	134	--	--	--	--	--	--
	Our modifiers	*all trees*	182	187	+5	0	+8	26	2	36
		susceptible trees	139	139	+4	0	+6	24	2	34
	STAMAN modifiers	*all trees*	188	217	+24	+6	+38	35	6	51
		susceptible trees	143	166	+20	+4	+32	31	5	44
	FVS-ACD	*all trees*	188	219	+24	+6	+41	37	7	53
		susceptible trees	144	168	+20	+5	+34	33	5	47

* The year of observation is 1985 while all predictions are for 1986. Susceptible trees are balsam fir, as well as red, black, and white spruce.

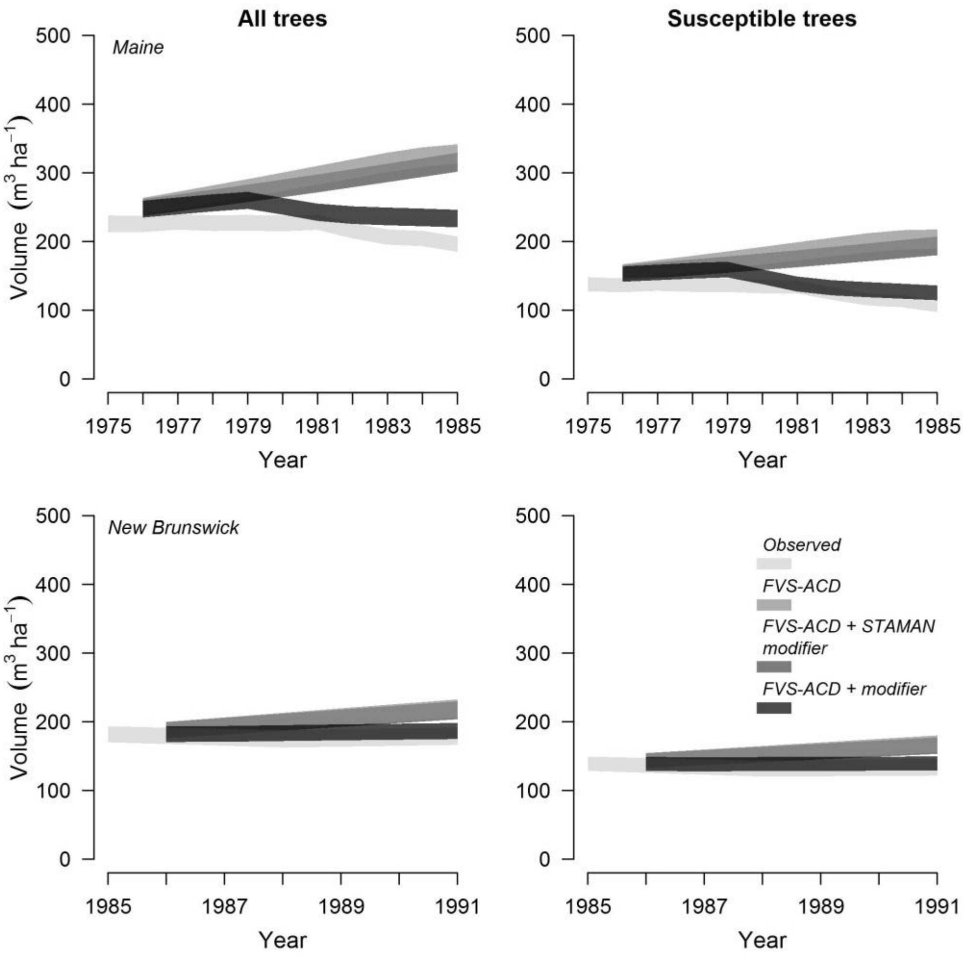

Figure 5.3. Comparisons of observed volume (m^3 ha^{-1}), as well as that predicted by the Forest Vegetation Simulator Acadian variant (FVS-ACD), FVS-ACD refined by our modifiers, and FVS-ACD refined by STAMAN modifier over time in Maine and New Brunswick.

5.3.3. Forty-year Projections of Stand Development Using Our Refined FVS-ACD

Without defoliation, stands with a greater percentage of susceptible trees were predicted by FVS-ACD to have higher volumes after 40 years. Specifically, stands with >75%, 50-75%, and <50% susceptible trees were predicted to have volumes of 498, 468, and 455 m^3 ha^{-1}, respectively (Figure 5.4). With defoliation, FVS-ACD refined by our modifiers predicted the above order of yield to reverse with the volumes being 375, 380, and 391 m^3 ha^{-1}, respectively. Peak annual defoliation was projected to have relatively little influence on stand development, with mean volumes in 2015 for stands with >70%, 30-70%, and <30% peak annual defoliation projected to be 377, 407, and 384 m^3 ha^{-1}, respectively. In addition, higher initial volume had higher yield in 2015 irrespective of whether the influence of defoliation was considered. Finally, growing stock volume under the influence of defoliation did not fully recover and reach the level without the influence of defoliation for any of the stand types examined during the 40-year projection period (Figure 5.4).

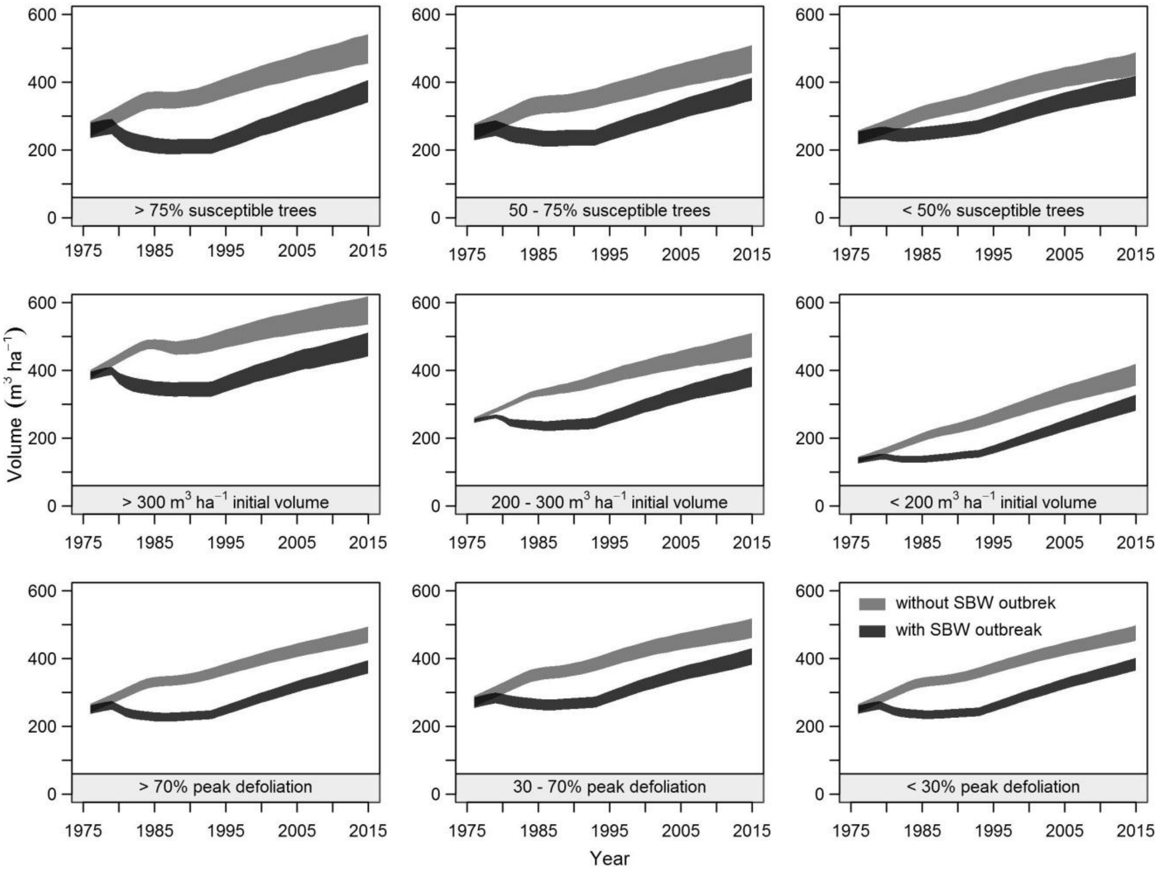

Figure 5.4. Forty-year projections of stand volume (m^3 ha^{-1}) of various types of stands with and without the influence spruce budworm (SBW) defoliation using the Forest Vegetation Simulator Acadian variant (FVS-ACD) refined by our SBW modifiers. Observed defoliation in 1975 was used as the input of the defoliation scenario.

5.4. Discussion

The major differences between FVS-ACD and the northeast variant of FVS (FVS-NE; Dixon and Keyser 2008), which has also been applied in the Acadian region, are the use of site indices related to climate attributes, not using the potential times modifier approach, and utilizing an annualization technique in model development (Weiskittel et al. 2017). Previous work has highlighted the key stand-level prediction differences between FVS-ACD and FVS-NE for common forest types in Maine, but the differences are more limited for typical spruce-fir stands where SBW would have the largest influence (Weiskittel et al. 2017). While it is potentially problematic to predict potential growth in mixed-species stands (Russell et al. 2014), the compounding effects of SBW defoliation make it even more difficult. In addition, the use of an annual time step in FVS-ACD allows for capturing the highly variable and cumulative effects of SBW defoliation, especially on mortality as it starts to increase after several years of defoliation (MacLean 1980, Chen et al. 2017a). A multi-year projection period (or a linearly interpolated annual prediction) could overestimate the influence of defoliation for the flat period of the first a few years and/or underestimate the relatively quick increase in mortality in the ensuing years of an SBW outbreak.

The metric of cumulative defoliation used in this study was designed to represent the compounding effect of SBW defoliation, and was highly compatible with the annualization technique used in FVS-ACD. Like many other insect and pathogen disturbance agents represented in FVS, a challenging aspect of representing the influences of SBW defoliation on forest development was to predict the temporal dynamics of defoliation itself. STAMAN projections use a scenario definition approach, where current annual defoliation is defined for each year of a SBW outbreak cycle, and then converted into a modified six-year moving-average of these defoliation values (MacLean et al. 2001). In the STAMAN modifiers, defoliation levels were thus predetermined for the assumed duration of an outbreak and fixed at the same value for each susceptible tree. This obviously ignores the long-observed individual tree spatio-temporal variability in SBW defoliation (e.g., MacLean and Lidstone 1982, Gray et al. 2000, Zhao et al. 2014, Doran et al. 2017) and the varying conditions of Acadian forests. Although relatively large errors existed in our predicted annual individual tree defoliation due to its highly variable nature, errors in our predicted totals of defoliation (i.e., cumulative defoliation) became smaller at a relative scale as the duration of FVS-ACD projection (i.e., sample size) increased since the predicted annual defoliation was generally unbiased (with a mean bias of +1.97%; Chen et al. In press). In general, our predicted cumulative defoliation performed well and generated predictions of the FVS-ACD components very close to those using observed defoliation.

The significant improvement in the predictions by the refined FVS-ACD was also due to a systematic modification of each component equations of FVS-ACD. Chen et al. (2017a, 2017b) showed that both various components of FVS-ACD and various species responded differently to SBW defoliation, which justified the approach used in this analysis. However, these responses also differed from those observed in most SBW impact studies under much higher levels of severe defoliation conditions. Some typical differences for an example with 100% cumulative defoliation (equivalent to removal of one age-class of foliage) are described in detail below.

