UNIVERSITÉ DU QUÉBEC À MONTRÉAL

SIMULATION AND ANALYSIS OF THE EFFECT OF SPRUCE BUDWORM ON FOREST CARBON DYNAMICS : NEW TRIPLEX-INSECT MODEL DEVELOPMENT AND APPLICATIONS

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SIMULATION ET ANALYSE DE L'EFFET DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE SUR LA DYNAMIQUE DU CARBONE FORESTIER : DÉVELOPPEMENT ET APPLICATIONS D'UN NOUVEAU MODÈLE TRIPLEX-INSECTE

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PREFACE

This dissertation is comprised of five chapters (three main articles) that present and discuss the effects of spruce budworm on carbon dynamics in the boreal forest of Québec. All three papers involved in the dissertation are my original contributions to my Ph.D. study in Environmental Sciences at Université du Québec à Montréal.

Chapters I and V are the general introduction and general conclusion, respectively. Chapters II to IV are correspondingly based on the following three publications:

1. **Liu, Z.,** Peng, C., De Grandpré, L., Candau, J.N., Zhou, X. and Kneeshaw, D., 2018. Development of a New TRIPLEX-Insect Model for Simulating the Effect of Spruce Budworm on Forest Carbon Dynamics. *Forests*, 9(9), p.513.
2. **Liu, Z.,** Peng, C., De Grandpré, L., Candau, J.N., Work, T., Huang, C. and Kneeshaw, D., 2019. Simulation and analysis of the effect of spruce budworm outbreak on carbon dynamics in boreal forests of Québec. *Ecosystems,* Under review.
3. **Liu, Z.,** Peng, C., De Grandpré, L., Candau, J.N., Work, T., Zhou, X. and Kneeshaw, D., 2019. Simulation and evaluation the efficacy of aerial spraying on carbon dynamics under spruce budworm disturbances. In prep.

Appendix I is the result of my Ph.D. comprehensive exam, which must be completed by Ph.D. candidates and is to answer a topical question indirectly related to their dissertation. This paper is:

4. **Liu, Z.,** Peng, C., Work, T., Candau, J.N., DesRochers, A. and Kneeshaw, D., 2018. Application of machine-learning methods in forest ecology: recent progress and future challenges. *Environmental Reviews*, 26(4), pp.339-350.

I developed all hypotheses with my Ph.D. supervisor, Dr. Changhui Peng and co-supervisor Dr. Daniel Kneeshaw. I designed the new insect disturbances sub-model under the framework of TRIPLEX 1.0 and programmed the model code with C++

Build. After the model development, I conducted the model validation and data analysis as well as wrote the three manuscripts (first author) and the dissertation. Dr. Louis De Grandpré, Dr. Timothy Work and Dr. Jean-Noël Candau constantly advised and discussed with me about my Ph.D. project, and commented on early versions of the manuscripts and this dissertation. Dr. Chunbo Huang discussed and commented on the data analyzed for Chapter III and Chapter IV. Dr. Xiaolu Zhou helped to explain the model code and discussed the programming problems. Dr. Louis De Grandpré also compiled the stand data (i.e. forest, defoliation and mortality data) used in Chapter II. Ms. Marie-Claude Lambert provided the climate data used in Chapters III. All coauthors contributed comments and suggestions, greatly improving the quality of the papers.

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RÉSUMÉ

Les épidémies de tordeuses des bourgeons de l'épinette (*Choristoneura fumiferana* (Clemens), *Lepidoptera*: *Tortricidae*, TBE) jouent un rôle important dans la forêt boréale de l'Amérique du Nord. La dynamique du carbone au sein de ces écosystèmes forestiers s'en trouve sévèrement affectée, les pertes en couvert forestier reliées à la défoliation et à la mortalité se chiffrant en millions de kilomètres carrés.

L'objectif général de ce projet est d'améliorer la compréhension et la quantification de l'impact des insectes sur la dynamique du carbone forestier. Spécifiquement, (1) un nouveau modèle basé sur un processus (TRIPLEX-Insect) a été développé pour quantifier l'effet des épidémies de TBE sur les flux de carbone forestier pour le sapin baumier (*Abies balsamea* (L.) Mill.). (2) En utilisant le modèle TRIPLEX-Insect combiné avec des données de parcelles d'inventaire forestier, des bases de données géospatiales, des données climatiques mensuelles et des données séquentielles de défoliation spatialement explicites, nous simulons et comparons la dynamique et les changements au niveau du carbone dans les forêts de la province de Québec sans et avec perturbation par la TBE sur une superficie de 65,746 km^2. (3) Le modèle a été ultérieurement utilisé pour évaluer la quantité de carbone pouvant être conservé au Québec en procédant à un épandage aérien d'insecticide (*Bacillus thuringiensis* ssp. Kurstaki – Btk) durant la période de 2010 à 2017.

Le modèle a été validé avec des données de mortalité observée dans la région de la Côte-Nord au Québec de même que par des données publiées de croissances volumique annuelle actuelle (CAI) pour l'île du Cape Breton en Nouvelle-Écosse au Canada. En comparaison à la simulation sans défoliation, la moyenne nette en productivité écosystémique (NEP) avec défoliation a diminuée de 91±7.3 g C m^{-2}année^{-1} dans 65,746 km^2 d'aire forestière défoliée au Québec de 2007 à 2017, alors que cette aire était de 21,046 km^2 et a été convertie en source de carbone en 2017. Cette étude démontre aussi que les peuplements de sapins baumiers plus jeunes perdent moins de carbone que les peuplements d'épinettes ou les peuplements mixte de sapin baumier et d'épinette. De plus, l'épandage aérien s'est avéré être une bonne méthode de sauvegarde de carbone sous perturbation par la TBE. L'année subséquente au traitement d'épandage, la NEP moyenne des forêts traitée a augmentée de 0.59 g C m^{-2}year^{-1} en comparaison aux forêts sans traitement. Les résultats ont aussi démontrés que davantage de carbone peut être conservé dans les peuplements de sapin baumier que dans ceux d'épinette et mixtes de sapin baumier et d'épinette.

En somme, le modèle TRIPLEX-Insect s'avère être un outil très utile pour assister les initiatives de gestion des épidémies d'insectes forestiers. Celui-ci s'applique bien pour la quantification de la dynamique du carbone de même qu'à l'évaluation de l'efficacité de l'épandage aérien lors d'épidémies de TBE.

Mots clés : mortalité des arbres, perturbations naturelles, productivité nette de l'écosystème, défoliation cumulative, sapin baumier, processus de photosynthèse

ABSTRACT

Spruce budworm (*Choristoneura fumiferana* (Clemens), Lepidoptera: Tortricidae, SBW) outbreaks play an important role in the boreal forests of North America. Carbon (C) dynamics in these forest ecosystems are severely affected by SBW outbreaks due to millions of square kilometers of forest loss from defoliation and mortality.

The overall aim of this research is to improve our quantitative understanding of the impact of insect disturbances on forest carbon dynamics. Especially, (1) a novel process-based model (TRIPLEX-Insect) was developed to quantify the effect of SBW outbreaks on forest carbon fluxes for balsam fir (*Abies balsamea* (L.) Mill.). (2) Using the TRIPLEX-Insect combined with forest inventory plots, geospatial databases, monthly climate data, and spatially explicit defoliation sequence data, we simulated carbon dynamics and changes between scenarios with and without SBW disturbances for 65,746 km^2 of Québec. (3) The model has been further used to evaluate how much carbon would be saved by aerial spraying (i.e. a biological insecticide: Bacillus thuringiensis ssp. Kurstaki -- Btk) during 2010~2017 in Québec.

The model was validated against observed mortality in the North Shore region of Québec and published current annual volume increment (CAI) in the Cape Breton Island in Nova Scotia, Canada. Compared to simulations without defoliation, the average net ecosystem productivity (NEP) with defoliation decreased by 91±7.3 g C m^{-2}year^{-1} in 65,746 km^2 defoliated areas of Québec from 2007 to 2017. While there were 21,046 km^2 of defoliated areas converted from C sink to source in 2017. This study also found that younger balsam fir stands lost less C than either spruce or mixed fir-spruce stands during the period of SBW outbreak 2007-2017 in Québec. Moreover, the aerial spraying was a good way to save C during the SBW attacks. In the year following spraying average NEP with spraying protection increased 0.59 g C m^{-2}year^{-1} more than without spraying. The results also showed more C to be saved in balsam fir than either spruce or mixed fir+spruce forests in the year following spraying.

Overall, the TRIPLEX-Insect model is a useful tool for informing forest insect management initiatives. It can be applied to quantify the carbon dynamics as well as to evaluate the efficacy of aerial spray during spruce budworm outbreaks.

Keywords: tree mortality, natural disturbances, net ecosystem productivity, cumulative defoliation, balsam fir, photosynthesis process

CHAPTER I

GENERAL INTRODUCTION

1.1. Background

1.1.1. Boreal forests and natural disturbances

Boreal forests contain 33% of the world's forest cover and a large portion of the Earth's boreal region lies in Canada (28% or 552 million hectares) (Brandt *et al.*, 2009 and 2013). Boreal forests play a key role and strongly impact the global carbon cycle through the exchange of carbon between the atmosphere and terrestrial ecosystems (Apps *et al.*, 1999; Chapin *et al.*, 2008) and have been estimated store about 60-70 Pg of carbon (Bonan 2008; Pan *et al.*, 2011; Peh *et al.*, 2015). It is well known that biogenic fluxes of carbon occur mainly through the abosorption of CO_2 by plants (photosynthesis processes) and the carbon emission return to the atmosphere by autotrophic and heterotrophic respiration (decomposition processes) (Amiro *et al.*, 2010). However, boreal forest ecosystems in Canada are subject to a variety of natural ecosystem disturbances, such as wildfire, insect outbreak, windthrows, drought, etc. These ecosystem disturbances cause changes in forest composition, forest structure, forest photosynthesis and landscape patterns (Seidl et al., 2018). Furthermore, these natural disturbances also affect carbon sequestration, biodiversity and future timber supply (Boucher *et al.*, 2018). Forecasting future natural disturbances under a global change context is also critical in international conformation strategy programs (Boulanger *et al.*, 2016).

Wildfire is the most important natural disturbance in Canada. From 1998 to 2017, 2.4 million hectares per year of forest area burned on average in Canada (Canadian Council of Forest Ministers 2018). The area burned annually in Canadian forests ranges from 626,420 hectares in 2001 to 4,614,287 hectares in 1998. Fire disturbance is mainly driven by some factors such as weather, forest composition (fuel) and fire control response policies (Lagerquist *et al.*, 2017). Although only 3%

of fires exceed 200 hectares of area, they account for more than 95% of the total area burned in Canada (Stocks *et al.*, 2003). As a result, large-scale wildfire may lead to reductions of the carbon sink in boreal forests of Canada (Lamberty *et al.*, 2007). Research in Canada has reported that wildfire may be directly responsible for average carbon emissions of 27±6 Tg/year in the forest from 1959-1999 (Amiro *et al.*, 2001).

Table 1.1. Summed area of moderate to severe damage (including beetle-killed trees) in Canada from 1997 to 2016 by insects (data from National Forestry Database, Canadian Council of Forest Ministers 2018).

Insect	Area (ha)	% of total area disturbed by insect
Spruce budworm	44,793,145	15
Forest tent caterpillar	83,597,574	28
Mountain pine beetle	80,460,054	27
Large aspen tortrix	22,659,243	7
Others	70,129,084	23
Total	301,639,100	100

After fire, insect outbreaks are the second most important natural disturbance in Canadian forests. The large areas of tree mortality or reduced tree growth that result from insect outbreaks have significant effects on the carbon cycle of Canada boreal forests. Over the 1997-2016 period currently reported by the national forestry database (Canadian Council of Forest Ministers 2018), the area of moderate-severe defoliation averaged 15 million hectares per year in Canada. Unlike wildfire, insect disturbances are selective and can cycle with a given periodicity. During outbreak periods, insects can cause more damage and carbon loss in a given area than fire. For example, forest tent caterpillar (*Malacosoma disstria* Hübner Lepidoptera: Lasiocampidae) defoliation caused the largest summed area over 20 years of disturbance at 83 million hectares (Table 1.1). By 2007, the mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae) outbreak was the predominant insect disturbance in West Canada, with 18 million hectares affected that year. Kurz *et al*., (2008a) reported that the cumulative effect of the mountain pine beetle outbrak will be 270 Mt carbon in the affected region of Canada from 2000 to 2020. The most damaging outbreaking insect pests typically undergo population increases over several years, reach a peak, and then decline to endemic levels (Hicke *et al*., 2012). Knowlwdge on the area defoliated and tree mortality is the first step to estimate the effects of insect outbreaks on forest ecosystems and carbon dynamics (MacLean 2016).