First, our modifier indicates 69%, 88%, and 100% reductions in DBH increment of balsam fir, red spruce, and white spruce, respectively, which correspond to predicted mean DBH increments of 0.07, 0.09, and 0.03 cm yr^{-1} of respective average-sized trees (i.e., DBH of 17.5, 19.6, and 20.7 cm, respectively). These percentage reductions are greater than the 20-60% reduction reported for years 3-5 of a SBW outbreak by MacLean (1979) and the maximum 50% reduction estimated by Pothier et al. (2005), although such a reduction was estimated to be 80% or more under severe cumulative defoliation levels of 400-600% (Ostaff and MacLean 1995). Piene (1980) probably has the best quantification of early outbreak (low-level) cumulative defoliation, and found that young balsam fir trees with 80-100% defoliation of a single age-class of foliage during the first year of defoliation (i.e., cumulative defoliation of 80-100%) had about 20% reduction of stem volume growth, and a loss of two age classes of needles (i.e., cumulative defoliation of 200%) resulted in about 50% reduction of the stem volume growth. Our predicted absolute DBH increments were generally lower than that of balsam fir of 0.06 to 0.17 cm yr^{-1} reported by MacLean (1988), as well as those of balsam fir, black spruce, and white spruce of 0.10-0.28, 0.10-0.24, and 0.10-0.36 cm yr^{-1}, respectively, indicated by Steinman and MacLean (1994). Second, our modifier indicates 79%, 100%, and 100% reductions in height increment of balsam fir, red spruce, and white spruce, respectively, which all correspond to predicted mean height increment of <0.05 m yr^{-1}. Although records of height increment influenced by SBW defoliation were not found in previous studies, our predictions agree with the large number of height growth cessations (76% of the observations) due to widespread top-kill observed in this study as well as suggested by Van Sickle (1987) and Ostaff and MacLean (1989). However, these previous data on top-kill were at higher cumulative defoliation levels. Similarly, there are no other references for measures of height to crown base and ingrowth influenced by SBW defoliation. In addition, our modifier suggests 7.4 trees ha^{-1} yr^{-1} ingrowth observed during the last SBW outbreak compared to the 22.8 trees ha^{-1} yr^{-1} ingrowth reported by Li et al. (2011) mainly for the period after the outbreak.

Finally, our modifier indicates 3.3, 2.4, and 25.8 times increases in mortality probability of balsam fir, red spruce, and white spruce, respectively, which correspond to predicted mean annual mortality probabilities of 2.0%, 0.3%, and 0.8% of respective average-sized trees indicated above. These are much lower than the cumulative mortality probabilities of 73%-100% for balsam fir and 27%-66% for spruce species under 336%-840% cumulative defoliation reported by a number of previous studies (e.g., Blais 1958, MacLean and Ostaff 1989, Piene 1989, MacLean et al. 1996). SBW-caused tree mortality is typically minimal until at least 3-4 years of severe (>70% current) defoliation have occurred (MacLean 1980), and thus at 100% cumulative defoliation should reflect normal, undefoliated mortality rates.

Overall, our results in Figure 5.1 indicate much higher reductions of growth and increases of mortality than other SBW impact literature (e.g., MacLean 1980, Piene 1980, Ostaff and MacLean 1989, 1995, Erdle and MacLean 1999, Pothier et al. 2005). Previous studies have generally showed little effect of annual defoliation less than 30% on growth or mortality. Mean needle longevity of balsam fir has been shown to range from a mean of 5.5 years on 22-27 year-old fir in Cape Breton, Nova Scotia (Fleming and Piene 1992) to 9.5 years on 50-year-old balsam fir with low defoliation in Quebec (Doran et al. 2017). Cumulative defoliation of 100% would equate to removal of only one age class out of approximately five to nine age classes of foliage on the tree, so our modifiers predict surprisingly strong effects on growth reduction and mortality for relatively low defoliation levels. This could reflect unusually large impacts given stand conditions during the 1970s-1980s SBW outbreak in Maine.

In general, SBW defoliation had a more significant influence on height growth than on diameter growth and had a more important role in affecting both mortality and ingrowth than survivor growth. The large percentage changes of FVS-ACD components under the influence of defoliation partly reflect the fact that FVS-ACD was calibrated using data collected after the SBW outbreak. Therefore, baseline values (i.e., without the influence of defoliation) in FVS-ACD likely are greater than those in studies conducted during SBW outbreaks. Nevertheless, these large changes confirmed that even low levels of SBW defoliation had significant effects on various components of forest dynamics (Chen et al. 2017a, 2017b). Therefore, species- and equation-specific modifiers developed for each component of FVS-ACD and each SBW host species likely have improved this model's ability to accurately represent the highly variable influences of SBW defoliation on forest development. In comparison, changes in ingrowth and height to crown base as well as differences in DBH and height increments among SBW host species were not previously considered in the STAMAN modifiers.

Projections by FVS-ACD and its STAMAN-modified version comprised significant and consistent over-prediction (Figure 5.2 and 5.3). This is understandable for the unmodified FVS-ACD, in which the reduced tree growth and survival due to SBW defoliation was not accounted for. It is also expected for FVS-ACD refined by STAMAN modifiers, which were calibrated using higher levels of severe defoliation data than ours from Canada (Erdle and MacLean 1999, MacLean et al. 2001). Consequently, mean defoliation was considered to start reducing tree survival at levels >30%, and this effect of reduced survival was also consistently smaller than that in our refined FVS-ACD at comparable defoliation levels (Hennigar et al. 2013a). In contrast, observed individual tree defoliation averaged 28% and 22% in Maine and New Brunswick, respectively, which means that SBW defoliation appeared to have no effect on predicted tree survival in many cases in FVS-ACD refined by STAMAN modifiers. This did not seem to agree with the observations, which suggest that even low levels of defoliation resulted in significant increases in mortality (Chen et al. 2017a, 2017b).

While projections of the volume of susceptible trees by our refined FVS-ACD were not significantly different from the observations, relatively small over-predictions existed in projections involving trees of all species in Maine (Figure 5.3). Possible causes could be the growth of living trees (that are not modified in the model) was not as fast as indicated by the model because their growth may still be limited by the standing dead trees recently killed by SBW defoliation, and growth of non-susceptible trees like eastern hemlock (*Tsuga canadensis* (L.) Carrière) may also have been slightly influenced by defoliation.

Overall, these biases (over-prediction) are believed to be the cause of the increasing errors of predictions over time, and could severely affect the accuracy of long-term projections by the models. These biases may be reduced by introducing additional modifiers, which are built upon predictions of these biases using some potential tree, stand, and defoliation variables as predictors. Subsequently, the above predicted values (i.e., modifier values) will be subtracted from the biases and consequently reduce them. For the mortality component in our refined FVS-ACD, we currently kill a tree when its mortality probability exceeds a threshold, which is the value that maximized the ratio of true positive rate over false positive rate of mortality. This could be an alternative to the approach that kills fractions of trees by reducing the expansion factors by the predicted mortality probability, which uses no criterion to protect against potential errors in predictions considering the fact that many trees lived through the projection period (i.e., the predicted mortality did not happen despite part of a tree being killed in the model). However, we believe that a stochastic component, which kills a tree based on a well-designed random process and the predicted mortality probability, may be developed to evaluate its ability to further reduce biases in the predictions of mortality.

Limitations in our refined FVS-ACD that require further improvements are mainly in four important aspects. First, FVS was developed for use in a static climate, and are generally incapable of reflecting the effects of climate change on stand dynamics (Crookston et al. 2010). In addition, climate change may also directly affect the dynamics of SBW defoliation (e.g., Gray 2008), which may already be evolving in response to changes of the Acadian forests. However, it is challenging to separate the changes of SBW defoliation dynamics from its usually high spatial and temporal variations, and update it in growth models. Second, it is important for growth models like FVS-ACD to incorporate the effects of SBW defoliation with forest management and protection activities, considering various silvicultural techniques have been proposed as long-term solutions to alleviating the influence of defoliation, as well as the control of SBW has largely relied on the application of insecticide (Baskerville 1975, Mott 1980, Blais 1983). Such data on effects of management (such as species composition changes from thinning or salvage activities) and protection activities (e.g., Hennigar et al. 2013b) could be incorporated into FVS-ACD. Third, the data used to develop the modifiers may not be fully representative of SBW outbreaks. As highlighted previously, the data in Maine were initiated after defoliation reached epidemic level and a significant portion of the landscape was sprayed with insecticide, which complicates the interpretation of our findings. Also, ground-based estimates of defoliation can be difficult and the observations in Maine were made by multiple observers, which could increase bias and underlying variability. Finally, the modifiers were developed using the base FVS-ACD equations, which are primarily based on data from more recent conditions. Consequently, the modifiers may be adjusting for additional factors above and beyond SBW defoliation. Ideally, the base and modifier equations would be developed using the same data to reduce this potential confounding influence. However, as mentioned above, the available data for this analysis were only after the start of the SBW outbreak and there were relatively few observations for non-defoliated trees. All of these above issues in addition to sampling design limitations may have contributed to large differences in defoliation dynamics of white spruce between this study and some previous studies (Table 5.1; Chen et al. In press).

In general, the refined FVS-ACD showed significant improvement compared to previous works like FVS-NE refined by STAMAN modifiers. This improvement includes more accurate predictions of volume, species composition, and diameter distribution, as well as a much closer resemblance of the patterns in volume increment (Figure 5.2 and 5.3). We believe that our refined FVS-ACD is suitable to predict forest stand dynamics and support management as well as protection activities against SBW defoliation in the Acadian region during future outbreaks similar to the one during the 1970s-1980s. Given the significant differences between the previous model and the model developed here, prior analyses (e.g. Hennigar et al. 2011) examining economic viability of insecticide spraying and potential growth losses in Maine may need to be further examined. To our knowledge, data used in this analysis are the best available data for assessing the effects of SBW defoliation on individual trees for this region. Only after the next SBW outbreak, new data for testing the developed relationships will be available. Until that time, we must assume that modifiers developed in this analysis reflect the general trends following SBW defoliation. The R code and parameters to run FVS-ACD with these developed modifiers are provided in Supplemental Materials D.1 and D.2. Overall, this work highlights the need and importance of effectively accounting for defoliation in growth and yield models.

CHAPTER 6

EPILOGUE

It was found in this dissertation that species was the primary factor in affecting both trees' growth responses and susceptibility to spruce budworm (*Choristoneura fumiferana* (Clem.); SBW) defoliation. Specifically, what levels of defoliation trees sustained and how much growth reduction as well as mortality occurred under these levels of defoliation were more determined by species than the common tree, stand, and site attributes examined. Although growth reduction and mortality observed in this dissertation appeared to be lower than those reported by many previous SBW studies, these effects of defoliation seemed to be relatively more significant considering our data represented relatively low levels of defoliation observed during the last SBW outbreak. Overall, our findings are largely consistent between Maine and New Brunswick with regional differences being primarily related to the fact that New Brunswick data were in the end of the last SBW outbreak. As more accurate and precise predictions of forest development were achieved using findings from this dissertation than a similar work from Canada, these findings appeared to be generally valid and will help advance our understandings of SBW defoliation dynamics and its influence on the Acadian forest.