In order to control damage by defoliating insects, biological insecticides were used on over 2 million hectares of boreal forest from 2006 to 2016, in Canada (Canadian Council of Forest Minister 2018). Bacillus thuringiensis ssp. Kurstaki (Btk), which is the most popular biological insecticide, has been used to protect forests affected by insect disturbances over the last four decades in Canada (Fuentealba et al., 2015). Protection programs aim not only maintain a trees' current-year foliage (e.g. 50% in Québec) but also ensure tree survival and reduce timber losses during pest outbreaks (van Frankenhuyzen et al., 2016). Furthermore, aerial spray programs can help forest managers protect the carbon sequestration capacity of Canadian forests (Fuentealba et al., 2019).

1.1.2. The roles of spruce budworm on boreal forests

The spruce budworm (*Choristoneura fumiferana* (Clemens), Lepidoptera: Tortricidae) is the major biotic disturbance in boreal forests of eastern North America (Bognounou *et al*., 2017). From 1997 to 2016, spruce budworm outbreaks defoliated a summed area exceeding 44 million hectares of Canadian forests (Table 1.1), of which there were about 19 million hectares in Québec (Canadian Council of Forest Ministers 2018). For behavioral and ecological reasons, the species that are the most vulnerable to the spruce budworm in descending order are balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg) and black spruce (*Picea mariana* (Mill.) B.S.P.) (Hennigar *et al*., 2008). One of the most cited reasons for the greater vulnerability of balsam fir over the spruces is that larvae emergence is closely related to host phenology (e.g.

the timing of bud break) (Rauchfuss and Ziegler 2011). The insect usually is multivoltine (i.e. it has a one year life-cycle) (Figure 1.1). The spruce budworm prefers current year foliage as well as feeding on staminate flowers (Blais 1958). Defoliation of the most photosynthetically productive current year foliage causes a number of changes within host trees, such as rebalancing cabonhydrate storage in different tree compartments (i.e. stem, foliage and roots). Tree strategies to respond to defoliation include rebuilding photosynthetic capacity (MacLean 2016). However, after 5-6 consecutive years of severe defoliation, mortality is observed in balsam fir, followed by white spruce and then red spruce and then black spruce (MacLean 1980; Erdle and MacLean 1999). In addition, forests with mixtures of host species alter the vulnerability of the hosts compared to pure forests (Bognounou *et al.*, 2017). For instance, black spruce is more susceptible to spruce budworm damage when surrounded by fir neighbours.

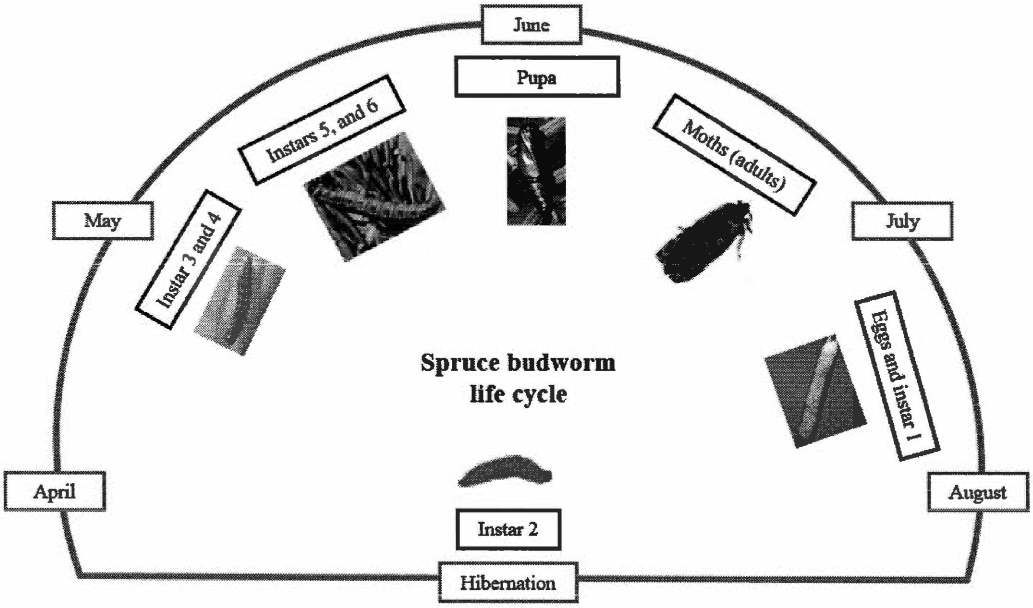

Figure 1. 1. Life cycle of the spruce budworm. Photos of spruce budworm stages are from the following sources: Rauchfuss and Ziegler (2011), and the website of the Southern Interior Forest Region (www.for.gov.bc.ca/ris/foresthealth/guide/WSBW.html, accessed on 19 December, 2018)

The outbreak cycles of spruce budworm are longer than most other defoliating species (e.g. forest tent caterpillar, etc) (Myers and Cory 2013). Outbreaks are generally synchronized within the region and occur on 30-40 years intervals in eastern Canada (Pureswaran *et al.*, 2015). The outbreak phase can last 5-15 years during which time the population density increases over several orders of magnitude (Morris 1963; Boulanger and Arseneault 2004). Defoliation by reducing tree growth and increasing tree mortality, results in large timber and economic losses. For instance, most of forests of Québec suffered spruce budworm defoliation from the 1960s to 1990s (Nealis 2015; Navarro *et al.*, 2018) and resulted in 250 million m^3 of wood-fiber losses (Grondin *et al.*, 1996) and \$12.5 billion in lost revenue (Coulombe *et al.*, 2004). Moreover, spruce budworm outbreaks also have a great influence on forest carbon budgets over broad areas. During outbreaks, extensive tree mortality reduces the carbon uptake of forests and increases carbon emissions from the decay of dead trees (Dymond *et al.*, 2010). This represents an important mechanism by which insect outbreaks may reduce the capability of boreal forests to absorb and store atmospheric carbon (Kurz *et al.*, 2008b).

1.2. MODELING INSECT DISTURBANCES

Challenges for evaluating the impact of insect, including spruce budworm, and forest response to climate changes in managed forests include quantifying the effects of different forest management strategies on carbon dynamics under insect attacks, and predicting annual defoliation at stand or landscape scales in the future. Using forest simulation models is an effective way to understand the long-term responses of forested landscapes to a given spruce budworm disturbance outbreak scenario (Hicke *et al.*, 2012; MacLean 2016; Boulanger *et al.*, 2016; Meyer *et al.*, 2018).

1.2.1. Modeling insect outbreaks

The current modelling of spruce budworm disturbances is mainly based on two different areas of study: (1) modeling budworm's population biology and dynamics;

and (2) building relationships between defoliation and forest response (i.e. tree growth, mortality and carbon dynamics) (Sturtevant *et al.*, 2015).

Researchers have modeled spruce budworm's population dynamics and biological processes in order to evaluate and provide guideance for insect population management. Indeed, understanding insect population dynamics is critical step in simulating temporal and spatial patterns of outbreaks (Régnière *et al.*, 2012). Spruce budworm outbreaks have temporal periodicity but strong randomness in the spatial distribution of annual defoliation. Because adult insects (i.e. moths) are able to both actively and passively disperse through short-distant and long-distance flights using wind currents to boost long-distance dispersal the trajectory of this process cannot be captured (Sturtevant *et al.*, 2013). For example, contrasting defoliation outbreak patterns (e.g. cumulative defoliation ranging from least to most severe) occured across New Bruswick (Zhao *et al.*, 2014). Therefore, there is an important challenge to accurately predicting and simulating the spatial distribution and intensity of annual defoliation of insect population dynamics. This limitation also affects most population dynamics models (e.g. Fleming 1996; 2002; Régnière and Nealis 2007; Candau and Fleming 2011; Régnière *et al.*, 2012).

Actually, defoliation is a function of insect numbers but it is easier to oberve and record directly than predicted based on population dynamics. Furthermore, tree growth reduction and mortality are strongly related to annual and cumulative defoliation of spruce budworm over several consecutive years (e.g. Ostaff and MacLean 1995; Zhao *et al.*, 2014). Therefore, researchers have built defoliation-growth reduction and defoliation-mortality relationship models to optimiz and reduce the impact of spruce budworm outbreaks on timber supply and carbon sequestration. For example, the Spruce Budworm Decision Support System (SBWDSS) is a feasible and valuable model for simulating the effects of budworm disturbances on tree growth, mortality, and timber supply (Erdle 1989; MacLean *et al.*, 2001; Hennigar *et al.*, 2007). Landscape disturbance and succession (LDSM) models have also been used to help forest managers evaluate the long-term and large-scale effects of spruce budworm outbreaks on forest dynamics (e.g. vegetation change, neighborhood effects, etc) (Scheller and Mladenoff 2007; James *et al*., 2011).

1.2.2. Modeling the influence of insect disturbances on forest carbon dynamics

Although challenges remain in the development of fully integrated predictive models of outbreaks, the carbon dynamic models can be used to study how insect defoliation may impact forest carbon dynamics across stand and landscape scales. In Canada, the Carbon Budget Model of the Canadian Forest Sector (CBM–CFS3) has been used in the past to simulate carbon dynamics (i.e. carbon fluxes and stocks) under different scenarios of defoliation and management practices in the boreal forest (Kurz *et al*., 2008b; 2009). For example, Hennigar and MacLean (2010) suggested that the CBM-CFS3 model can be applied to identify the quantity of insecticide application that would lead to carbon sequestration compared to a scenario without pest and forest management. Based on results from the CBM-CFS3 model, it was found that the spruce budworm is able to significantly convert the forest from a carbon sink to a source over large regions (Dymond *et al*., 2010). In addition, Chen *et al*., (2016) integrated CBM-CFS3 into the Carbnon and Nitrogen coupled Canadian Land Surface Scheme (CN-CLASS) and used this method to estimate the effects of climate variability and insect disturbance on carbon dynamics over 6275 ha of boreal forest in eastern Canada from 1928 to 2008. Moreover, combining GIS and forest models could also have several benefits for forest insect assessment and management (Senf *et al*., 2017). Foster (2011) used LANDIS-II, which is a spatially interactive forest succession and disturbance model (Scheller and Mladenoff 2004), and remote sensing analyses to simulate long-term changes in forest carbon under insect defoliation. They found that understanding the spatial variability of disturbance intensity will enable us to more accurately quantify and simulate the impact of defoliation on carbon accumulation at the landscape-level.

Empirical models (i.e. CBM-CFS3, LANDIS-II) do not help us well understand the relationship between insect disturbances and carbon dynamics. Therefore, we need more process-based models to study the impacts of defoliation on forest carbon dynamics. For example, Meyer *et al.*, (2018) applied the 3-PG model to simulate the influence of mountain pine beetle disturbance on net ecosystem productivity (NEP) at the stand level. They suggeted that the management approach of not harvesting disturbed forests is beneficial for carbon recovery and the carbon balance of boreal forest ecosystems. Landry *et al.*, (2016) used the Integrated Biosphere Simulator (IBIS) process-based model to find that there is a stronger effect on outbreak severity than outbreak return interval for mountain pine beetle.

1.3. General questions and hypotheses

There are three primary knowledge gaps in the research of the role of spruce budworm outbreaks on forest carbon dynamics. First, there is little known about the responses of carbon fluxes and stocks following different outbreak duration and intensity. Second, there is a lack of understanding of the effect of spruce budworm outbreaks on carbon dynamics for different host species. Third, high uncertainties exist as to the effect of forest management strategies on the protection of carbon sequestration in boreal forests during insect outbreaks.

In order to better understand the effect of spruce budworm disturbances on forest carbon dynamics, it is necessary to answer the following two questions:

(1) What features of insect outbreak can be quantified in the process-based models?

(2) Can we estimate the potential impact of spruce budworm outbreaks on forest carbon budgets?

In this dissertation, I hypothesize that (1) spruce budworm disturbance will reduce the capacity of carbon sequestration for balsam fir and spruce forests; (2) pure balsam fir forests will lose more carbon than either pure spruce or mixed fir+spruce forests during the same period of spruce budworm outbreak across large regional areas; (3) forest management strategies such as aerial spraying with insecticide could benefit the carbon budgets of boreal forest as well as reduce the risk of wood losses to insect outbreaks.

1.4. Thesis structure and specific objectives

In this dissertation, there are three manuscripts related to the investigation of the impacts of spruce budworm disturbances on carbon dynamics (i.e. carbon fluxes and stocks) of boreal forest in Québec. Chapters I and V are the general introduction and the general conclusion, respectively. The main structure of this thesis is shown in Figure 1.2.

The specific objectives of this dissertation are as follows:

1) Chapter II: Develop a novel process-based TRIPLEX sub-model to quantify the effects of forest carbon dynamics in response to spruce budworm outbreaks in balsam fir at the stand level; and validate this model against mortality data and published current annual volume increment (CAI) data.

2) Chapter III: use the newly developed TRIPLEX-Insect model, based on TRIPLEX 1.0 in Chapter II, to quantify and analyse the effects of spruce budworm outbreaks from 2007 to 2017 on carbon fluxes (i.e. gross primary productivity, net primary productivity, autotrophic respiration, heterotrophic respiration and net ecosystem productivity) and stocks (i.e. aboveground biomass, belowground biomass, soil organic and total litterfall) at a regional scale in boreal forests of Québec.

3) Chapter IV: quantify how much carbon could be maintained by aerial spraying protection by comparing the differences in carbon dynamics between forest management strategies with and without aerial spray protection for three different forest compositions of host species (balsam fir, spruce, and mixed fir+spruce) during the period of spruce budworm outbreaks.

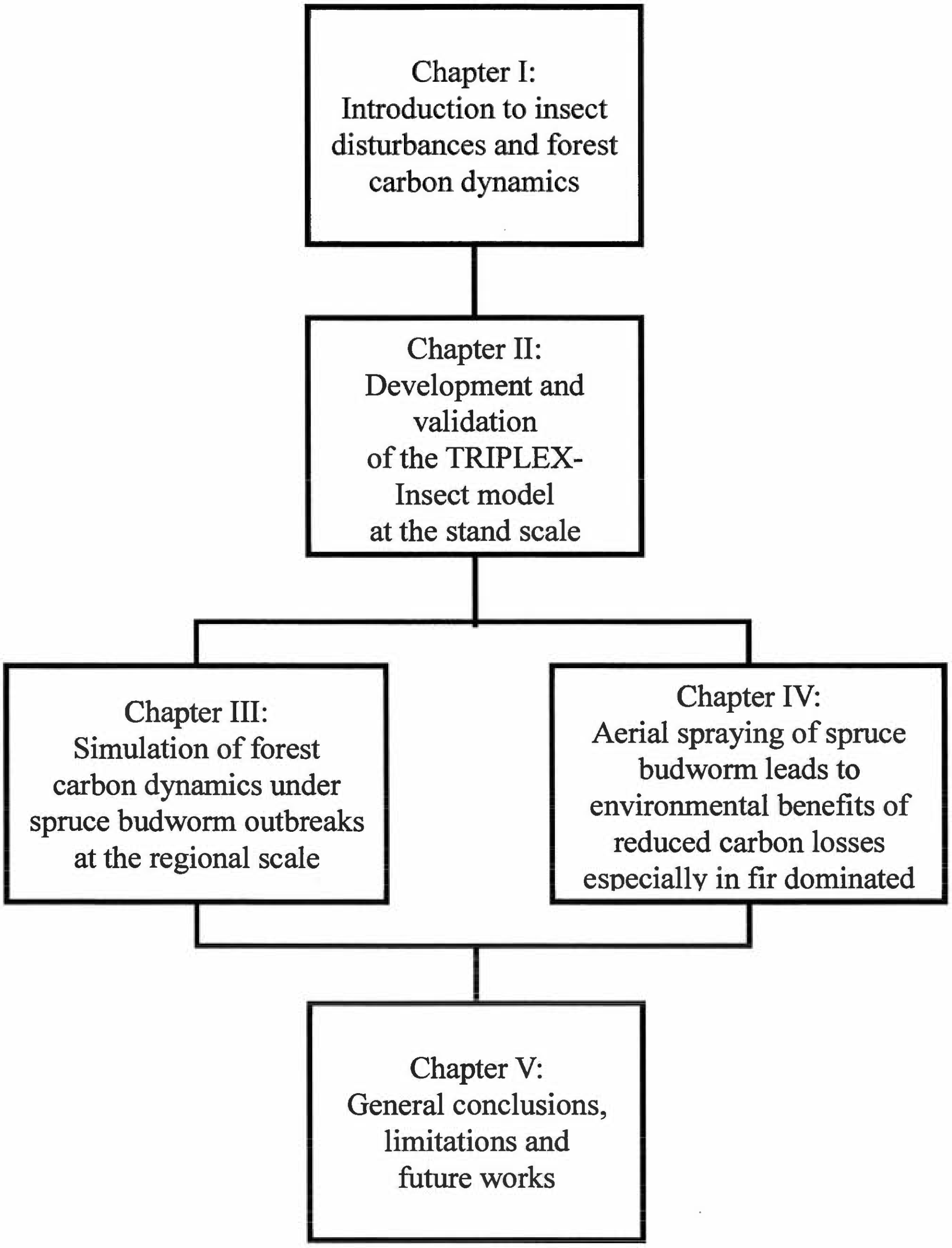

Figure 1. 2. Structure of the dissertation.

1.5. Study area

This study is conducted in different forested area of Québec using available data to respond to the different objectives (Figure 1.3). Chapter II was based on three balsam fir sites in the North Shore region of Québec. The mean annual temperature and the mean annual precipitation is 1.7°C and 1001mm, respectively, from 1981 to 2010.

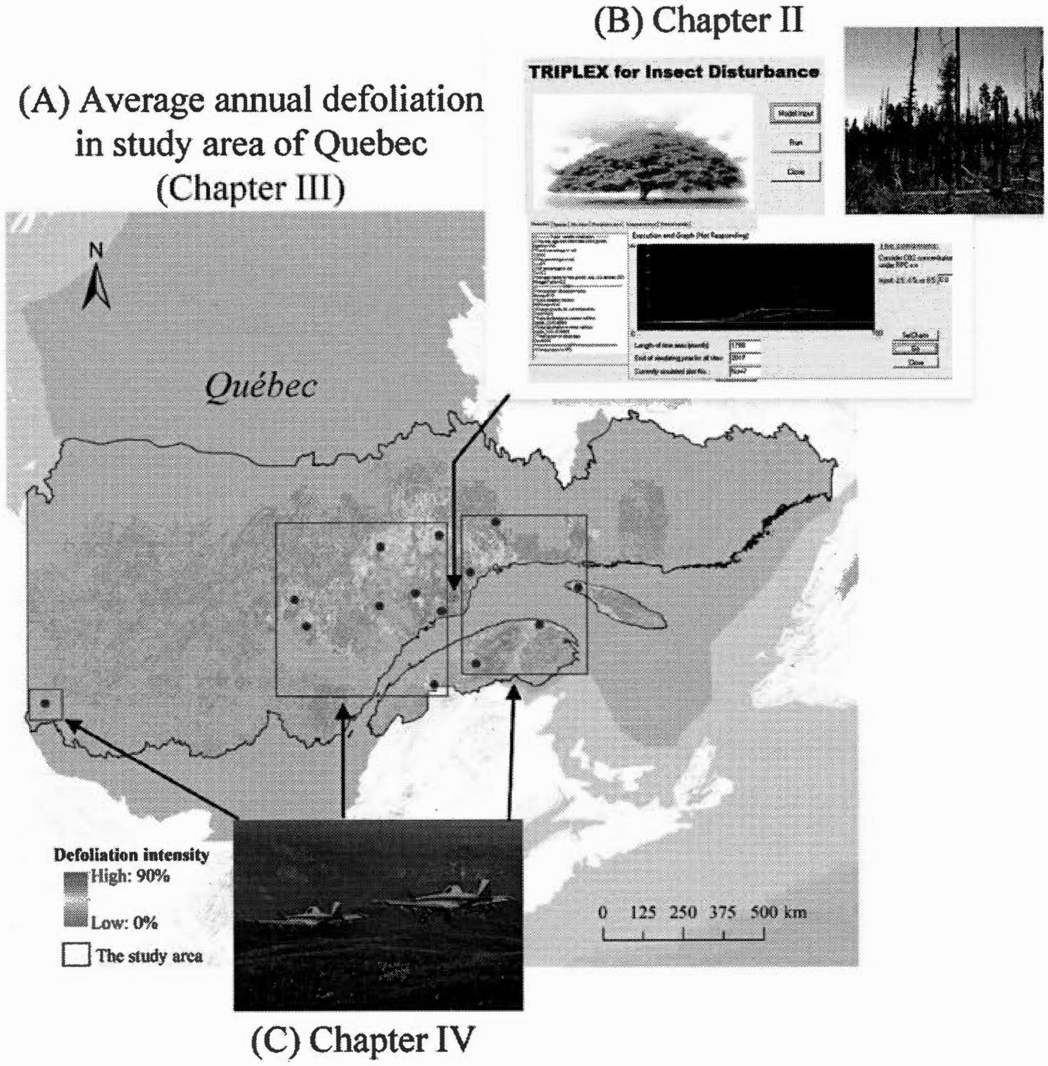

Figure 1. 3. Study area for each of the chapters. The figure introductions are as follows: (A), Average annual defoliation in study area of Quebec from 2007-2017; (B), the model interface and the image of defoliated forest (from https://www.forestpests.org/vd/116.html); and (C), an image of aerial spraying (from http://www.sopfim.qc.ca/en/photo-gallery.html).

Chapter III focused on 218,665 km^2 of balsam fir-spruce forests in Québec. While Chapter IV estimated fourteen sample units located in various regions of the study area in Chapter III. The dominate species include balsam fir, black spruce, white spruce and red spruce. The mean annual temperature varied from 1 to 3°C. Precipitation is generally range 800-1000mm.

Note: This thesis is written as a collection of published or submitted peer-reviewed journal articles. Consequently, there is little overlap in the texts between the General Introduction, General Conclusion and the main body of the Chapters.

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CHAPTER II

DEVELOPMENT OF A NEW TRIPLEX-INSECT MODEL FOR SIMULATING THE EFFECT OF SPRUCE BUDWORM ON FOREST CARBON DYNAMICS

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2.1. Résumé

La tordeuse des bourgeons de l'épinette (TBE) défolie et induit de la mortalité chez les conifères, affectant conséquemment les échanges de carbone (C) entre la surface terrestre et l'atmosphère. Nous avons développé un nouveau sous-modèle TRIPLEX-Insect pour quantifier l'impact des épidémies d'insecte sur les flux de C. Nous avons modélisé la défoliation annuelle (DA), la défoliation cumulative (DC) et la mortalité des arbres. Le modèle a été validé avec des données de mortalité observée et des données publiées à l'échelle du peuplement pour la région de la Côte-Nord du Québec et de l'île du Cape Breton en Nouvelle-Écosse au Canada. Les résultats suggèrent que TRIPLEX-Insect performe très bien dans l'évaluation suivant une épidémie de TBE et sous-estime légèrement la croissance volumique annuelle actuelle (CAA). Dans les forêts matures et immatures, la simulation du modèle suggère une plus grande réduction en productivité primaire brute (PPB) qu'en respiration autotrophique (Ra) pour un même niveau de défoliation lorsque la mortalité des arbres est faible. Suite à une épidémie de TBE, la reprise de croissance des arbres survivants contribuent à la restauration de la productivité écosystémique annuelle nette (PEN) basée sur l'âge de la forêt si la mortalité n'est pas excessive. Dans l'ensemble, le modèle TRIPLEX-Insect a la capacité de simuler la dynamique du C du sapin baumier suivant une perturbation par la TBE et peut être utilisé en tant qu'outil efficace dans la gestion des insectes forestiers.

2.2. Abstract

The spruce budworm (SBW) defoliates and kills conifer trees, consequently affecting carbon (C) exchanges between the land and atmosphere. Here, we developed a new TRIPLEX-Insect sub-model to quantify the impacts of insect outbreaks on forest C fluxes. We modeled annual defoliation (AD), cumulative defoliation (CD), and tree mortality. The model was validated against observed and published data at the stand level in the North Shore region of Québec and Cape Breton Island in Nova Scotia, Canada. The results suggest that TRIPLEX-Insect performs very well in capturing tree mortality following SBW outbreaks and slightly underestimates current annual volume increment (CAI). In both mature and immature forests, the simulation model suggests a larger reduction in gross primary productivity (GPP) than in autotrophic respiration (Ra) at the same defoliation level when tree mortality was low. After an SBW outbreak, the growth release of surviving trees contributes to the recovery of annual net ecosystem productivity (NEP) based on forest age if mortality is not excessive. Overall, the TRIPLEX-Insect model is capable of simulating C dynamics of balsam fir following SBW disturbances and can be used as an efficient tool in forest insect management.

2.3. Introduction

Spruce budworm (*Choristoneura fumiferana* (Clemens), Lepidoptera: Tortricidae) (SBW) outbreaks play a key role in the dynamics of eastern North America's boreal and temperate forest biome (Ludwig *et al.*, 1978; Fleming *et al.*, 2002; Gray 2013; MacLean 2016). In recent centuries, SBW outbreaks have occurred cyclically every 30–40 years in eastern North America (Boulanger *et al.*, 2012) with a new outbreak beginning in 2006 (Aires infestees par la tordeuse des bourgeons de l'epinette au Québec en 2017). Balsam fir (*Abies balsamea* (L.) Mill.), an important conifer in Canada's boreal forest, is also the tree species most vulnerable to SBW (MacLean 1996; Hennigar *et al.*, 2008; Zhao *et al.*, 2014; MacLean 2016). A modification of carbon (C) exchanges occurs in balsam fir forests during outbreaks as the defoliator destroys photosynthetic tissues, resulting in a reduction of tree growth and an increase in mortality (Richards 1993; Pothier and Mailly 2006; Dymond *et al.*, 2010).