This dissertation was based on extensive data from Maine and New Brunswick, which had large spatio-temporal extents and comprised wide ranges of forest conditions as well as detailed individual tree measurements and defoliation observations. Consequently, these data provided strong support to the findings of this dissertation. In the meantime, differences in scales and resolutions of data likely played an important role in the discrepancies in the findings among SBW studies. In particular, many studies based their conclusions on data disproportionally incomparable to the extents and variability of SBW defoliation during its outbreaks. Insufficient data are a general limitation of SBW studies including this dissertation mainly in the following aspects: 1) data do not have a temporal extent to cover the transition from extremely low levels of defoliation (endemic SBW populations) to high levels of defoliation (endemic SBW populations), and to show how the development of forests have modified after defoliation subsides; 2) data generally cannot facilitate the investigation of the effects of forest management and protection activities like insecticide spraying and salvage (pre-salvage) cutting on defoliation and consequent forest development; and 3) sampling designs such as the spatial distribution and size of sample plots are insufficient to investigate the spatio-temporal dynamics of defoliation, which are highly variable at a range of scales.

While the influences of SBW defoliation on the growth and mortality of trees have been rather intensively studied, the dynamics and variation of defoliation have been less investigated. Recent hypothesis of SBW population dynamics suggests that SBW defoliation was more synchronized at regional scale and more variable at smaller scales, and immigration as well as emigration played an important role in both the synchrony and variation of defoliation hence the high fluctuation in its temporal dynamics. Therefore, it is unrealistic to predict local defoliation risk (or development) and its influences without understanding the spatial dynamics of defoliation. Although we have discussed the variation in individual tree defoliation in Chapter 4 from a non-spatial perspective, it is worth further investigating how this variation in defoliation changes spatially and how this spatial dynamics interact and influence local defoliation and its temporal developments in the future.

Our data contain relatively large numbers of wind throws of trees, which may be partly related to the fact that sustained SBW defoliation has weakened trees and made them more prone to wind damage. It is also likely that defoliation has affected the regimes of other forest disturbances such as disease and fire by weakening trees and accumulating dead wood as fuel. It is beneficiary to forest protection and management planning to understand how different forest disturbances interact with each other and potentially cause secondary impacts following SBW outbreaks. Likewise, forest management activities like salvage (pre-salvage) cutting, which resembles natural disturbances, are also important elements in helping understand the interactions and consequences of human and natural disturbances proceeding and ensuing SBW outbreaks.

SBW defoliation probably has as much influences on the growth and mortality of trees as on forest ecosystems. SBW defoliation likely has influences on forest development at a much larger temporal scale considering SBW has a longer history in the Acadian region than its current hosts. It will be interesting to know whether spruce-fir (*Picea-Abies*) forests and SBW together are in a stable state or just transit to such a state. In addition, would human activities and/or climate change significantly alter this long-term forest development? Consequently, whether some species or forest ecosystems are dependent on periodic SBW outbreaks, how these outbreaks affected forest carbon and nutrition cycles, and how these altered cycles affect future climate and its interactions with the Acadian forests are also interesting and important topics worth investigation following this dissertation.

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APPENDIX A: SUPPLEMENTAL MATERIALS OF CHAPTER 2

A.1. Temporal Variation in Defoliation

The following graph presents how annual spruce budworm (SBW) defoliation changed at each of our sample plots over time, where each line represents one sample plot and n is the year that defoliation peaked at this sample plot. It shows that there is a large amount of temporal variation in defoliation. Despite this variation, there is a rather clear pattern such that defoliation rises, peaks, and declines rapidly, and unlikely remains at high levels over time in contrary to some previous assumptions (Intermittent insecticide spraying at different locations may also have contributed to this pattern). In addition, the graph indicates that New Brunswick was mainly in the later phase of the SBW outbreak.

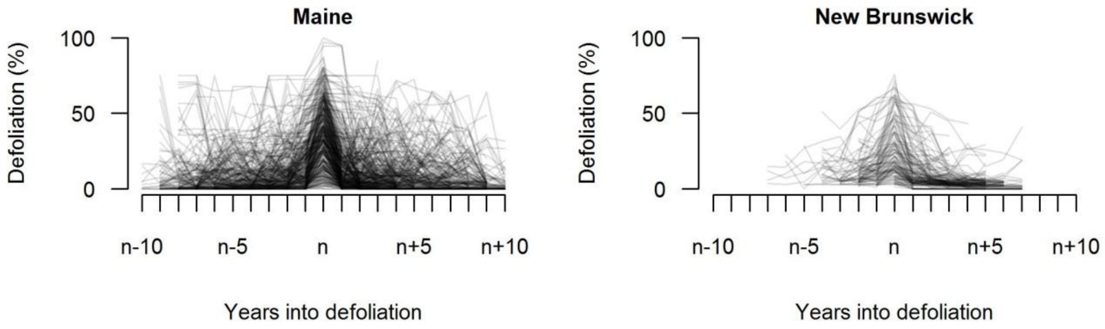

Figure A.1. Temporal variation in defoliation.

A.2. The Effects of Insecticide Spraying on the Stand Growth Components

The following graph compares stand growth components of net growth, mortality, and ingrowth between sample plots with and without insecticide spraying in Maine during the last spruce budworm (SBW) outbreak, and shows that the effects of insecticide spraying were minimal and not significant. MacLean et al. (1984) also found that spraying did not result in significant difference in mortality rates of black, red spruce, and their hybrids in New Brunswick. However, since spraying was more likely to be applied to areas facing higher defoliation pressure, it was possible that such areas would otherwise have been more influenced by SBW defoliation without the protection of spraying.

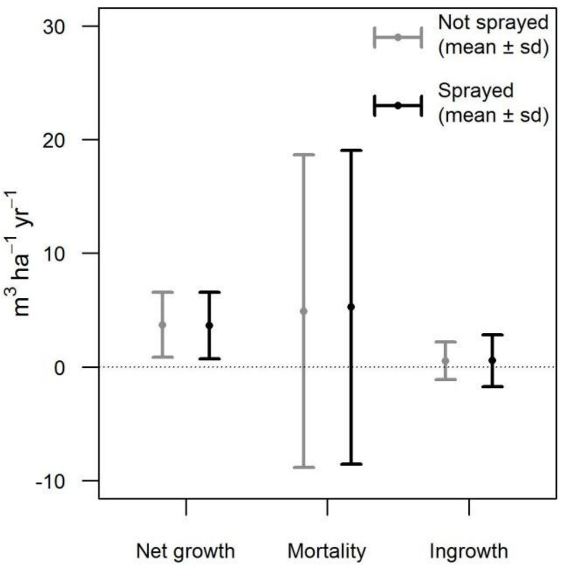

Figure A.2. The Effects of Insecticide Spraying on the Stand Growth Components.

A.3. A Summary of the Data

A summary of the attributes derived from the data used in this analysis is shown in the following table.

Table A.1. A summary of the data.

	Maine (n = 3 846)					New Brunswick (n = 753)				
Attributes	**Mean**	**Median**	**SD**	**Min.**	**Max.**	**Mean**	**Median**	**SD**	**Min.**	**Max.**
Net growth (m^3 ha^{-1} year^{-1})	3.70	3.09	2.88	0.00	41.13	5.36	4.93	3.36	0.00	55.32
Mortality (m^3 ha^{-1} year^{-1})	4.96	0.00	13.76	0.00	231.68	3.11	0.00	5.85	0.00	59.73
Mortality rate in volume (% year^{-1})	2.42	0.00	7.03	0.00	100.00	1.69	0.00	3.55	0.00	44.64
Ingrowth (m^3 ha^{-1} year^{-1})	0.53	0.00	1.76	0.00	40.20	0.80	0.00	2.62	0.00	43.42
Ingrowth rate in volume (% year^{-1})	0.40	0.00	2.27	0.00	82.52	0.47	0.00	1.49	0.00	20.34
Standing volume (m^3 ha^{-1})	224.58	214.56	112.00	1.93	625.78	193.89	190.46	69.23	23.61	393.60
Stand density index	583.17	586.79	237.20	15.73	1394.51	618.62	622.33	186.14	97.19	1226.12
Relative density	0.30	0.30	0.12	0.01	0.66	0.30	0.30	0.09	0.05	0.61
Dominant height (m)	19.23	19.20	2.85	6.71	28.04	17.93	17.61	3.00	12.64	31.97
Cumulative defoliation (%)	84.98	58.51	86.36	0.00	585.63	64.28	47.18	53.50	5.31	321.87
Proportion of balsam fir in volume	0.26	0.21	0.24	0.00	1.00	0.33	0.30	0.24	0.00	0.89
Proportion of white spruce in volume	0.03	0.00	0.11	0.00	1.00	0.09	0.04	0.14	0.00	0.78
Proportion of black spruce in volume	0.03	0.00	0.13	0.00	1.00	0.11	0.00	0.24	0.00	1.00
Proportion of red spruce in volume	0.25	0.15	0.27	0.00	1.00	0.22	0.10	0.26	0.00	0.98
Proportion of hardwood in volume	0.19	0.11	0.21	0.00	1.00	0.10	0.04	0.13	0.00	0.50
Biomass growth index	1.95	2.00	0.34	0.94	2.74	--	--	--	--	--
Climate Site Index	13.47	13.37	1.37	9.23	19.03	11.63	11.59	1.26	8.61	14.90
Wetness Index	7.27	7.37	2.86	0.75	15.84	10.60	10.61	1.49	7.07	14.02
Slope (%)	9.76	5.24	14.04	0.00	132.70	6.59	2.62	6.10	0.00	27.97
Aspect (degree)	174.00	174.51	113.11	0.00	360.00	176.20	186.34	98.17	0.00	358.80
Elevation (m)	263.20	284.57	129.62	41.02	691.30	202.40	188.75	133.97	0.00	577.50

A.4. Comparisons between Our Mortality and Ingrowth Models with Zero-one-inflated Models

We built zero-one-inflated beta regression models for mortality and ingrowth in the following customary way to compare with our mortality and ingrowth models:

$$[1]\; y = p_0 \cdot 0 + (1 - p_0) \cdot (1 - p_1) \cdot \mu + (1 - p_0) \cdot p_1 \cdot 1$$

where *y* is the proportion of mortality/ingrowth; p_0 and $(1 - p_0) \cdot p_1$ are the probabilities of y = 0 and y = 1, respectively; and μ is the mean of a beta distribution.

p_0, p_1, and μ were all modeled through logit link functions, while the precision parameter φ of the beta distribution was modeled by a log link function as follows:

$$[2]\; log\left(\frac{p_0}{1 - p_0}\right) = x_0\beta_0$$

$$[3]\; log\left(\frac{p_1}{1 - p_1}\right) = x_1\beta_1$$

$$[4]\; log\left(\frac{\mu}{1 - \mu}\right) = x\beta$$

$$[5]\; log(\varphi) = x_\varphi\beta_\varphi$$

where x_0, x_1, x, and x_φ are predictors for p_0, p_1, μ, and φ, respectively; and β_0, β_1, β, and β_φ are corresponding parameters.

Parameter estimation was conducted in the following Bayesian setting using R package "zoib" (Liu and Kong 2016):

$$[6]\; p\big(\beta_0, \beta_1, \beta, \beta_\varphi \vee y\big)$$

$$\propto \left({p_0}^{I(y=0)} \cdot \big((1 - p_0) \cdot (1 - p_1)\big)^{I(0<y<1)} \cdot Beta(a, b) \cdot \big((1 - p_0) \cdot p_1\big)^{I(y=1)}\right) \cdot N(0, 10^{-3})$$

where $a = \mu \cdot \varphi;\; b = (1 - \mu)\varphi$; *I* indicates an indicator variable; and $N(0, 10^{-3})$ is the multivariate normal prior distribution of the parameters.