Defoliation varies with SBW population density and can be measured in terms of annual defoliation (AD) incurred. SBW mainly consumes foliage produced in the current year. Given that needles typically remain on the tree for five to six years, it can take many years for the SBW to kill a tree, especially at moderate or low defoliation levels (i.e., when not all foliage produced within a given year is consumed) (Sainte-Marie 2016). The last SBW outbreak started in the 1970s and 1980s in eastern North America, continued for almost two decades and was considered extremely severe (e.g., 80%–100% annual defoliation) (Gray *et al.*, 2000). Tree defoliation and ultimately mortality vary greatly between stands during an outbreak as well as between outbreaks themselves (Kneeshwa and Bergeron 2016). Older stands are more vulnerable than younger, more vigorous stands (Hennigar *et al.*, 2008a). Generally, C dynamics and insect disturbances lead to temporary changes in environmental conditions. However, insect outbreaks can cause long-term changes to ecosystem structure and function (Seidl *et al.*, 2011; Goetz *et al.*, 2012; Flower and Conzalez-Meler 2015), which can result in long-term impacts in C dynamics. We therefore need to better understand how insect outbreaks interact with stand structure (e.g., how defoliation severity and duration interact with stand age) to improve our estimates of forest C losses and our understanding of regional and global C cycles.

Modeling is a complementary tool to traditional observation and experimental approaches that can provide long-term and large spatial-scale perspectives on the effects of forest insect epidemics as well as evaluate interactions among multiple factors (Landry *et al.*, 2016). In recent years, there are some studies that have been conducted on C dynamics following insect outbreaks (Hicke *et al.*, 2012; Flower *et al.*, 2013). For example, Albani *et al.* (2010) used an ecosystem demography model in conjunction with a stochastic model to predict the impact of hemlock woolly adelgid (*Adelge tsugae*, Annand) on C dynamics in the eastern United States. Medvigy *et al.* (2012) also simulated a linear decrease in net ecosystem productivity (NEP) with increasing defoliation intensity by the gyspsy moth (*Lymantria dispar* L.). In addition, Edburg *et al.* (2011) used the Community Land Model version 4 (CLM4) to simulate coupled C and nitrogen (N) dynamics following mountain pine beetle (*Dendroctonus ponderosae* (Hopkins), Coleoptera: Curculionidae, Scolytinae) outbreaks in the western United States of America. They found that the severity of the outbreak itself was an important factor which led to the initial decline in NEP, and required 80 to 100 years or more following the disturbance to recover. However, because CLM4 does not explicitly contain an age-class distribution model for trees, the impact of tree age on C dynamics following insect outbreaks is not known. In Canada, the Carbon Budget Model of the Canadian Forest Sector (CBM–CFS3) has been used to simulate and forecast ecosystem C dynamics impacted by SBW disturbances (Kurz *et al.*, 2008; Dymond *et al.*, 2010; Hennigar and MacLean 2010). Such studies found that a decrease in NEP may convert boreal forests from C sinks into C sources after SBW outbreaks. However, CBM–CFS3 is an empirically driven model that is not designed to estimate gross primary productivity (GPP) and respiration in forest ecosystems. It is therefore unable to explain in detail the flow of C dynamics under such conditions.

TRIPLEX, a process-based hybrid model (Liu *et al.*, 2002; Peng *et al.*, 2002), integrates the advantages of both empirical and mechanistic components. TRIPLEX 1.0 is able to simulate both short- and long-term forest growth and C and N dynamics and has been successfully calibrated and validated for different forest ages (Peng *et al.*, 2002; Zhou *et al.*, 2006), tree species (Zhou *et al.*, 2004; Sun *et al.*, 2008), and harvest disturbance types (Wang *et al.*, 2011 and 2012) in boreal ecosystems. However, the current version of TRIPLEX model is unable to simulate the impacts of insect disturbances due to the lack of corresponding modules. The main objective of our study was to develop a new process-based model (TRIPLEX-Insect) to quantify forest mortality and C sequestration in response to SBW outbreaks at the stand level. Specifically, this study (1) provides and tests a novel approach to integrate the relationship between defoliation and mortality, and (2) confirms that our sensitivity experiments contribute to the evaluation and understanding of how defoliation affects the capacity of C sequestration in forest stands.

2.4. Materials and methods

2.4.1. Study Site Description

The study area is located within the boreal forest of the North Shore region of Québec, Canada. The dominant species are black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir, which are both host species of the SBW (Hennigar *et al.*, 2008b). In 2006, the first signs of a SBW outbreak were observed in the North Shore region of Québec, and subsequent tree mortality has been observed in recent years (Aires infestees par la tordeuse des bourgeons de l'epinette au Québec en 2017). Three sample plots of mainly balsam fir were established in 2006 (see Table 2.1) in the epicenter of the outbreak to study long-term forest response to the current SBW outbreak. We sampled AD on a 45-cm branch segment sampled in the mid-crown (MacLean and Lidstone 1982) of each tree (20 balsam fir per stand) in each plot in August of each year. We assessed AD in the laboratory using the Fettes method (Fettes 1951) for each year since 2006 (Bognounou *et al.*, 2017).

We obtained monthly climate data, including air temperature, precipitation, and relative humidity from 1913–2016 from the CAUSAPSCAL (48.37° N, 67.23° W) meteorological station. Environment Canada has published the relevant climate data on their website (http://climate.weather.gc.ca/). We also used monthly data from 30-year averages (1913–1942) to replace earlier (1805–1912) climate data.

Table 2.1. Stand location, soil type, and observed defoliation of the balsam fir study sites in the North Shore region of Québec, Canada.

Plot ID	**QC_1**	**QC_2**	**QC_3**
Longitude	67.82° W	68.12° W	67.66° W
Latitude	49.58° N	49.71° N	49.48° N
Plot size	4000 m^2	4000 m^2	4000 m^2
Soil type	Thick glacial till	Thick glacial till	Thick glacial till
Primary Species	61% balsam fir	72% balsam fir	67% balsam fir
Observed defoliation (year)	2006–2016	2006–2016	2006–2016
Stand origin (year)	1805	1805	1930
Average annual temperature (1981–2010)	1.7 °C	1.7 °C	1.7 °C
Average annual precipitation (1981–2010)	1001 mm	1001 mm	1001 mm

Our study also used published data including plot locations and methods of annual assessments of defoliation in various regions of Cape Breton Island as well as density, basal area, volume, DBH and height per plot (Ostaff and MacLean 1989 and 1995).

2.4.2. Model development

2.4.2.1. Model Structure

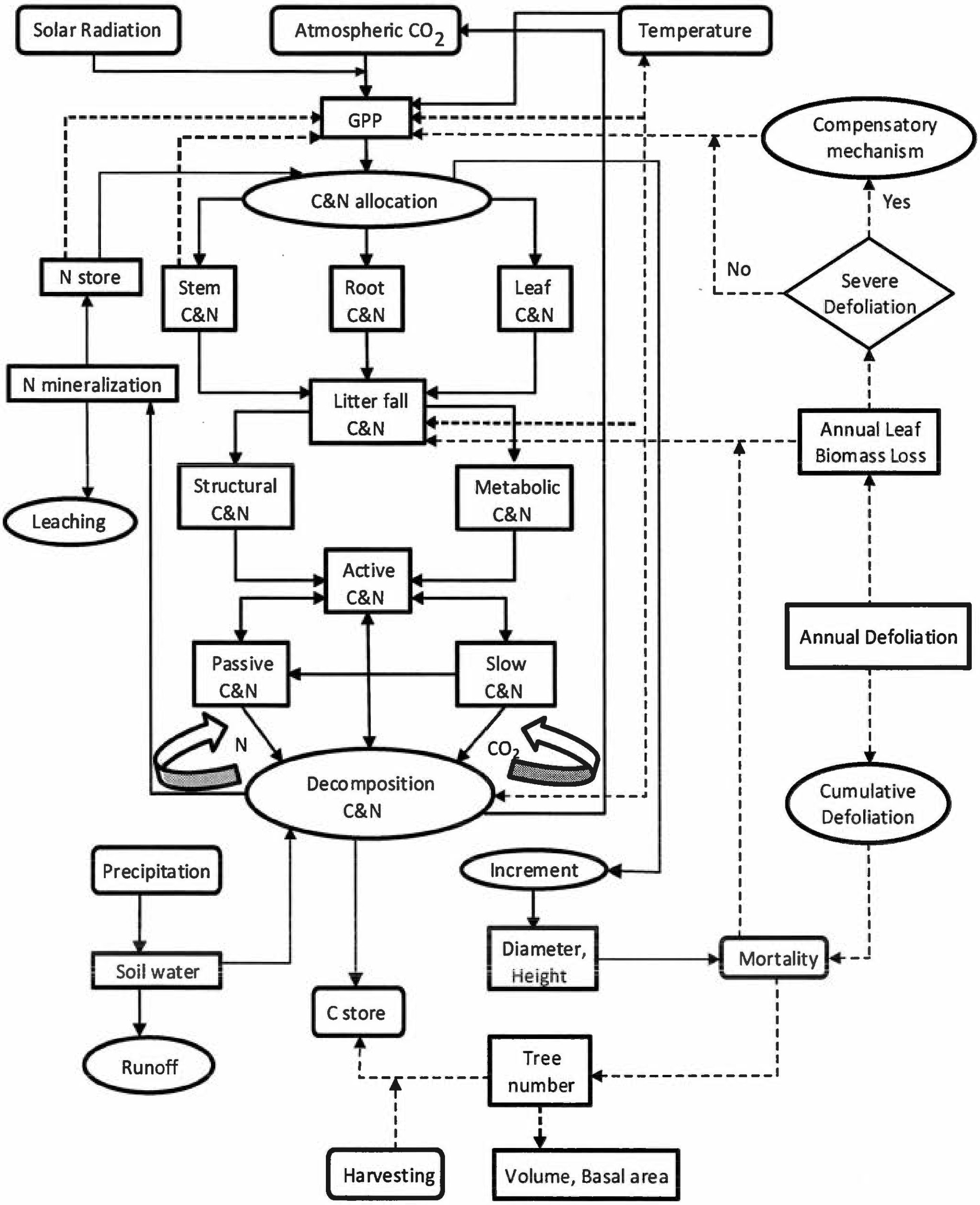

Figure 2.1. Framework and flow chart of TRIPLEX-Insect model (modified from Peng *et al.* 2002). Rectangles represent pools or state variables; ovals represent simulated processes; diamond-shaped boxes represent judgment process; dotted lines represent controls; and solid lines represent carbon (C), nitrogen (N), and water flow.

TRIPLEX 1.0 integrates three well-established models: 3-PG (Landsberg and Waring 1997), TREEDYN3.0 (Bossel 1996), and CENTURY4.0 (Parton *et al.*, 1993). TRIPLEX 1.0 can simulate forest growth and key C and N cycling processes which mainly include forest production, particularly GPP, net primary productivity (NPP), and NEP (see Figure 2.1) (Peng *et al.*, 2002; Zhou *et al.*, 2004 and 2006). Model simulations were conducted using a monthly time step, and monthly GPP was calculated from photosynthetically active radiation (PAR), leaf area index (LAI), forest age, mean air temperature, soil water, and the percentage of frost days per month. Boreal forest NPP was estimated using Equation (2.1):

$$\mathrm{NPP} = \mathrm{GPP} - \mathrm{Ra} \qquad (2.1)$$

where Ra is autotrophic respiration, which is estimated using N, air temperature, and component C pools (e.g., wood, branches, foliage, coarse roots, and fine roots) (Zhou *et al.*, 2006). NEP is calculated as GPP subtracted by ecosystem respiration (ER), which is comprised of Ra and heterotrophic respiration (Rh). Rh is calculated by subtracting root respiration from soil respiration, expressed as the exponential function of temperature and Q_{10} (Zhou *et al.*, 2006). Annual values are estimated by summing monthly results. In TRIPLEX 1.0, soil C and N are based on the CENTURY soil decomposition sub-model (Parton *et al.*, 1993). This sub-model provides realistic estimates of both C and N mineralization rates for Canadian boreal forest ecosystems (Peng *et al.*, 1998). More detailed information on TRIPLEX 1.0 is described in Peng *et al.* (2002) and Liu *et al.* (2002). Although the insect sub-model is designed to resolve how C dynamics respond to SBW outbreaks, many potentially confounding factors, such as climate change, forest fires, and land-use changes, are not directly considered.

2.4.2.2. Tree Mortality Resulting from Defoliation

Observed annual defoliation (AD) can be considered as a measure of the percentage of leaf biomass lost to insects. Since this variable causes a decrease in LAI, it subsequently impacts forest ecosystem photosynthesis. Every year, SBW produces one generation that is divided into nine life stages comprised of eggs, larvae (which include stage one through six), pupa, and moth. Damage from the SBW mainly occurs from May to July when the larvae are in stage three through six (Royama 1984; Sanders *et al.*, 1985; Rauchfuss and Ziegler 2011). Temperature impacts the beginning of SBW feeding. We estimated that defoliation commenced in May when the mean temperature is generally greater than 5 °C in the study area (Lysyk 1989; Volney and Fleming 2007; Rauchfuss and Ziegler 2011). Thus, AD was distributed over a period of two to three months by setting different weights to AD in our model (see Table 2.2) to account for differences in SBW phenology (Régnière and You 1991).

Table 2.2. Monthly distribution of annual defoliation (AD) in May, June, and July based on the mean temperature in May.

Mean Temperature in May	**Proportion of Annual Defoliation**		
	May	**June**	**July**
<5 °C		50% AD	50% AD
≥5 °C	10% AD	40% AD	50% AD

Defoliation caused mortality (DM; %/year) is defined in our model and described by Equation (2.2):

$$DM = K \times (exp(DS \times S \times A) - 7)/100 \qquad (2.2)$$

where K = 6.6774 is a parameter derived from empirical data taken from literature (Foster 2011). The defoliation stress (DS) index was calculated by cumulative defoliation (CD) and the weight of current annual defoliation (WAD) using Equation (2.3):

$$DS = CD \times WAD \qquad (2.3)$$

If annual current defoliation levels for the last five years were 0.25, 0.25, 0.5, 0.75, and 1, then CD would be 0.25, 0.5, 1, 1.75, and 2.75 (Blais 1958). The WAD estimates will equal 3 × AD, 1.07 × AD, 1.6 × AD, and 0.52 when annual defoliation levels are 1 (AD: 0%–5%), 2 (AD: 6%–30%), 3 (AD: 31%–60%), and 4 (AD: 61%–100%), respectively. Additionally, both tree species (S) and ages (A) influence mortality during SBW outbreaks (MacLean 1980). For balsam fir forests, we used observed basal area data from 2010–2016 for the North Shore region of Québec to compare with model simulation results from the model (see Table 2S.1) and then calibrated S = 0.4 and A as Equation (2.4):

$$A = 1.27/(1.75 + exp(-0.001 \times Age)) \qquad (2.4)$$

There are two mortality rates in the original TRIPLEX 1.0 model: natural mortality (NM; %/year) and competition mortality (CM; %/year). The CM rate is estimated based only on canopy competition for sunlight (Peng *et al.*, 2002) and be given an initial value as 1.2%/year. In addition, we assume that DM rates greater than 3%/year means all dead trees are caused by severe defoliation, where the rates of NM and CM are zero (Table 2.3). Note that in this study we did not add new trees when defoliation caused mortality and dead trees were transferred to the litter pool in the next iteration. SBW preferentially eats flower cones, resulting in little to no seed production during an outbreak (Schooley 1978).

Table 2.3. Key parameter values used in simulations of the TRIPLEX-Insect model. Parameters including Etas, EtaCR, EtaF, and EtaFR during endemic periods are based on the default values in TRIPLEX 1.0. For alpha carbon (Cα), EtaF, and EtaFR, severe defoliation was defined when LAI in December was less than 20% of LAI in January during the same year. For NM and CM, severe defoliation means DM greater than 0.03.

Parameter	Description	Without Defoliation	Severe Defoliation
		Balsam Fir	Balsam Fir
Cα	Canopy quantum efficiency	0.12 [a]	0.12×exp(-0.02×Age) ×3.5
Max Height	Max height (m)	25 [b]	-------
Age Max	Max stand age (year)	250 [b]	-------
Height at 5 year	Growth height during the first 5 year	2.1 [a]	-------
EtaS	Stem fraction from NPP	(1-exp(−0.04×age)) × (1-Height/MaxHeight)	-------
EtaCR	Coarse root fraction from NPP	0.25*EtaS	-------
EtaF	Leaf fraction from NPP	(1-EtaS-EtaCR) ×0.4	(1-EtaS-EtaCR) ×0.6
EtaFR	Fine root fraction from NPP	(1-EtaS-EtaCR) ×0.6	(1-EtaS-EtaCR) ×0.4
NM	Normal mortality (%/year)	0.6 [b]	0 [b]
CM	Competition mortality (%/year)	1.2 [b]	0 [b]

[a] Calibrated based on data from the Cape Breton Island study sites.

[b] Denotes an assumed value.

2.4.2.3. Biomass Loss Resulting from Mortality and Defoliation

The TRIPLEX-Insect model can simulate forest biomass loss by monthly time steps through the two following processes: (1) Mortality calculated in the Insect sub-model is sent to TRIPLEX 1.0 for NPP sub-model simulation. The DM is used to recalculate the survival and dead forest biomass, including branches, stems, and roots. Dead biomass becomes litter, which is then used in the simulation of soil C and N dynamics. (2) Leaf biomass loss is calculated based on AD (not mortality). When SBW-induced defoliation occurs, foliage is destroyed but not all foliage is consumed by insects; thus, we used a waste constant ($W = 0.4$) taken from Régnière *et al.* (1991) to estimate supernumerary foliage litter. In other words, 40% of total C from defoliation is transferred directly to litter as litterfall, and 60% is distributed to insect lifecycles (e.g., insect biomass and insect respiration).

2.4.2.4. Compensatory Mechanisms of Foliage Loss

Typically, the physiological response to defoliation activates multiple compensatory mechanisms that increase total crown photosynthesis in evergreen species (Eyles *et al.*, 2011). In this study, we considered three compensatory methods when defoliation occurred, by (1) an increase in the photosynthetic efficiency of remaining leaves when December LAI was less than 20% of January LAI in the same year (Eyles *et al.*, 2011). For example, we recalculated alpha carbon (Cα) using Equation (2.5):

$$\mathrm{C\alpha} = 0.12 \times \exp(-0.02 \times \mathrm{Age}) \times 3.5 \qquad (2.5)$$

(2) Defoliators reduced leaf biomass, resulting in more consumption of nonstructural carbohydrate (NSC), which was transferred to the growth of new leaves (Anderegg *et al.*, 2015). Here, we assumed and estimated this following Equation (2.6):

$$\mathrm{NL} = \mathrm{F} \times \mathrm{IAD} \qquad (2.6)$$

where NL is increment biomass of new leaves converted by NSC from other aspects of trees (i.e., stems, coarse roots and fine roots). F is the index of NL that is based on different CD conditions. For example, defoliation increases NSC consumption and reduces NSC production (Vanderklein and Reich 1999), we assumed NSC is exhausted when $CD \geq 4.5$, so $F = 0$ in this case. The index of annual defoliation (IAD) was calculated by annual defoliation, and the biomass of new leaves scales the conversion from biomass of stems (85%), coarse roots (10%) and fine roots (5%). (3) A change in the nutritional distribution of foliage and roots (Mediene *et al.*, 2002; Eyles *et al.*, 2011), for example, we increased the leaf fraction (EtaF) from NPP using Equation (2.7), while we decreased the fine root fraction (EtaFR) from NPP using Equation (2.8):

$$EtaF = (1 - \mathrm{EtaS} - \mathrm{EtaCR}) \times 0.6 \qquad (2.7)$$

$$EtaFR = (1 - \mathrm{EtaS} - \mathrm{EtaCR}) \times 0.4 \qquad (2.8)$$

where EtaS is stem fraction from NPP and EtaCR is the coarse roots fraction from NPP. We selected data that included mean diameter at breast height (DBH), mean tree height, mean volume, and mean basal area from primarily balsam fir stands (greater than 85% balsam fir) in Cape Breton Island to calibrate the compensatory setting in our model (see Table 2S.2).

2.4.3. Sensitivity Experiments

Using the TRIPLEX-Insect model, we conducted sensitivity experiments in order to test the effects of defoliation on C dynamics under different outbreaks durations, different initial forest age, and different defoliation severity in defoliated forests of balsam fir. Six different periods were estimated in which the duration of the outbreaks (10 or 20 years) and started stand ages (41, 101 or 161 years) varied given that younger stands are less vulnerable than older stands. Defoliation took 10 years in Short-Young (from 41 to 50 years tree age), Short-Mature (from 101 to 110 years stand age), and Short-Old (from 161 to 170 years stand age), while defoliation took 20 years in Long-Young (from 41 to 60 years stand age), Long-Mature (from 101 to 120 years stand age), and Long-Old (from 161 to 180 years stand age). We used five different defoliation scenarios representing a gradient from light to severe defoliation (no defoliation (control), 20% AD, 40% AD, 60% AD, and 80% AD) under the same AD severity level for the entire period of the outbreak. The TRIPLEX-Insect model was initialized using tree seedlings from the year of germination in all cases.

2.5. Results

2.5.1. Model Validation

Although there are no direct data to verify C flux estimations made by the TRIPLEX-Insect model from 2006 to 2016 in the North Shore region of Québec, Canada, we surveyed 16 records of tree mortality in the QC1 (yearly record from 2014 to 2016), QC2 (yearly record from 2008 to 2016), and QC3 (yearly record from 2011 to 2014). We compared simulated mortality to field measurements to evaluate the accuracy of the TRIPLEX-Insect model. The model predictions fitted quite well the observed data (Figure 2.2 A). In addition, we verified the compensatory mechanism in our model by using the current annual volume increment (CAI) data published by Ostaff and MacLean (1989 and 1995) from Cape Breton Island, Nova Scotia, Canada. Overall, TRIPLEX-Insect seems to underestimate the observed CAI by 10%–20% (Figure 2.2 B).

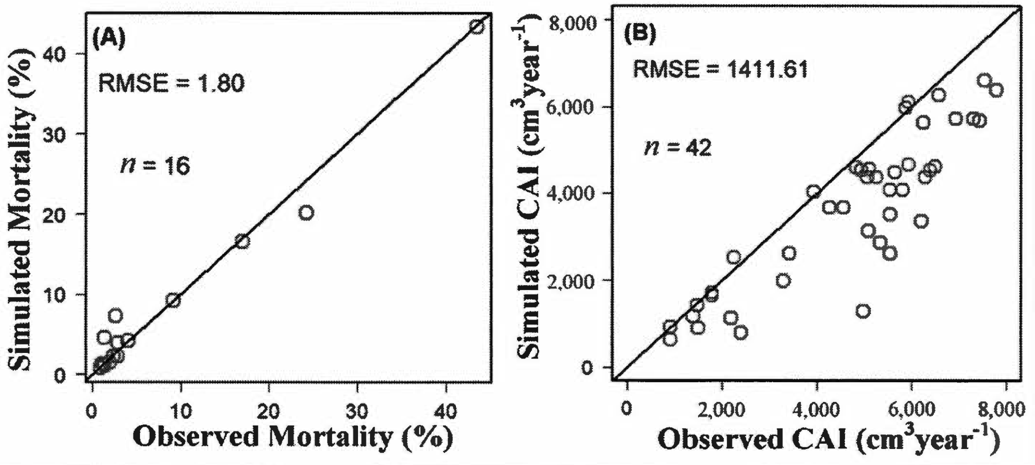

Figure 2.2. Comparison of observed and simulated values of (A) tree mortality (%), and (B) the current annual volume increment (CAI) (cm^3 $year^{-1}$).

Table 2.4. Simulated total changes of GPP and Ra at 5 years and 10 years after the beginning of an outbreak compared to no defoliation (control) in the balsam fir forest. AD denotes annual defoliation.

	5 Years of GPP Change				5 Years of Ra Change			
Tree Ages	20% AD	40% AD	60% AD	80% AD	20% AD	40% AD	60% AD	80% AD
41–60 ages	5.80%	1.32%	−35.78%	−53.68%	4.81%	0.74%	−32.18%	−46.36%
101–120 ages	6.25%	2.16%	−78.02%	−84.95%	3.91%	−0.49%	−65.04%	−76.07%
161–180 ages	11.15%	4.25%	−93.16%	−95.42%	6.23%	−1.64%	−89.62%	−93.01%
	10 Years of GPP Change				**10 Years of Ra Change**			
Tree Ages	20%AD	40%AD	60%AD	80%AD	20%AD	40%AD	60%AD	80%AD
41–60 ages	4.94%	−6.76%	−100%	−100%	4.30%	−8.06%	−100%	−100%
101–120 ages	7.88%	−4.76%	−100%	−100%	4.86%	−8.62%	−100%	−100%
161–180 ages	12.74%	−23.37%	−100%	−100%	7.37%	−29.47%	−100%	−100%

2.5.2. Sensitivity Analysis

Simulated outputs of GPP and Ra exhibited significant sensitivity to the level of defoliation. Five or 10 years after the beginning of an outbreak, we found a greater increase in GPP than Ra with 20% AD, while a greater loss in GPP compared to Ra with 60% AD and 80% AD (Table 2.4). Changes in GPP compared to no defoliation (control) increased from 1.32% to 4.25% while changes in Ra ranged from 0.74% to −1.64% as 40%AD levels after 5 years of an outbreak starting (Table 2.4). In addition, in all scenarios, with 60% and 80% AD, total GPP and Ra loss reached 100% because no trees survived. Indeed, medium and severe defoliation (40%–80% AD) led to the mortality of all trees when the SBW outbreak was programmed to last for 20 years. Therefore, we ended the simulation when all trees were dead.The sensitivity experiments simulated negative NEP following defoliation for all scenarios evaluated (Figure 2.3 A–F). Although we observed a pattern of rapid decline for all defoliation levels, more severe AD (from 20% to 80%) led to a greater decrease in annual NEP in balsam fir forests (Figure 2.3 A–F).