Different combinations of predictors derived from various tree, stand, and site attributes were tested in Equations [2] – [5]. The root mean squared error (RMSE) of the predictions on mortality using parameters estimated from Equation [6] ranged from 0.0998 (where *x* comprised only cumulative defoliation; and x_0, x_1, and x_φ comprised only intercept) to 0.0750 (where *x* comprised standing volume, relative density, proportion of balsam fir · cumulative defoliation, and proportion of spruce · cumulative defoliation; x_0 comprised cumulative defoliation and proportion of hardwood; and x_1, and x_φ comprised only intercept). In comparison, RMSE of our mortality model was 0.0682 and 0.0584 (with random effects).

More importantly, our model outperformed the above zero-one-inflated beta model in terms of predicting excessive zero and over-dispersed observations. First, our model had 904 close-to-zero predictions ($\hat{y} < 0.01$ when *y* = 0) comparing to 385 the zero-one-inflated beta model has (albeit being named as zero-one-inflated beta model, predicted values of the above specific model obviously cannot be either zero or one). Second, the maximum predicted value of our model is 0.41, which is 0.23 in the zero-one-inflated beta model.

The following graphs compare the predictions of mortality between the zero-one-inflated beta model and our model. Specifically, Graph A shows that predictions from our model better resembles the distribution of the observed mortality. Graphs A and B both show that our model yields closer predictions of large observed values. Graph C shows that our model has a larger number of close-to-zero predictions. In Graphs B and C, x-axis values were jittered by Uniform (-0.01, 0.01) and Uniform (-0.0005, 0.0005), respectively, to show overlapping observations.

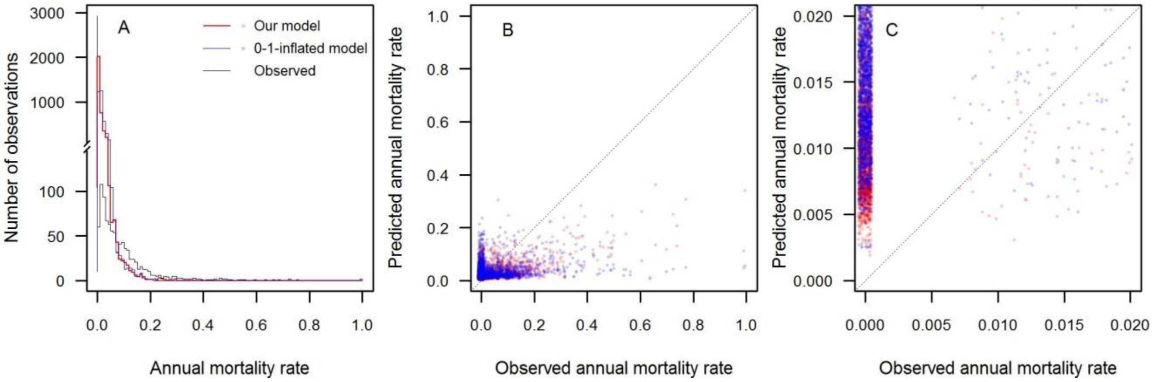

Figure A.3. Comparisons between our mortality and ingrowth models with zero-one-inflated models.

Similarly, consistent findings as for mortality in terms of model performance were also found for ingrowth analysis. The minimum RMSE of the predictions on ingrowth from zero-one-inflated beta model was 0.0262 comparing to 0.0233 and 0.0222 (with random effects) of our model. Overall, we evaluated the more traditional zero-inflated approach and found it to not be superior to our approach. More importantly, our findings in terms of parameter significance and magnitude of influence were consistent with the zero-inflated approach.

A.5. The Effects of Site Characteristics on the Stand Dynamics Examined

Site characteristics represented by the variables of *Slope*, cos(*Aspect*), *Slope* · cos(*Aspect*), *Elevation*, *Wetness index*, *Climate site index*, and *Biomass growth index* were initially tested in our models. However, none of them yielded significant effects or accounted for more than 1% of the variation in the response variables in both regions. The following table shows correlations between these characteristics and the response variables (and their residuals) in our models. It demonstrates that the correlations were generally negligible (especially with the residuals) and sometimes contradicting between the two regions. After these tests, dominant height appeared to be a better proxy of site potential productivity than the other covariates mentioned above. Hence, dominant height was used in our models.

Table A.2. The effects of site characteristics on the stand dynamics examined.

	Slope	**cos(*Aspect*)**	***Slope* ·cos(*Aspect*)**	***Elevation***	***Wetness index***	***Climate site index***	***Biomass growth index***
			Maine				
Annual net growth	0.045	-0.089	-0.024	0.013	-0.054	-0.046	0.007
Residuals of annual net growth	-0.003	0.074	0.009	0.013	-0.078	-0.003	-0.015
Annual mortality rates	0.028	0.007	0.039	0.003	-0.005	-0.032	-0.009
Residuals of annual morality rates	-0.006	0.019	0.023	0.010	0.022	0.015	-0.027
Annual ingrowth rates	0.006	-0.014	-0.025	-0.040	-0.023	-0.012	0.056
Residuals of annual ingrowth rates	0.027	-0.041	0.019	0.009	0.007	0.002	0.015
			New Brunswick				
Annual net growth	0.201	-0.030	0.030	0.210	-0.020	0.141	--
Residuals of annual net growth	0.006	0.028	0.023	-0.019	-0.031	0.022	--
Annual mortality rates	0.037	0.030	-0.041	-0.009	0.013	-0.003	--
Residuals of annual morality rates	0.047	-0.036	0.011	-0.008	0.051	0.018	--
Annual ingrowth rates	0.034	0.009	0.031	-0.058	-0.042	-0.038	--
Residuals of annual ingrowth rates	-0.023	0.002	-0.002	-0.026	-0.002	0.022	--

A.6. The Fit of Our Models

In addition to the statistics presented in the text and tables, the following graphs illustrate the fit of our models by plotting predicted values of net growth, mortality, and ingrowth over corresponding observed values (a few large observations were truncated to show details in the fit).

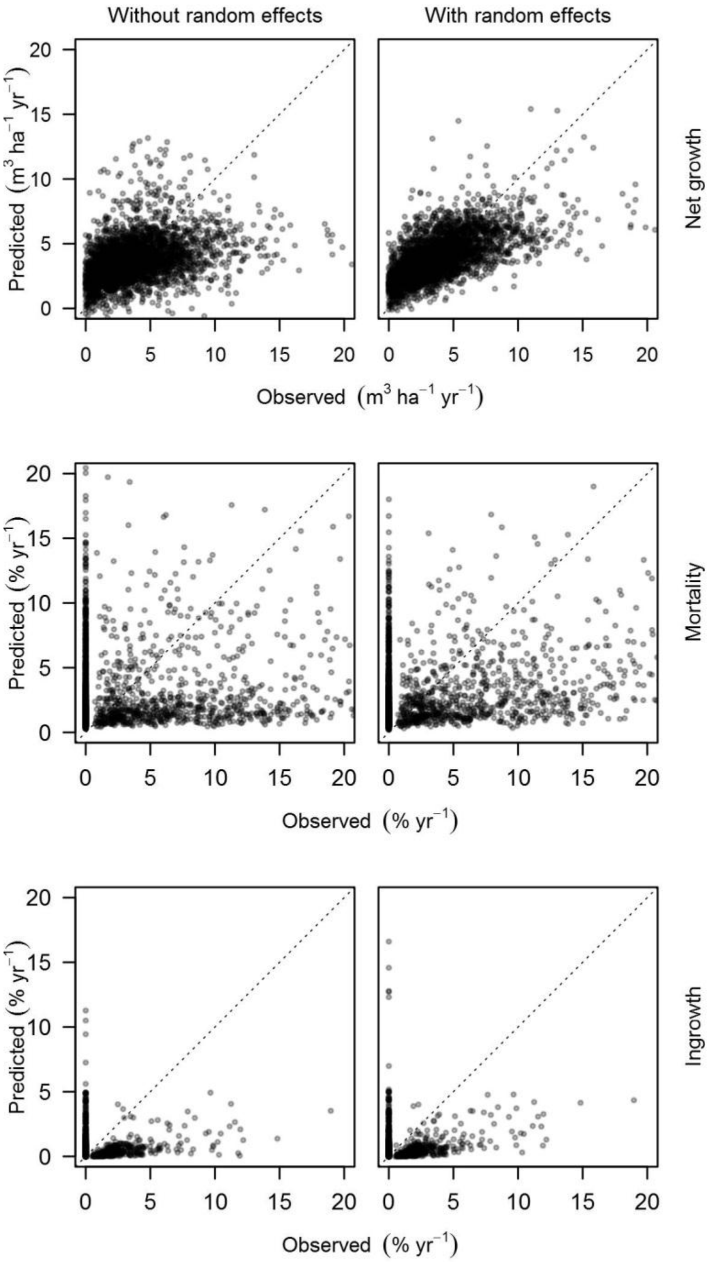

Figure A.4. The fit of our models for the Maine data.

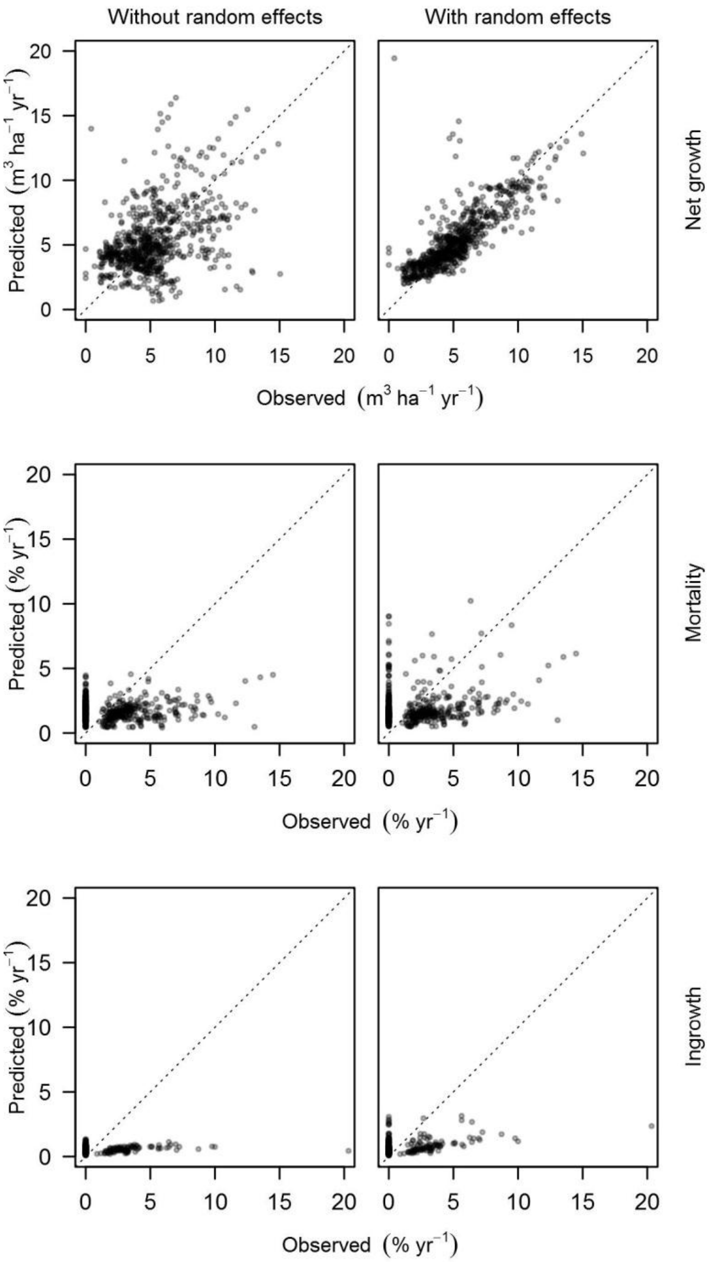

Figure A.5. The fit of our models for the New Brunswick data.

A.7. Cumulative Mortality Probability of Different Host Species

Our data indicated differences in host species' vulnerability to SBW defoliation. The following graph illustrates the observed cumulative mortality probability (%) over the observed cumulative defoliation (%) by species. It shows that cumulative mortality probability of red/black spruce surpasses that of balsam fir at high levels of defoliation. Since the beginning part of the SBW outbreak was not recorded, the actual cumulative mortality probability should be stretched to the right for New Brunswick.

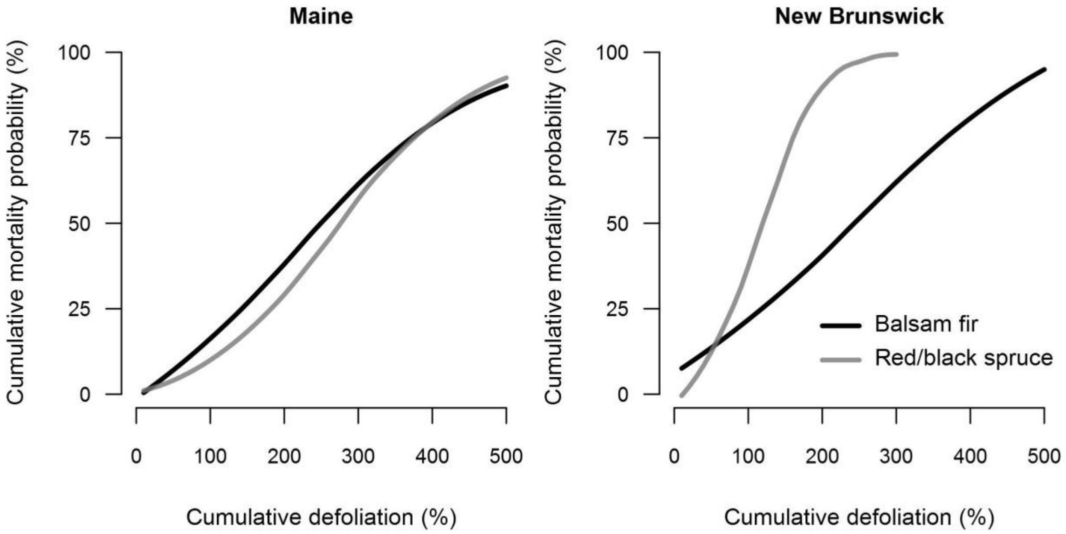

Figure A.6. Cumulative mortality probability of different host species.

APPENDIX B: SUPPLEMENTAL MATERIALS OF CHAPTER 3

B.1. A Summary of the Data

A summary of individual trees attributes of various host species, where BAL is basal area of trees larger than the subject tree in DBH (m^2 ha^{-1}); cumulative defoliation is cumulative sums of the percentage defoliation of current-year foliage from all previous years until current year (%).

Table B.1. A summary of the data.

	Maine					New Brunswick				
Attributes	**Mean**	**Median**	**SD**	**Min.**	**Max.**	**Mean**	**Median**	**SD**	**Min.**	**Max.**
						Balsam fir				
			n = 89 976					*n = 2 819*		
DBH (cm)	17.49	16.51	4.55	11.43	53.85	19.21	18.30	6.16	9.00	43.50
ΔDBH (cm $year^{-1}$)	0.13	0.08	0.13	0.00	1.52	0.27	0.23	0.19	0.00	1.80
Height* (m)	14.51	14.63	3.04	2.13	26.52	12.05	12.00	3.13	2.60	25.00
ΔHeight (m $year^{-1}$)	0.07	0.00	0.21	0.00	13.41	--	--	--	--	--
Height to crown base (m)	11.48	11.28	4.47	0.00	26.21	--	--	--	--	--
ΔHeight to crown base (m $year^{-1}$)	0.22	0.00	0.69	0.00	14.63	--	--	--	--	--
Crown ratio	0.22	0.20	0.23	0.00	1.00	--	--	--	--	--
Mortality (% $year^{-1}$)	5.81	--	--	--	--	2.76	--	--	--	--
BAL of softwood (m^2 ha^{-1})	17.10	15.38	11.22	0.00	63.11	12.13	10.60	8.64	0.00	44.35
BAL of hardwood (m^2 ha^{-1})	5.35	2.78	6.92	0.00	42.34	4.50	3.35	4.47	0.00	24.61
Cumulative defoliation (%)	193	158	146	0	845	148	120	115	10	700

(Table B.1. continued)

	Maine					**New Brunswick**				
Attributes	**Mean**	**Median**	**SD**	**Min.**	**Max.**	**Mean**	**Median**	**SD**	**Min.**	**Max.**
Black spruce										
			n = 8 584					*n = 1 240*		
DBH (cm)	17.32	16.00	4.83	11.43	36.58	18.65	17.50	5.99	7.30	46.80
ΔDBH (cm year^{-1})	0.12	0.08	0.13	0.00	1.27	0.16	0.13	0.13	0.00	0.97
Height* (m)	12.91	12.50	2.68	6.40	20.73	12.71	12.50	2.97	5.50	21.50
ΔHeight (m year^{-1})	0.04	0.00	0.12	0.00	2.44	--	--	--	--	--
Height to crown base (m)	9.53	9.45	3.96	0.00	20.73	--	--	--	--	--
ΔHeight to crown base (m year^{-1})	0.12	0.00	0.45	0.00	10.36	--	--	--	--	--
Crown ratio	0.27	0.28	0.26	0.00	1.00	--	--	--	--	--
Mortality (% year^{-1})	1.43	--	--	--	--	1.56	--	--	--	--
BAL of softwood (m^{2} ha^{-1})	11.99	10.71	8.40	0.00	43.92	12.96	12.15	8.35	0.00	43.46
BAL of hardwood (m^{2} ha^{-1})	0.47	0.00	2.20	0.00	33.62	1.83	0.74	2.90	0.00	14.34
Cumulative defoliation (%)	65	38	89	0	620	41	35	32	10	375
Red spruce										
			n = 83 563					*n = 2 257*		
DBH (cm)	19.57	18.03	6.41	11.43	59.69	22.65	20.90	8.30	8.60	61.90
ΔDBH (cm year^{-1})	0.14	0.13	0.14	0.00	1.52	0.22	0.20	0.19	0.00	3.70
Height* (m)	14.59	14.63	3.09	3.96	26.82	13.48	13.50	3.83	4.00	30.00
ΔHeight (m year^{-1})	0.05	0.00	0.15	0.00	6.10	--	--	--	--	--
Height to crown base (m)	11.05	10.36	4.17	0.00	26.82	--	--	--	--	--
ΔHeight to crown base (m year^{-1})	0.14	0.13	0.14	0.00	1.52	--	--	--	--	--
Crown ratio	0.25	0.28	0.23	0.00	1.00	--	--	--	--	--
Mortality (% year^{-1})	1.24	--	--	--	--	0.96	--	--	--	--
BAL of softwood (m^{2} ha^{-1})	16.84	15.34	11.93	0.00	63.74	9.51	7.89	7.49	0.00	36.54
BAL of hardwood (m^{2} ha^{-1})	3.29	0.00	5.61	0.00	42.34	2.28	0.71	3.88	0.00	19.28
Cumulative defoliation (%)	100	70	104	0	659	51	45	40	10	360

(Table B.1. continued)

	Maine					New Brunswick				
Attributes	**Mean**	**Median**	**SD**	**Min.**	**Max.**	**Mean**	**Median**	**SD**	**Min.**	**Max.**
					White spruce					
			n = 9 154					*n = 845*		
DBH (cm)	20.67	19.05	7.43	11.43	50.55	24.04	23.00	8.41	9.70	63.60
ΔDBH (cm year^{-1})	0.15	0.13	0.16	0.00	1.27	0.29	0.25	0.19	0.00	1.20
Height* (m)	14.58	14.33	3.51	6.71	25.60	12.75	12.50	3.83	4.00	25.50
ΔHeight (m year^{-1})	0.06	0.00	0.18	0.00	3.35	--	--	--	--	--
Height to crown base (m)	10.53	10.06	4.51	0.00	25.60	--	--	--	--	--
ΔHeight to crown base (m year^{-1})	0.19	0.00	0.59	0.00	9.75	--	--	--	--	--
Crown ratio	0.28	0.31	0.26	0.00	1.00	--	--	--	--	--
Mortality (% year^{-1})	0.38	--	--	--	--	1.13	--	--	--	--
BAL of softwood (m^2 ha^{-1})	15.48	13.47	12.16	0.00	54.85	8.75	6.66	7.56	0.00	34.00
BAL of hardwood (m^2 ha^{-1})	4.61	1.19	7.40	0.00	42.34	2.39	1.43	3.26	0.00	22.91
Cumulative defoliation (%)	5	0	28	0	280	114	85	91	10	640

APPENDIX C: SUPPLEMENTAL MATERIALS OF CHAPTER 4

C.1. Correlation between Tree-level as well as Stand-level Characteristics and Defoliation

Table C.1. Correlation coefficients between some common tree-level as well as stand-level characteristics and individual tree defoliation.

Individual tree defoliation (%)	DBH (cm)	Height (m)	Crown ratio	BAL (m^2 ha^{-1})	BA (m^2 ha^{-1})	BA_{HW}/BA	Height/MHT_{SW}
Maine	-0.07	0.00	0.03	0.03	-0.02	-0.02	-0.02
New Brunswick	0.00	-0.03	--	0.07	0.16	0.04	0.06

BAL is basal area of trees larger than the subject tree in DBH at a location (m^2 ha^{-1}); BA and BA_{HW} are basal area and that of hardwoods in a plot (m^2 ha^{-1}), respectively; MHT_{SW} is mean height of softwood trees at a location (m). Height (MHT_{SW}) in New Brunswick is of the initial measurements obtained during 1976-1979.