We found that the duration of the outbreak and stand age also influence forest recovery. Following the end of the outbreak, younger (ages range from 40 to 60 years) stands (Figure 2.3 A and D) recovered C sinks (NEP > 0) more rapidly and achieved higher levels of NEP compared to scenarios with older stands. Shorter duration of outbreaks resulted in a greater tree survival (20% AD and 40% AD in Figure 2.3A–C). For outbreaks lasting 20 years, only scenarios with 20% AD were able to recover (Figure 2.3 D–F) because the other scenarios resulted in total tree mortality.

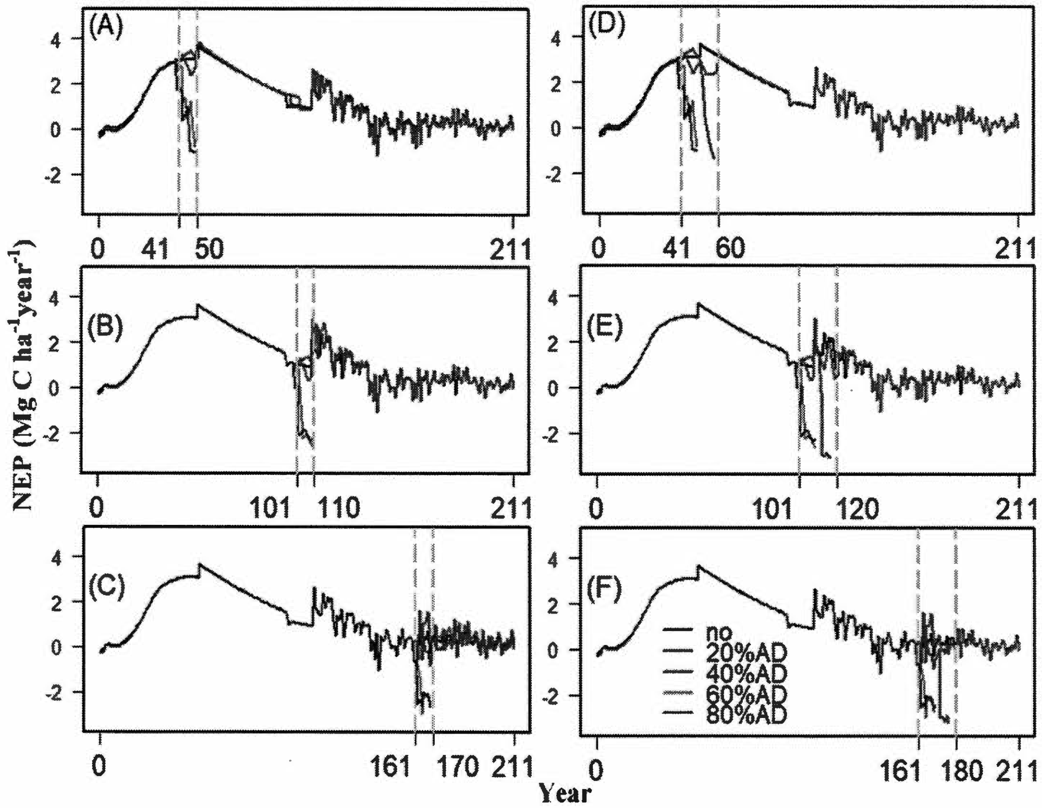

Figure 2.3. Simulated annual NEP started from different stand ages (41, 101 or 161 years) under two different durations of outbreaks (10 or 20 years) and five different defoliation scenarios (no defoliation (control), 20% AD, 40% AD, 60% AD, and 80% AD). AD denotes annual defoliation. (A) Short-Young; (B) Short-Mature; (C) Short-Old; (D) Long-Young; (E) Long-Mature; and (F) Long-Old.

2.5.3. Effects of Defoliation on Carbon Fluxes and Stocks

The lowest GPP and NPP values from our model simulations occurred in 2014 for QC1 and QC3, and in 2015 for QC2 in the North Shore region of Québec, Canada. In comparing simulated results of insect disturbances to conditions of no defoliation (control), Figures. 2.4 A–C show that annual GPP had decreased 98.23% (in 2014), 99.41% (in 2015), and 43.1% (in 2014), respectively, in the QC1, QC2, and QC3 plots. On the other hand, annual NPP decreased by 99.4% (Figure 2.4 D), 99.99% (Figure 2.4

E), and 44.44% (Figure 2.4 F), which was slightly higher compared to GPP losses. NEP was sensitive to changes in the severity of AD and CD (Figure 2.4 G–I). Two of the stands (QC1 and QC2) showed signs of weak recovery whereas QC3 did not. The simulation of NEP for all stands changed from positive to negative following the commencement of defoliation, which resulted in all plots becoming significant C sources after only a few years of SBW-induced defoliation.

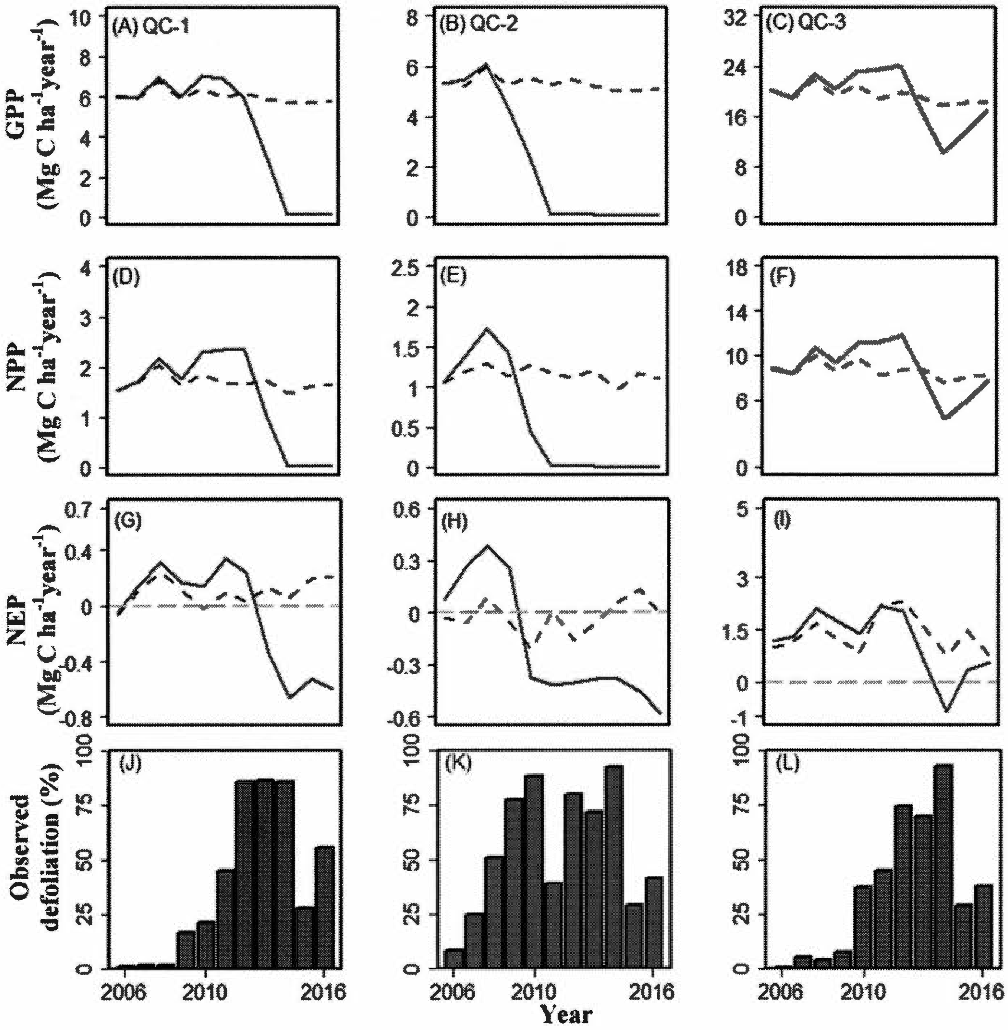

Figure 2.4. Simulated annual GPP, NPP, and NEP under conditions of insect disturbance (red line) and no disturbance (control; green dotted line) by the TRIPLEX-

Insect model using observed annual defoliation scenarios (red bar plot) from the QC1 (A, D, G, and J), QC2 (B, E, H, and K), and QC3 (C, F, I, and L) plots from 2006 to 2016.

When compared with control, SBW outbreaks simulations resulted in above (AGB) and below (BGB) ground decline in biomass for all plots (Figure 2.5 A and B). In contrast, total litterfall (TL) stocks showed increasing trends for all simulations 2006 to 2016 (Figure 2.5 D). The differences in litter fall were 28.09%, 252.56% and 7.97% higher than in scenarios with no defoliation for QC1, QC2 and QC3, respectively, in 2016. In addition, soil carbon (SC) stocks indicated almost no change for all plots compared to no defoliation (control) (Figure 2.5 C).

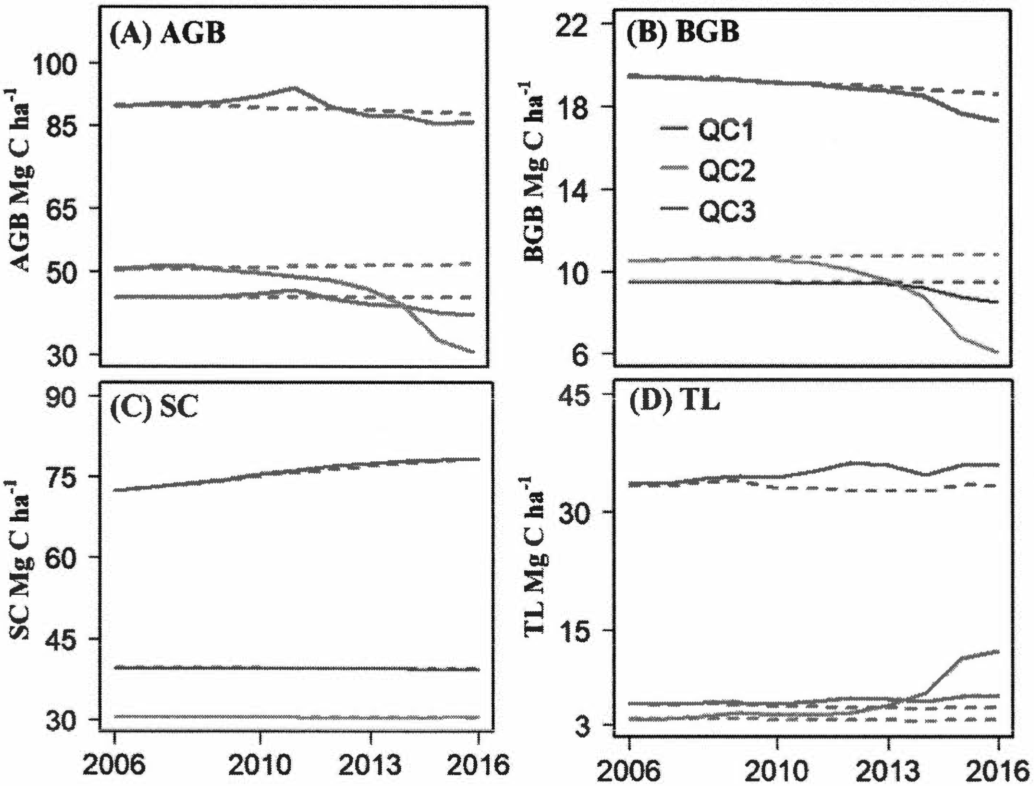

Figure 2.5. Simulated AGB (A), BGB (B), SC (C) and TL (D) on QC1, QC2 and QC3 plots from 2007 to 2017. Dotted lines represent results for no disturbance (control) and

solid lines represent results for insect disturbance. Legend: AGB—aboveground tree biomass; BGB—belowground tree biomass; SC—soil organic carbon; TL—total litterfall.

2.5.4. Prediction of Mortality and NEP with Different Defoliation Scenarios

Simulated results showed cumulative mortality was 24.4%, 88.1% and 24.6%, respectively, for QC1, QC2 and QC3 from 2006 to 2016. We used 30 years (1981–2010) of averages of monthly climate data and three different defoliation scenarios (no defoliation (control), 20% AD per year, and 45% AD per year) to forecast mortality from 2017 to 2025 in the North Shore region of Québec, Canada. In our predicted results, balsam fir mortality should reach 100% if continuous moderate defoliation (45% AD per year) occurs at QC1 until 2021, at QC2 until 2018, and at QC3 until 2022. This means that the risk for balsam fir stands will be significant if AD cannot be lowered.