C.2. Locations of Sample Plots and Some Characteristics of Samples

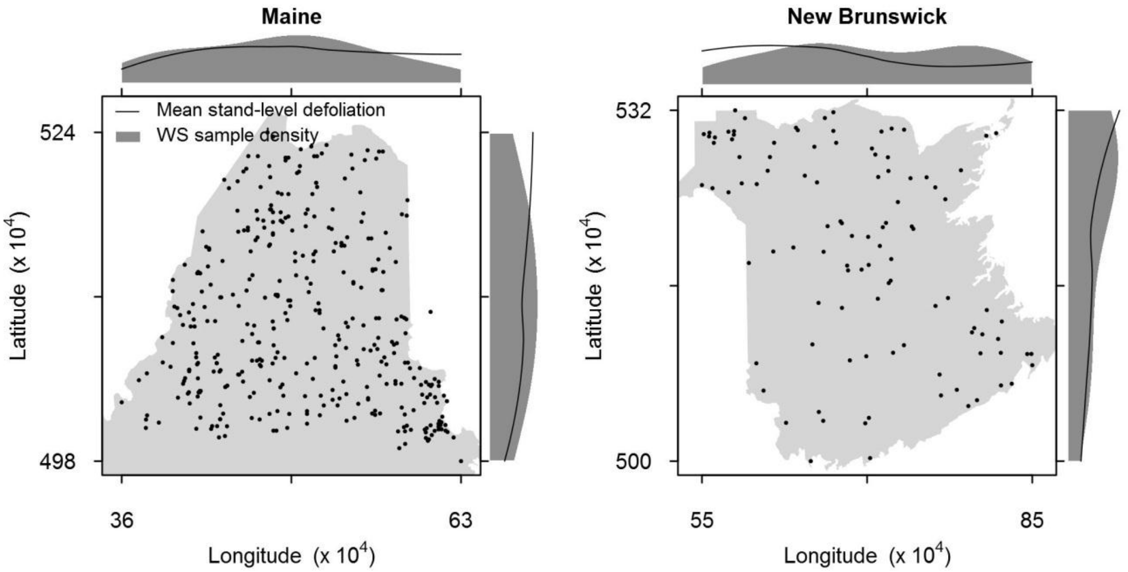

Figure C.1. Locations of sample plots as well as distributions of white spruce (WS) sample density (trees per plot) and mean stand-level defoliation (%) by region. Ideally, white spruce samples would be uniformly distributed over the regions and ranges of defoliation (i.e., balanced samples). However, white spruce sample density was slightly higher in southeastern Maine (where defoliation was lower), and was much higher in northern New Brunswick (where defoliation was also much higher). These patterns in samples likely contributed to the observed regional difference in white spruce' susceptibility.

C.3. Standard Deviation in Individual Tree Defoliation

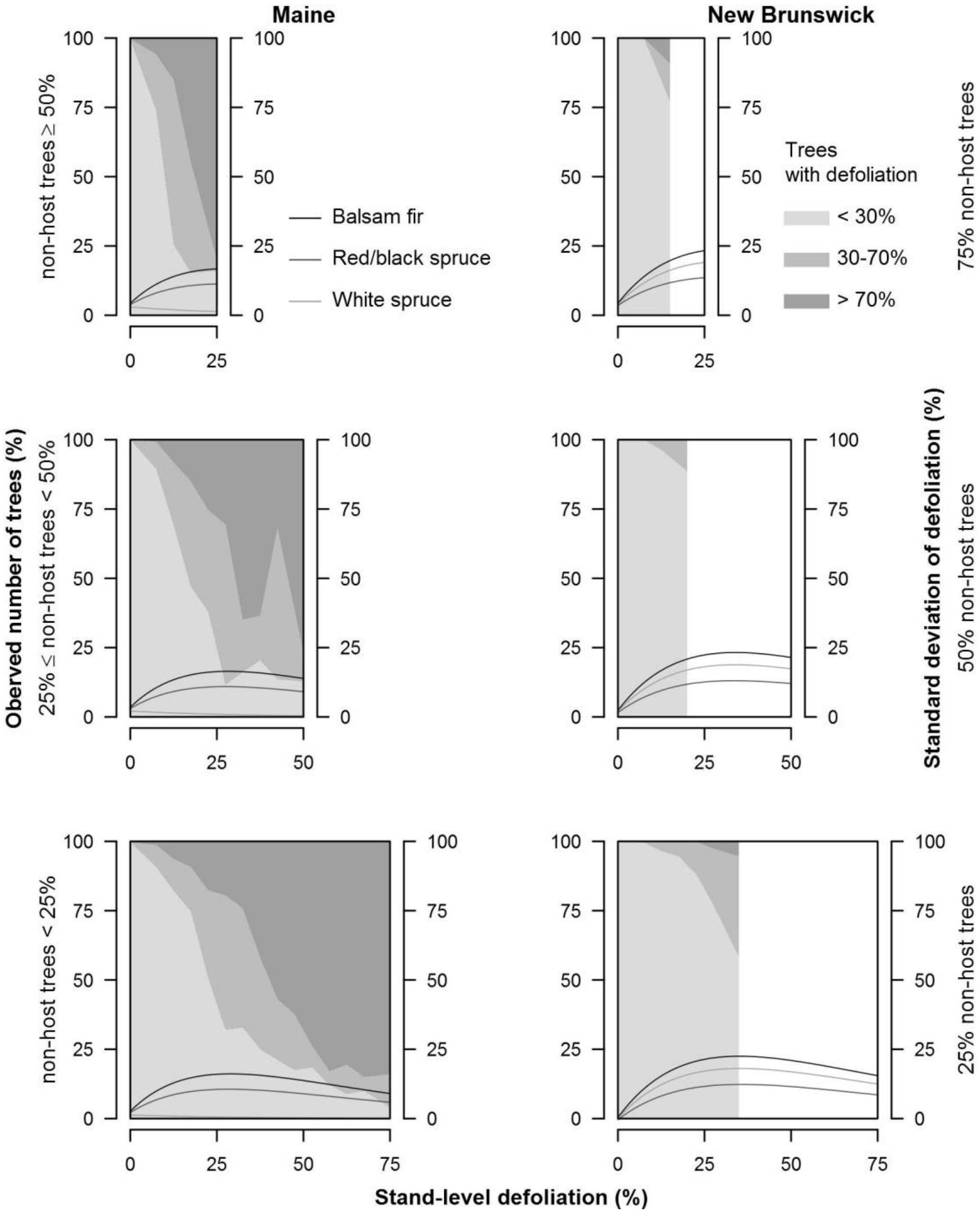

Figure C.2. Observed distribution of trees in different defoliation classes with various percentages of non-host trees by region (left axes; shown by shaded background). Predicted standard deviation of individual tree defoliation (%) as a function of stand-level defoliation (%) by percentage of non-host trees at a location (right axes; shown by lines, with all the other covariates at their means).

APPENDIX D: SUPPLEMENTAL MATERIALS OF CHAPTER 5

D.1. Developed R code to implement the Forest Vegetation Simulator Acadian variant (FVS-ACD) refined by our spruce budworm modifiers

```
# FVS_ACD(): performing growth and yield projections using FVS-ACD.
# Usage: FVS_ACD(PLOT, SPP, DBH, HT, CR, DEF, CSI, EXPF, CutPoint, T=0,
N_YEAR)
# Arguments:
      # PLOT: numeric or character (do not use factor), sorting is not
      required;
      # SPP: species, numeric or character (do not use factor);
      # DBH: diameter at breast height (cm), numeric;
      # HT: height (m), numeric;
      # CR: crown ratio, numeric;
      # DEF: cumulative defoliation observed (%), 0 if not defoliated,
      numeric;
      # CSI: climate site index, numeric;
      # EXPF: expansion factor of each plot, numeric;
      # CutPoint: the cut point DBH of ingrowth (cm), numeric;
      # T: years into defoliation, default value of 0 indicates the
      first year of defoliation, value of 999 indicates not applying
      defoliation modifiers, numeric;
      # N_year: duration of projection (year), numeric.
# Value: return a list of the length indicated by N_YEAR, each element
of the list is a data.frame representing projections at that year with
columns of PLOT, SPP, DBH, HT, CR, and DEF.
FVS_ACD <- function(PLOT, SPP, DBH, HT, CR, DEF, CSI, EXPF, CutPoint,
T=0, N_YEAR)
{
```

```
      PROJ <- vector("list", N_YEAR)
      N <- MORT <- ING <- 0
      DEF_I <- DEF
      HW_SPP <- c("YB","RM","SM","BT","AB","OH","PB")
      SW_SPP <- c("EH","RS","WC","BF","BS","WP","OS","WS")
      while(N_YEAR-N >= 1)
      {
            m <- match(SPP, PARA$SPP)
            m[is.na(m)] <- 1
            n <- length(PLOT)
            ID <- ID.new <- ID.int <- 1:n
            MCW <- PARA$b1.MCW[m]*DBH^PARA$b2.MCW[m]
PBA <- BAL.SW <- BAL.HW <- BA.SW <- BA.HW <- tph <- topht <- SDI <-
SDImax <- CCF <- numeric(n)
for(i in 1:n)
{
      PBA[i] <- 0.25*pi*sum(DBH[PLOT==PLOT[i] &
SPP==SPP[i]]^2)/10^4*EXPF
      BAL.SW[i] <- 0.25*pi*sum(DBH[PLOT==PLOT[i] & DBH>DBH[i] &
      SPP%in%SW_SPP]^2)/10^4*EXPF
      BAL.HW[i] <- 0.25*pi*sum(DBH[PLOT==PLOT[i] & DBH>DBH[i] &
      SPP%in%HW_SPP]^2)/10^4*EXPF
      BA.SW[i] <- 0.25*pi*sum(DBH[PLOT==PLOT[i] &
      SPP%in%SW_SPP]^2)/10^4*EXPF
      BA.HW[i] <- 0.25*pi*sum(DBH[PLOT==PLOT[i] &
      SPP%in%HW_SPP]^2)/10^4*EXPF
      tph[i] <- length(DBH[PLOT==PLOT[i]])*EXPF
      topht[i] <- max(HT[PLOT==PLOT[i]])
      SDI[i] <- sum((DBH[PLOT==PLOT[i]]/25.4)^1.605)*EXPF
```

```
      SDImax[i] <- -6017.3*mean(PARA$SG[m][PLOT==PLOT[i]]) + 4156.3
      CCF[i] <- 100*0.25*pi*sum(MCW[PLOT==PLOT[i]]^2)/10^4*EXPF
      }
            BAL <- BAL.SW + BAL.HW
            BA <- BA.SW + BA.HW
            RS <- sqrt(10000/tph)/topht
            BAperc <- 1 - BAL/BA
            BALmod <- (1-BAperc)/RS
            pBAL.SW <- BAL.SW/(BAL+0.1)
            RD <- SDI/SDImax
            PBA <- PBA/BA
PLOT_add <- data.frame(PLOT=PLOT, SPP=SPP, CSI=CSI, ID=ID,
stringsAsFactors=FALSE)[!duplicated(data.frame(PLOT=PLOT, SPP=SPP,
CSI=CSI, ID=ID, stringsAsFactors=FALSE)[,1:2]),]
if(T!=999)
{
      dDEF <- T*(1-exp(PARA$p1.DEF[m]*(T-PARA$p2.DEF[m]))) +
      PARA$p3.DEF[m]*T*exp((PARA$p4.DEF[m]*DEF_I+PARA$p5.DEF[m]*CR)*T)
      + (SPP=="WS")*T
      DEF <- DEF + dDEF
      DEF[dDEF<0] <- DEF[dDEF<0]-dDEF[dDEF<0]-100
      DEF[DEF<0] <- 0
      mod_DBH <- exp(PARA$p.DBH[m] * DEF)
      mod_HT <- exp(PARA$p.HT[m] * DEF) *
      ifelse(runif(n)>PARA$p.HTc[m], 1, 0)
      mod_HCB <- exp(PARA$p1.HCB[m]*DEF + PARA$p2.HCB[m]*CR)
      mod_MORT <- PARA$p.MORT[m] * DEF
      mod_IPH <- PARA$p1.IPH[1] * c(unlist(by(DEF, list(PLOT),
      function(x) rep(mean(x),length(x))))) + PARA$p2.IPH[1]
```

```
      names(mod_IPH) <- ID[match(c(unlist(by(PLOT, list(PLOT),
      function(x) x))), PLOT)]
      mod_IPH <- mod_IPH[match(ID[!duplicated(PLOT)], names(mod_IPH))]
      mod_IPH[mod_IPH==0] <- 1
      mod_Icomp <- PARA$p1.Icomp[1] * c(unlist(by(DEF, list(PLOT,SPP),
      function(x) rep(mean(x),length(x))))) + PARA$p2.Icomp[1]
      names(mod_Icomp) <- ID[match(c(unlist(by(PLOT, list(PLOT, SPP),
      function(x) x))), PLOT)]
      mod_Icomp <- mod_Icomp[match(rownames(PLOT_add),
names(mod_Icomp))]
      mod_Icomp[mod_Icomp==0] <- 1
      mod_DBH[is.na(mod_DBH)] <- mod_HT[is.na(mod_HT)] <-
      mod_HCB[is.na(mod_HCB)] <- mod_IPH[is.na(mod_IPH)] <-
      mod_Icomp[is.na(mod_Icomp)] <- 1
      mod_MORT[is.na(mod_MORT)] <- 0
      } else
            {
            mod_DBH <- mod_HT <- mod_HCB <- mod_IPH <- mod_Icomp <- 1
            mod_MORT <- 0
            }
dDBH <- exp(-1.6331538+PARA$b0.DBH[m] + (0.0070441+PARA$b1.DBH[m])*DBH
-0.0002784*DBH^2 + 0.1257197*log(CR+0.001) + (-
0.2705499+PARA$b4.DBH[m])*log(BALmod+0.001) + 0.2941056*log(CSI) + (-
0.0616965+PARA$b6.DBH[m])*sqrt(BA*RD) -0.1465285*sqrt(pBAL.SW)) *
mod_DBH
dDBH[dDBH<0] <- 0
dHT <- exp(-3.925083+PARA$b0.HT[m] + (-0.061691+PARA$b1.HT[m])*HT +
0.255589*log(HT) + 0.199307*log(CR+0.001) + (-
0.091328+PARA$b4.HT[m])*log(BALmod+0.001) + 1.025877*log(CSI) +
```

```
(0.115358+PARA$b6.HT[m])*log(BA*RD) +
(0.098963+PARA$b7.HT[m])*sqrt(pBAL.SW) + 0.003199*BA*RD) * mod_HT
dHT[dHT<0] <- 0
HCB <- HT/(1+exp((0.29070+PARA$b0.HCB[m])+0.00636*DBH-
0.02288*HT+0.08232*DBH/HT-0.03086*log(CCF+1)-
0.01701*(BAL.SW+BAL.HW+1))) * mod_HCB
ID.index <- ID[ID%in%ID.int]
HCB[ID.index][HCB[ID.index]<(1-CR[ID.index])*HT[ID.index]] <- ((1-
CR[ID.index])*HT[ID.index])[HCB[ID.index]<(1-
CR[ID.index])*HT[ID.index]]
dMORT <-
1/(1+exp(PARA$b0.MORT[m]+PARA$b1.MORT[m]*DBH+PARA$b2.MORT[m]*DBH^2)) *
(0.010591127*BALmod + 0.049789571*sqrt(pBAL.SW) - 0.124299218*CR -
0.199434641*log(CSI) + 0.523150752 + mod_MORT)
CR <- (HT-HCB)/HT
CR[CR<0] <- 0
DBH <- DBH + dDBH
HT <- HT + dHT
MORT <- MORT + dMORT
link1 <- -0.2116-0.0255*(BA.SW+BA.HW)-0.1396*BA.HW/(BA.SW+BA.HW)-
0.0054*(tph/1000)+0.0433*CSI+0.0409*CutPoint
PI <- 1/(1+exp(-link1))
eta <- 3.8982-0.0257*(BA.SW+BA.HW)-
0.3668*BA.HW/(BA.SW+BA.HW)+0.0002*(tph/1000)+0.0216*CSI-0.0514*CutPoint
IPH <- exp(eta)*PI
names(IPH) <- 1:n
IPH <- IPH[match(ID[!duplicated(PLOT)], names(IPH))] * mod_IPH
```

```
perc <-
PARA$b0.ING[m]+PARA$b1.ING[m]*(BA.SW+BA.HW)+PARA$b2.ING[m]*PBA+PARA$b3.
ING[m]*CSI+PARA$b4.ING[m]*CutPoint
perc <- 1/(1+exp(-perc))
names(perc) <- 1:n
perc <- perc[match(rownames(PLOT_add), names(perc))] * mod_Icomp
IPH <- IPH[match(names(perc), names(IPH))]
dING <- IPH*perc/EXPF
dING[is.na(dING)] <- 0
names(dING) <- names(perc)
if(length(ING)==1)
{
      ING <- ING + dING
      names(ING) <- names(dING)
      ING.new <- data.frame(PLOT=PLOT_add$PLOT[match(names(ING),
      rownames(PLOT_add))], SPP=PLOT_add$SPP[match(names(ING),
      rownames(PLOT_add))], ING=ING)
      } else
            {
            dING <- data.frame(PLOT=PLOT_add$PLOT[match(names(dING),
            rownames(PLOT_add))], SPP=PLOT_add$SPP[match(names(dING),
            rownames(PLOT_add))], ING=dING, ID=names(dING))
            ING.new <- merge(ING.new, dING, by=c("PLOT","SPP"),
      all=FALSE)
            ING <- ING.new$ING <- ING.new$ING.x + ING.new$ING.y
            rownames(ING.new) <- ING.new$ID
            ING.new <- ING.new[,c("PLOT","SPP","ING")]
            }
ING.add <- which(ING>=1)
```

```
if(length(ING.add)>0)

{

      DBH <- c(DBH, rep(CutPoint, sum(trunc(ING[ING.add]))))

      HT <- c(HT, rep(11.10, sum(trunc(ING[ING.add]))))

      CR <- c(CR, rep(0.204, sum(trunc(ING[ING.add]))))

      MORT <- c(MORT, rep(0, sum(trunc(ING[ING.add]))))

      ID.new <- c(ID, (n+1):(n+sum(trunc(ING[ING.add]))))

      CSI <- c(CSI, rep(PLOT_add$CSI[match(rownames(ING.new[ING.add,]),

      rownames(PLOT_add))], trunc(ING.new$ING[ING.add])))

      SPP <- c(SPP, rep(PLOT_add$SPP[match(rownames(ING.new[ING.add,]),

      rownames(PLOT_add))], trunc(ING.new$ING[ING.add])))

      PLOT <- c(PLOT,

      rep(PLOT_add$PLOT[match(rownames(ING.new[ING.add,]),

      rownames(PLOT_add))], trunc(ING[ING.add])))

      if(sum(DEF==0)<n)

      {

            DEF <- c(DEF,

            rep(ifelse(PLOT_add$SPP[match(rownames(ING.new[ING.add,]),

            rownames(PLOT_add))]%in%c("BF","BS","RS","WS"), 29, 0),

            trunc(ING[ING.add])))

            DEF_I <- c(DEF_I,

            rep(ifelse(PLOT_add$SPP[match(rownames(ING.new[ING.add,]),

            rownames(PLOT_add))]%in%c("BF","BS","RS","WS"), 29, 0),

            trunc(ING[ING.add])))} else

                        {

                        DEF <- c(DEF, rep(0, sum(trunc(ING[ING.add]))))

                        DEF_I <- c(DEF_I, rep(0,

                        sum(trunc(ING[ING.add]))))

      }}
```

```
ING[ING.add] <- ING.new$ING[ING.add] <- ING[ING.add] -
trunc(ING[ING.add])
MORT.drop <- which(MORT>=0.214)
if(length(MORT.drop)>0)
{PLOT <- PLOT[-MORT.drop]; SPP <- SPP[-MORT.drop]; DBH <- DBH[-
MORT.drop]; HT <- HT[-MORT.drop]; CR <- CR[-MORT.drop]; MORT <- MORT[-
MORT.drop]; DEF <- DEF[-MORT.drop]; DEF_I <- DEF_I[-MORT.drop]; CSI <-
CSI[-MORT.drop]; ID.new <- ID.new[-MORT.drop]}
ID.int <- intersect(ID, ID.new)
ID <- ID.new
N <- N+1
T <- T+1
PROJ[[N]] <- data.frame(PLOT=PLOT, SPP=SPP, DBH=DBH, HT=HT, CR=CR,
DEF=DEF, stringsAsFactors=FALSE)
}
      PROJ
      }
```