In our predictions, both QC1 and QC2 showed increasing trends in NEP with no defoliation (control) and with 20% AD from 2017 to 2025 (Figure 2.6 A and B). However, we also found that there was still a slight C source (NEP < 0) at both QC1 and QC2 between 2017and 2025. Given its younger ages, a more rapid recovery was observed at QC3 compared to both QC1 and QC2 for all defoliation scenarios. Recovery in NEP reached 1.91 Mg C ha^{-1}year^{-1} (no defoliation; control) and 2.22 Mg C ha^{-1}year^{-1} (20% AD) in 2020. Predicted showed C sink (NEP > 0) occurred again and kept with no defoliation (control) at QC3 from 2017 to 2025 (Figure 2.6 C); however, QC3 quickly converted from a C sink (NEP > 0) to a source (NEP < 0) again with 20% AD.

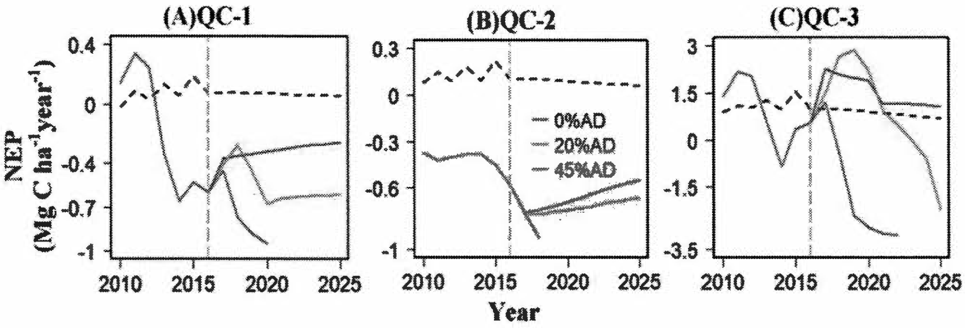

Figure 2.6. Simulated NEP from 2010 to 2016 (on the left side of the vertical dotted line) and predicted NEP under three different defoliation levels (0% AD, 20% AD and 45% AD) from 2017 to 2025 (on the right side of the vertical gray dotted line) for the QC1 (A), QC2 (B), and QC3 (C) sites. Horizontal dotted line represent results for disturbance (control).

2.6. Discussion

2.6.1. Impact of Defoliation Intensity and Duration

Defoliated forests are predicted to lose C because photosynthesis is interrupted by the removal of foliage while respiration and decomposition continue (Hoogesteger and Karlsson 1992; Gough *et al.*, 2016). The model simulations showed that more severe defoliation and a longer outbreak duration would result in a higher mortality level, lower recovery capacity, and thus more C loss in balsam fir forest ecosystems. Gray (2008) reported that more severe outbreaks and a longer duration would result young and rapid carbon-accumulating trees replacing old and slow carbon-accumulating trees. In our study, annual GPP and NPP recovered significantly only at QC3 in 2015 and 2016 (Figure 2.4 C and F), and this was perhaps due to the fact that QC3 had both the younger age and lower CD than both QC1 and QC2.

In our sensitivity experiments, we found that when defoliation severity increases, both GPP and Ra decrease. However, we did not find any correlation between GPP or Ra dynamics and the various forest ages investigated under the same defoliation intensity (see Table 2.4). These results suggest that when defoliation-driven tree mortality is not excessively high, GPP's response to defoliation severity is greater than Ra's in both mature and immature balsam fir forest stands. The possible reason for this difference is that leaves are the only organ of photosynthesis rather than respiration, so defoliation should have a greater and direct impact on GPP than Ra.

When AD is low, it tends to act as a thinning mechanism, such that NEP exceeds that found in non-defoliated stands. Virgin and MacLean (Virgin and MacLean 2017) also found that subsequent forest structure depends on defoliation severity, although SBW outbreaks caused a "patchier" response compared to forestry (thinning) operations. In our simulations, C fluxes (i.e., GPP, NPP and NEP) had a rapid decrease when DM occurred in 2013 (at QC1 and QC3) and in 2010 (at QC2). However, the C fluxes were higher under outbreak conditions compared to the no disturbance scenario before DM occurred (Figure 2.4).

Medvigy *et al.* (2012) reported that forest ecosystems respond strongly to C sequestration when defoliation duration varies from 5 to 15 years, but they exhibit a relatively weak response when defoliation duration varies by more than 15 years. In our study, simulated and predicted results also found that defoliation duration influences C losses and recovery in balsam fir forest stands. Long-term defoliation duration results in higher mortality and a lower recovery capacity in forests (Figure 2.3 D, 2.3 E, and 2.3 F). However, when the defoliation duration is less than 10 years, tree mortality is low because CD remains below lethal levels with the exception of the most severe defoliation cases.

Many studies have shown that insect damage could convert forests from C sinks to C sources (Dymond *et al.*, 2010; Landry *et al.*, 2016; Kautz *et al.*, 2017), and this is consistent with our simulation and sensitivity experimental results. However, we observed a rapid recovery trend in annual NEP if defoliation is reduced (red line after 2015 in Figure 2.6 A–C). In other words, the C source period may not protract following insect outbreaks if defoliation intensity is not excessively high and the duration is relatively short. Albani *et al.* (2010) predicted similar impacts of the hemlock wooly adelgid on eastern United States forests, i.e., an 8% decrease in NEP during the period 2000–2040 and a 12% increase without disturbance during the period 2040–2100.

2.6.2. Model Performance, Limitations, and Future Research

To improve the ability of TRIPLEX to model impacts of insect disturbances, we developed the new TRIPLEX-Insect model which is able to simulate and predict C dynamics and tree mortality caused by defoliation. This ability to test scenarios will be useful in planning SBW management. The TRIPLEX-Insect model is inherited from the original model (TRIPLEX 1.0) and expands its capabilities to simulate key variables related to SBW disturbances, such as changes in mean DBH, mean height, total stand volume, biomass, and C dynamics. The extensive application of this model, however, will first require further research on the five following aspects:

(1) To accurately model the influence of defoliation on regional forest C dynamics, a comprehensive understanding of the spatial and temporal development of insect outbreaks is required (Foster 2011; Robert *et al.*, 2012). In our study, we only calibrated and validated the model at the stand level, yet spatial processes that drive outbreaks to cross thresholds and become catastrophic disturbances have not been completely simulated and are difficult to predict using the current version of the TRIPLEX-Insect model. In the future, we intend to link our model to remote sensing analyses to scale up the model from a stand level to a landscape level for regional-level applications.

(2) Another key element that will need to be included in our model is the influence of species composition. In the current application, we tested the model in balsam fir stands whereas the SBW has been observed to have a reduced effect in mixed-host hardwood stands (Bergeron *et al.*, 1995; Su *et al.*, 1996; Campbell *et al.*, 2008). To more fully

understand forest level C losses, we will also need to include other host species, such as white and black spruce. Even if these species are less vulnerable to mortality caused by the SBW (Hennigar *et al.*, 2008b), it has recently been shown that associational susceptibility occurs when spruce trees are mixed with fir trees, and as outbreak severity and duration length increase (Bognounou *et al.*, 2017).

(3) Climate can also influence SBW outbreak characteristics, such as duration and intensity. For instance, seasonal temperatures and precipitation impact SBW life cycles (e.g., feeding and survival rates) (Régnière and You 1991; Régnière and Duval 1998; Bouchard *et al.*, 2017) and population dynamics (e.g., dispersal area and develop rate) (Greenbank *et al.*, 1980; Régnière and You 1991; Weber *et al.*, 1999). To more accurately predict ecosystem response to SBW disturbances in the future, forthcoming modeling research should investigate the effects of future climate change on defoliation dynamics.

(4) Although our model is not capable of considering all SBW dynamics which impact ecosystem C budgets (e.g., insect respiration processes and decomposition of dead larvae), our method of simulating defoliation directly as an input parameter will be easily applicable to similar pest species from which defoliation data are regularly collected. Furthermore, since the TRIPLEX-Insect model can run with only an AD input, it should be possible to modify weights of monthly defoliation distribution and foliage waste for other defoliator species.

(5) TRIPLEX did not initially consider the concurrent simulation of tree mortality and regeneration; thus, the accuracy of the long-term simulations on C dynamics is limited. In this study, we only predicted short-term C dynamics (from 2017 to 2020) at sites in the North Shore region of Québec, Canada. This approach of only modeling C dynamics during the outbreak when establishment of new balsam fir was chosen so that we could avoid uncertainty, linked to the post-disturbance establishment of new trees, when testing our model. This could also cause some uncertainty related to model

simulations due to simple assumptions concerning C pool totals and regeneration deficiencies.

2.7. Conclusions

There is currently a lack of accurate C budget quantification methods in conjunction with insect disturbances. Accordingly, we successfully developed the TRIPLEX-insect model, which is a new process-based sub-model that takes into account AD, CD, and tree mortality inputs to ascertain C dynamic response to balsam fir forests under SBW disturbances. This study found that the capacity of C sequestration is highly correlated with both defoliation intensity and duration in forest ecosystems. Furthermore, our sensitivity experiments also showed that tree age was a key factor which determined the capacity of recovery in the boreal forest following SBW outbreaks. Additionally, we found that GPP was more sensitive to defoliation intensity compared to Ra during outbreaks for both mature and immature forests. The simulated results showed that C fluxes (i.e., GPP, NPP and NEP) would increase to higher levels under conditions of insect disturbance than no disturbance (control) before DM occurred. The predicted results also indicated that the C source period would not be protracted if DM is not excessively high. Overall, our results demonstrated that the TRIPLEX-Insect model can be a useful tool for assisting forest insect management initiatives and provides more accurate C budget assessments of balsam fir forests under spruce budworm disturbances.

2.8. Author contributions

Z.L., C.P., and D.K. conceived and designed the model; Z.L. performed the model and analyzed the data; Z.L., L.D. and D.K. provided or collected the data; X.Z. contributed technical advice for TRIPLEX model; Z.L., L.D. J-N.C. and D.K. interpreted the analyses and all authors wrote the manuscript.

2.9. Founding

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2.10. Acknowledgements

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2.11. Supplementary materials

Table 2S.1. Calibration results for TRIPLEX-Insect model using basal area data during the 2010–2016 from the North Shore region of Québec.

		Basal Area (m^2 ha^{-1})	
Plot ID	**Year**	**Observed**	**Simulated**
QC_1	2010	13.30	13.34
QC_1	2015	11.65	12.36
QC_2	2010	18.65	18.73
QC_2	2015	13.77	11.9
QC_3	2010	20.25	20.3
QC_3	2015	19.19	19.2

Table 2S.2. Calibration results for TRIPLEX-Insect model using data from Cape Breton Island study sites. Values provided before the parentheses are published values from Ostaff and MacLean (1995). Values provided in the parentheses were simulated using the TRIPLEX-Insect model. The details about Group 2 and 3 were represented by Ostaff and MacLean (1989 and 1995).

	1976					**1985**	
	Density	**Basal Area $(m^2 ha^{-1})$**	**Volume (m^3)**	**DBH (cm)**	**Height (m)**	**DBH (cm)** [a]	**Height (m)** [a]
Group 2	1300 (1294)	38 (44.8)	184 (199.3)	21 (21)	11 (11.1)	22.7 ± 0.9 (21.7)	10.2 ± 0.4 (11.5)
Group 3	900 (896)	21 (40.5)	92 (147)	24 (24)	9 (9.1)	23 ± 2.2 (25.1)	8 ± 0.6 (9.6)

[a] Mean ± standard error of the mean.

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CHAPTER III

SIMULATION AND ANALYSIS OF THE EFFECT OF A SPRUCE BUDWORM OUTBREAK ON CARBON DYNAMICS IN BOREAL FORESTS OF QUÉBEC

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3.1. Résumé

Dans le contexte des changements climatiques, la séquestration de carbone (C) atmosphérique en forêt est un élément clé pour l'atteinte des objectifs d'émission de gaz à effet de serre. Il est donc critique de comprendre comment les perturbations à grande échelle affectent les réservoirs de C forestier. La dynamique du C dans la forêt boréale de l'Amérique du Nord est fortement affectée par la défoliation et la mortalité ayant lieu durant les épidémies de tordeuse des bourgeons de l'épinette (TBE). Nous avons utilisé des données géospatiales issues d'inventaires forestiers, des données climatiques mensuelles, des données séquentielles de défoliation spatialement explicites et le TRIPLEX-Insect pour simuler la dynamique du C avec et sans perturbation par la TBE dans la forêt boréale du Québec. Nos résultats montrent que la défoliation par la TBE et la mortalité qui lui est associée ont causé une réduction moyenne de la biomasse aérienne et souterraine respectivement par 5.96% et 6.94% en 2017. Au même moment, une aire défoliée atteignant 21,046 km2 a été convertie de puit à source de C. Cette étude fournit la première analyse quantitative de l'effet des épidémies de TBE sur la dynamique du C à l'échelle régionale pour trois différents peuplements évoluant dans la forêt boréale (i.e. sapin baumier, épinette, et mixte sapin baumier-épinette). Nos résultats suggèrent que les peuplements de sapins baumiers plus jeunes ont perdu moins de C que les peuplements mixtes ou les pessières durant les épidémies de TBE entre 2007 et 2017 au Québec. Cela souligne l'importance de prendre en compte la composition en espèces lors de l'évaluation de la vulnérabilité ou de la résilience.