D.2. Parameters (PARA) used in the R code for the Forest Vegetation Simulator Acadian variant refined by our spruce budworm modifiers

```
PARA <- rbind(
data.frame(SPP="All of the others", SG=0.3, b0.DBH=0, b1.DBH=0,
b4.DBH=0, b6.DBH=0, b0.HT=0, b1.HT=0, b4.HT=0, b6.HT=0, b7.HT=0,
b0.MORT=2.6967072576, b1.MORT=-0.001250889, b2.MORT=0.0007521152,
b1.MCW=2.24262, b2.MCW=0.462653333, b0.HCB=0, b0.ING=0, b1.ING=0,
b2.ING=0, b3.ING=0, b4.ING=0, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0,
p5.DEF=0, p.DBH=0, p.HT=0, p.HTc=0.8948422, p1.HCB=0, p2.HCB=0,
p.MORT=0, p1.IPH=-0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053,
p2.Icomp=1.245914),
data.frame(SPP="AB", SG=0.64, b0.DBH=-0.034977457, b1.DBH=0.007276127,
b4.DBH=0.117697955, b6.DBH=-0.0382661, b0.HT=-0.415979307,
b1.HT=0.0274010197, b4.HT=0.196582208, b6.HT=-0.164287184,
b7.HT=0.17710536, b0.MORT=2.152681379, b1.MORT=-0.0269825907,
b2.MORT=0.0002203177, b1.MCW=2.93, b2.MCW=0.434, b0.HCB=-0.218384027,
b0.ING=-2.9832, b1.ING=-0.0020, b2.ING=2.4837, b3.ING=0.0673, b4.ING=-
0.0167, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0,
p.HT=0, p.HTc=0.9226306, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-
0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="BF", SG=0.35, b0.DBH=0.124494862, b1.DBH=0.00123841,
b4.DBH=0.021706955, b6.DBH=-0.012162306, b0.HT=-0.252382258,
b1.HT=0.0100278394, b4.HT=-0.115915182, b6.HT=-0.019904875,
b7.HT=0.35826384, b0.MORT=2.5743949775, b1.MORT=-0.0851930923,
b2.MORT=0.0015971909, b1.MCW=1.37, b2.MCW=0.572, b0.HCB=0.093585699,
b0.ING=-3.0291, b1.ING=0.0027, b2.ING=2.7779, b3.ING=0.0211,
b4.ING=0.0221, p1.DEF=0.0175090638, p2.DEF=11.9561909843, p3.DEF=-
0.0442501199, p4.DEF=-0.0009501345, p5.DEF=-0.2969766902, p.DBH=-
```

```
0.0116125, p.HT=-0.0155001, p.HTc=0.8689313, p1.HCB=0.007474090,
p2.HCB=-0.929648888, p.MORT=0.002153933, p1.IPH=-0.0011637, p1.Icomp=-
0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="BS", SG=0.46, b0.DBH=-0.032226829, b1.DBH=-0.01442781,
b4.DBH=-0.021477635, b6.DBH=-0.001507636, b0.HT=0.09727877, b1.HT=-
0.0270708651, b4.HT=0.034082833, b6.HT=0.023416841, b7.HT=-0.27796473,
b0.MORT=1.9568828063, b1.MORT=0.0535388009, b2.MORT=-0.0010376306,
b1.MCW=0.535, b2.MCW=0.742, b0.HCB=-0.227771445, b0.ING=-1.2500,
b1.ING=-0.0132, b2.ING=2.0470, b3.ING=-0.0514, b4.ING=0.0351,
p1.DEF=0.004462929, p2.DEF=18.161944433, p3.DEF=-0.021691545, p4.DEF=-
0.003606711, p5.DEF=-0.087007898, p.DBH=-0.0236663, p.HT=-0.1373007,
p.HTc=0.9119572, p1.HCB=0.007364462, p2.HCB=-0.627453191,
p.MORT=0.007823319, p1.IPH=-0.0011637, p1.Icomp=-0.007686,
p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="BT", SG=0.39, b0.DBH=0.107871306, b1.DBH=-0.0004487118,
b4.DBH=-0.049918635, b6.DBH=0.049907667, b0.HT=0.097631862, b1.HT=-
0.0019892345, b4.HT=-0.033205181, b6.HT=0.178102299, b7.HT=-0.42712909,
b0.MORT=2.1791849646, b1.MORT=-0.0125375225, b2.MORT=0.0008529794,
b1.MCW=4.04, b2.MCW=0.308, b0.HCB=0.010040571, b0.ING=-2.9832, b1.ING=-
0.0020, b2.ING=2.4837, b3.ING=0.0673, b4.ING=-0.0167, p1.DEF=0,
p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0, p.HT=0,
p.HTc=0.9171139, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-0.0011637,
p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="EH", SG=0.4, b0.DBH=-0.073679869, b1.DBH=0.01541532,
b4.DBH=0.176123957, b6.DBH=-0.070655479, b0.HT=-0.338641101,
b1.HT=0.0149152575, b4.HT=0.042828473, b6.HT=-0.023914376, b7.HT=-
0.02984288, b0.MORT=4.5205542708, b1.MORT=-0.0670350692,
b2.MORT=0.0012041907, b1.MCW=2.44, b2.MCW=0.408, b0.HCB=0.403937729,
b0.ING=-4.7182, b1.ING=0.0070, b2.ING=3.2269, b3.ING=0.1000,
```

```
b4.ING=0.0188, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0,
p.DBH=0, p.HT=0, p.HTc=0.9189400, p1.HCB=0, p2.HCB=0, p.MORT=0,
p1.IPH=-0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053,
p2.Icomp=1.245914),
data.frame(SPP="OH", SG=0.5121, b0.DBH=0.182086574, b1.DBH=0.004291105,
b4.DBH=0.031149091, b6.DBH=-0.038283159, b0.HT=0.190850506,
b1.HT=0.008856123, b4.HT=0.096511731, b6.HT=-0.179549618,
b7.HT=0.11449758, b0.MORT=4.552236589, b1.MORT=-0.5204997134,
b2.MORT=0.0125996045, b1.MCW=4.04, b2.MCW=0.308, b0.HCB=-0.042894377,
b0.ING=-2.9832, b1.ING=-0.0020, b2.ING=2.4837, b3.ING=0.0673, b4.ING=-
0.0167, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0,
p.HT=0, p.HTc=0.9104781, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-
0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="OS", SG=0.445, b0.DBH=0, b1.DBH=0, b4.DBH=0, b6.DBH=0,
b0.HT=0, b1.HT=0, b4.HT=0, b6.HT=0, b7.HT=0, b0.MORT=2.6967072576,
b1.MORT=-0.001250889, b2.MORT=0.0007521152, b1.MCW=1.597128571,
b2.MCW=0.513957143, b0.HCB=0, b0.ING=-4.7182, b1.ING=0.0070,
b2.ING=3.2269, b3.ING=0.1000, b4.ING=0.0188, p1.DEF=0, p2.DEF=0,
p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0, p.HT=0, p.HTc=0.8592058,
p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-0.0011637, p1.Icomp=-0.007686,
p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="PB", SG=0.55, b0.DBH=0.147672195, b1.DBH=-0.01733291,
b4.DBH=-0.121852844, b6.DBH=0.002444024, b0.HT=-0.130932583, b1.HT=-
0.0078414315, b4.HT=0.111669147, b6.HT=-0.044044815, b7.HT=0.11333075,
b0.MORT=2.5863343441, b1.MORT=-0.0518497247, b2.MORT=0.0021853588,
b1.MCW=1.48, b2.MCW=0.623, b0.HCB=-0.180946077, b0.ING=-2.5645,
b1.ING=0.0020, b2.ING=2.6624, b3.ING=-0.0010, b4.ING=-0.0127, p1.DEF=0,
p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0, p.HT=0,
```

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p.HTc=0.8744374, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-0.0011637,
p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="RM", SG=0.54, b0.DBH=-0.053329455, b1.DBH=-
0.0000425553, b4.DBH=-0.018221214, b6.DBH=0.02432616, b0.HT=0.12732005,
b1.HT=-0.0245368295, b4.HT=0.053246849, b6.HT=0.00579006,
b7.HT=0.14672003, b0.MORT=2.1674971386, b1.MORT=0.0557266595, b2.MORT=-
0.0010435394, b1.MCW=2.17, b2.MCW=0.491, b0.HCB=-0.202478201, b0.ING=-
0.6566, b1.ING=0.0123, b2.ING=1.7669, b3.ING=-0.0421, b4.ING=-0.0283,
p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0, p.HT=0,
p.HTc=0.9213483, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-0.0011637,
p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="RS", SG=0.4, b0.DBH=0.040808688, b1.DBH=0.004242409,
b4.DBH=-0.004858248, b6.DBH=-0.008108392, b0.HT=-0.048412618, b1.HT=-
0.0079040397, b4.HT=-0.145815645, b6.HT=0.060567801, b7.HT=0.0797388,
b0.MORT=2.0420797297, b1.MORT=0.0425701678, b2.MORT=-0.0004901795,
b1.MCW=1.80, b2.MCW=0.461, b0.HCB=-0.121308265, b0.ING=-1.2500,
b1.ING=-0.0132, b2.ING=2.0470, b3.ING=-0.0514, b4.ING=0.0351,
p1.DEF=0.004462929, p2.DEF=18.161944433, p3.DEF=-0.021691545, p4.DEF=-
0.003606711, p5.DEF=-0.087007898, p.DBH=-0.0213097, p.HT=-0.2907858,
p.HTc=0.9008300, p1.HCB=0.006873691, p2.HCB=-0.630759428,
p.MORT=0.001598985, p1.IPH=-0.0011637, p1.Icomp=-0.007686,
p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="SM", SG=0.63, b0.DBH=0.12397129, b1.DBH=0.006428658,
b4.DBH=0.0137845, b6.DBH=-0.047456949, b0.HT=0.088620046,
b1.HT=0.0258811205, b4.HT=0.073470611, b6.HT=-0.218583608, b7.HT=-
0.14200099, b0.MORT=2.7069022565, b1.MORT=0.0086263655,
b2.MORT=0.0007235392, b1.MCW=3.31, b2.MCW=0.356, b0.HCB=-0.16382426,
b0.ING=-2.9832, b1.ING=-0.0020, b2.ING=2.4837, b3.ING=0.0673, b4.ING=-
0.0167, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0,
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p.HT=0, p.HTc=0.9097510, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-
0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="WC", SG=0.31, b0.DBH=-0.414076962, b1.DBH=0.01074121,
b4.DBH=0.145425792, b6.DBH=-0.001819793, b0.HT=0, b1.HT=0, b4.HT=0,
b6.HT=0, b7.HT=0, b0.MORT=3.647647507, b1.MORT=-0.0606735724,
b2.MORT=0.0008507857, b1.MCW=1.597128571, b2.MCW=0.513957143,
b0.HCB=0.419622685, b0.ING=-4.7182, b1.ING=0.0070, b2.ING=3.2269,
b3.ING=0.1000, b4.ING=0.0188, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0,
p5.DEF=0, p.DBH=0, p.HT=0, p.HTc=0.9217702, p1.HCB=0, p2.HCB=0,
p.MORT=0, p1.IPH=-0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053,
p2.Icomp=1.245914),
data.frame(SPP="WP", SG=0.35, b0.DBH=0.133589236, b1.DBH=0.008688826,
b4.DBH=0.064063728, b6.DBH=-0.011417414, b0.HT=0.004458537,
b1.HT=0.0069854589, b4.HT=-0.079402408, b6.HT=0.031357732,
b7.HT=0.16043057, b0.MORT=3.3383526175, b1.MORT=-0.0294498474,
b2.MORT=0.0009561864, b1.MCW=1.597128571, b2.MCW=0.513957143, b0.HCB=-
0.146685117, b0.ING=-5.1074, b1.ING=-0.0117, b2.ING=3.8817,
b3.ING=0.0501, b4.ING=0.0726, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0,
p5.DEF=0, p.DBH=0, p.HT=0, p.HTc=0.9076621, p1.HCB=0, p2.HCB=0,
p.MORT=0, p1.IPH=-0.0011637, p1.Icomp=-0.007686, p2.IPH=0.1397053,
p2.Icomp=1.245914),
data.frame(SPP="WS", SG=0.4, b0.DBH=0.286219598, b1.DBH=-0.00003104828,
b4.DBH=-0.049962785, b6.DBH=-0.027217847, b0.HT=-0.004902983,
b1.HT=0.001696414, b4.HT=-0.204246802, b6.HT=0.058944828,
b7.HT=0.15403836, b0.MORT=0.5437824528, b1.MORT=0.1052397713,
b2.MORT=0.0006332627, b1.MCW=1.50, b2.MCW=0.496, b0.HCB=0.100275538,
b0.ING=-1.2500, b1.ING=-0.0132, b2.ING=2.0470, b3.ING=-0.0514,
b4.ING=0.0351, p1.DEF=0, p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0,
p.DBH=-0.1359938, p.HT=-0.6065810, p.HTc=0.8662084, p1.HCB=0.009869723,
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p2.HCB=-0.654718900, p.MORT=0.016924216, p1.IPH=-0.0011637, p1.Icomp=-
0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914),
data.frame(SPP="YB", SG=0.62, b0.DBH=0.09393567, b1.DBH=0.003789904,
b4.DBH=0.087753032, b6.DBH=-0.047504164, b0.HT=0.052168661, b1.HT=-
0.0178393926, b4.HT=0.048486031, b6.HT=-0.001779362, b7.HT=0.00445344,
b0.MORT=2.6967072576, b1.MORT=-0.001250889, b2.MORT=0.0007521152,
b1.MCW=4.04, b2.MCW=0.308, b0.HCB=0.003235064, b0.ING=-2.5645,
b1.ING=0.0020, b2.ING=2.6624, b3.ING=-0.0010, b4.ING=-0.0127, p1.DEF=0,
p2.DEF=0, p3.DEF=0, p4.DEF=0, p5.DEF=0, p.DBH=0, p.HT=0,
p.HTc=0.9160839, p1.HCB=0, p2.HCB=0, p.MORT=0, p1.IPH=-0.0011637,
p1.Icomp=-0.007686, p2.IPH=0.1397053, p2.Icomp=1.245914)
)
```

BIOGRAPHY OF THE AUTHOR

Cen Chen has a bachelor's degree in horticulture and a master's degree in environmental monitoring and assessment (forest inventory). Information regarding his place of birth, place of high school graduation, place and date of college graduation, professional or employment experience, scholarly publications, and memberships in professional or honorary societies is not available. He is a candidate for the Doctor of Philosophy degree in Forest Sciences and Biology from the University of Maine in December 2019.