3.2. Abstract

In a climate change context, the sequestration of atmospheric carbon (C) in forests is key for achieving emission targets. It is thus critical to understand how large-scale disturbances are affecting the overall forest C stocks. C dynamics in North American boreal forest ecosystems are strongly affected by the defoliation and mortality that occurs during a spruce budworm (SBW) outbreak. We used forest inventory geospatial databases, monthly climate data, spatially explicit defoliation sequence data and the TRIPLEX-Insect model to simulate C dynamics with and without SBW disturbances in stands with different vulnerability to the SBW in the boreal forest of Québec. Our results showed SBW defoliation and related mortality decreased the average aboveground biomass and belowground biomass by 5.96% and 6.94% by 2017, respectively. At the same time, there were 21,046 km^2 of forest were converted from C sink to a source. This study provides the first quantitative analysis of the effect of a SBW outbreak on carbon dynamics for three different boreal stand types (i.e. fir, spruce, and mixed fir-spruce) at a regional scale. Our results suggested that younger fir forests lost less C than either fir-spruce or spruce forests during SBW attacks between 2007 and 2017 in Québec. This highlights the importance of considering species composition when assessing vulnerability or resilience.

3.3. Introduction

Northern American boreal forests are large carbon (C) sinks, which are affected by a wide range of natural disturbances including fire, drought and insect outbreaks (Kurz *et al.*, 2008). Such disturbances can create large variability in short term predictions of global C (Seidl *et al.*, 2011). Over longer timeframes, disturbances affect spatial patterns of forest composition and structure which ultimately affect the capacity of forests to sequestrate C (Franklin *et al.*, 2002; Forman 2014).

Outbreaks of forest insect influence C dynamics by destroying photosynthetic tissues, reducing tree growth and causing mortality over vast areas (Dymond *et al.*, 2010; Hicke *et al.*, 2012). The spruce budworm (*Choristoneura fumiferana* (Clemens), Lepidoptera: Tortricidae) (SBW) is one of the dominant biotic disturbances in North America's boreal forests (Fleming *et al*, 2002; Gray, 2013) whether measured by total area affected (Hicke *et al.*, 2012), frequency and duration of outbreaks (Blais 1983), or volume of wood lost (Hall *et al.*, 1994). The SBW defoliates primarily balsam fir (*Abies balsamea* (L.) Mill.) and spruces (*Picea*), and can kill nearly all trees in dense, mature stands during outbreaks, which occur at intervals of 30-40 years on average (Boulanger *et al.*, 2012). The previous SBW outbreak in Québec lasted from the late 1960s until the mid-1990s (Nealis 2015) causing timber and wood-fiber losses of 250 million m^3 (Grondin *et al.*, 1996) and $12.5 billion in loss of revenue (Coulombe *et al.*, 2004). Since 2006, a new SBW outbreak has developed in the Côte Nord region of Québec and has been steadily expanding throughout much of the provincially managed forest (Ministère des Ressources naturelles et de la Faune, Government of Québec 2018).

Dymond *et al.*, (2010) predicted that the current SBW outbreaks could transform 106,000 km^2 of forested land within this region from a net C sink to a source by 2024. In their study, Dymond *et al.*, (2010) assumed that future spatial-temporal patterns of SBW defoliation would be similar to the 1960s-1990s outbreak. These predictions were derived using simulation of SBW defoliation in the Carbon Budget Model of the

Canadian Forest Sector (CBM-CFS3). The CBM-CFS3 model (Kurz *et al.*, 2009) calculates C as a system of forest C pools related through a set of empirical equations that simulate annual changes in each pool's C stock due to forest dynamics and disturbances. TRIPLEX, on the other hand, is a process-based hybrid model (Peng *et al.* 2002). As such, it is able to simulate both short- and long-term forest C and nitrogen (N) dynamics (e.g. gross primary productivity, autotrophic respiration) derived from monthly climate variables (i.e. temperature, precipitation and relative humidity) (Peng *et al.* 2002). In comparison, CBM-CFS3 is not able to consider the dynamics of these key processes.

TRIPLEX-Insect (Liu *et al.*, 2018) is a new version of TRIPLEX recently developed to quantify forest mortality and C sequestration in response to a SBW outbreak. The TRIPLEX-Insect model has been previously validated at the stand level in Québec (Liu *et al.*, 2018). The objectives of this study were to: (1) use Québec's geospatial forest inventory databases, monthly climate data, spatially explicit defoliation sequences and the TRIPLEX-Insect model to estimate the C budget at the regional scale from 2007 to 2017; (2) compare scenario with and without SBW over a decade (2007-2017) to quantify the relative contribution of SBW to the regional C budget; (3) quantitatively compare the impact of a SBW outbreak on C dynamics for different host species (i.e. fir, fir-spruce, and spruce forests) at the regional scale. Moreover, as balsam fir is more vulnerable to SBW than spruces (Hennigar *et al.*, 2008), we hypothesize that during an outbreak landscapes with a greater proportions of balsam fir will lose more C than those where spruces are more abundant. In this study, we focus exclusively on changes in C caused by SBW as an initial validation of TRIPLEX-Insect at the regional scale. As a result, we did not consider potential confounding factors, such as forest harvesting, fire disturbances, or land-use changes.

3.4. Materials and methods

3.4.1. Study areas

The study area corresponds to the managed boreal forest of Quebec which covers an area of 683,000 km^2 (Figure 3.1, top panel). The dominant species are balsam fir and black spruce (*Picea mariana* (Mill.) B.S.P.). Other important species include white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), white birch (*Betula papyrifera* Ehrh.) and jack pine (*Pinus banksiana* Lamb.). Most of this area suffered some level of defoliation during the previous SBW outbreak of the 1970s and 1980s (https://mffp.gouv.qc.ca/forets/fimaq/insectes/pdf/tord-1967.pdf, accessed Nov. 5, 2018). In 2006, a new spruce budworm outbreak began in the North Shore region of Québec, Canada (Ministère des Ressources naturelles et de la Faune du Québec 2006). In subsequent years, the area defoliated increased almost exponentially to reach 82,000 km^2 by 2018 (Ministère des Forêts de la Faune et des Parcs du Québec 2018). As opposed to the previous outbreak (1960-90), the onset of the current one was much further to the north, in regions previously only lightly affected by the insect (Pureswaran *et al.*, 2015).

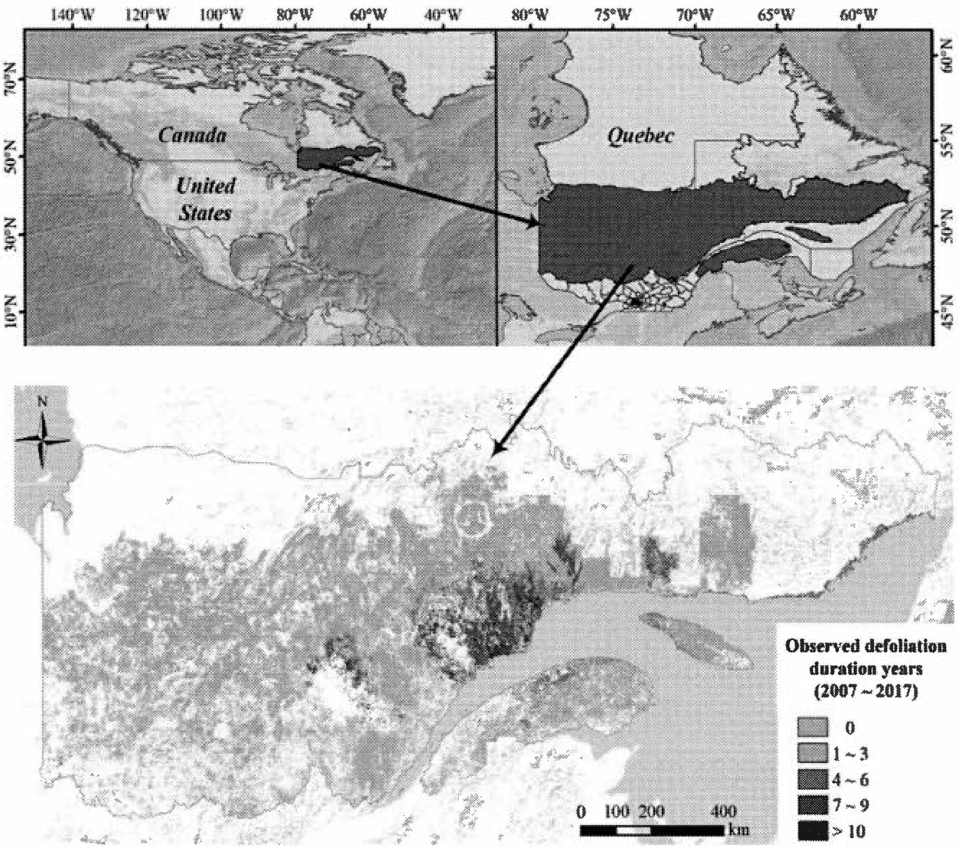

Figure 3. 1. Study areas (top) and estimates of outbreak duration at 1×1km resolution in SBW-host dominate forests (i.e. fir, spruce, and mixed fir+spruce; 218665 km^2) in Québec from2007-2017 (bottom).

3.4.2. Modeling

3.4.2.1. Model structure

TRIPLEX-Insect is a process-based hybrid model that simulates forest growth and key C and N cycling processes with SBW defoliation using a monthly time step (Liu *et al.*, 2018). This model is based on TRIPLEX model (Peng *et al.*, 2002). Forest gross primary productivity (GPP) is estimated using Equation (3.1):

$$\text{GPP} = k \times f(\text{PAR}) \times f(\text{age}) \times f(\text{temp}) \times f(\text{w}) \times f(\text{d}) \times \text{LAI} \quad (3.1)$$

where *k* is a conversion constant; *f*(PAR), *f*(age), *f*(temp), *f*(w) and *f*(d) are functions of monthly received photosynthetically active radiation (PAR), forest age, monthly air temperature, soil water content, and mean percentage of frost days in a month, respectively; and LAI is leaf area index. Monthly net primary productivity (NPP) is calculated as GPP minus autotrophic respiration (Ra) which is estimated using nitrogen (N), air temperature, and component C pools (e.g., wood, branches, foliage, coarse roots, and fine roots) (Zhou *et al.*, 2008). Ecosystem respiration (ER) is comprised of Ra and heterotrophic respiration (Rh), which is calculated by subtracting root respiration from soil respiration, expressed as the exponential function of temperature and Q_{10} (Zhou *et al.*, 2008). We estimated net ecosystem productivity (NEP) by subtracting ER from GPP.. The simulations of soil C and N are based on the CENTURY4.0 model (Parton *et al.*, 1993) which realistically estimates both C and N mineralization rates in forest ecosystems.

Tree mortality is estimated annually from natural mortality (NM; %/year), competition caused mortality (CM; %/year) and defoliation caused mortality (DM; %/year). In this study, NM is based on mean DBH and the number of stems in a plot while CM is estimated based on canopy competition for sunlight (Peng *et al.*, 2002). DM is calculated using Equation (3.2):

$$DM = K \times (exp(DS \times \mathrm{S} \times f(\mathrm{A})) - 7)/100 \qquad (3.2)$$

where *K*=6.6774 is a parameter derived from empirical data taken from the literature (Foster *et al.*, 2011). The defoliation stress (DS) index is calculated using cumulative defoliation (CD) and the weight of current annual defoliation (Liu *et al.*, 2018). S is the index of tree species for defoliation caused mortality and *f*(A) is a function of tree ages. TRIPLEX-Insect uses litterfall rates and tree mortality to represent the transfer of the dead biomass to the litterfall pools that include litter from foliage (LF), litter from branches (LB), litter from wood (LW), litter from fine roots (LFR) and litter from coarse roots (LCR).

To reflect the true range of physiological response, TRIPLEX-Insect considers three compensatory mechanisms when defoliation occurs. We estimated (1) an increase in the photosynthetic efficiency of remaining leaves (Eyles *et al.*, 2011), (2) nonstructural carbohydrates (NSC) transferred to the growth of new leaves (Anderegg *et al.*, 2015) and, (3) the nutritional distribution of foliage and roots that is changed when defoliation occurs (Mediene *et al.*, 2002; Eyles *et al.*, 2011). In addition to defoliating current year needles, SBW also feeds on flower cones, resulting in little to no seed production during an outbreak (Schooley 1978). For this reason, we did not consider new natural regeneration in the study areas. More detailed information on TRIPLEX-Insect is described in Liu *et al.*, (2018).

3.4.2.2. Model initialization

Provincial forest inventory information was obtained from Le Système d'Information Forestière par Tesselle (SIFORT) (Lord *et al.*, 2009; Berger 2015). In this study, the SIFORT geospatial database consists of variables from the last twol forest inventories (1990-now) of the Ministère des Ressources naturelles et de la Faune du Québec (MRNF). These data thus include an inventory of all forests in the study area. We stratified the study area into 683,000 standard grids of 1 km^2. Based on the SIFORT database, we selected 218,665 grid cells for which host species (balsam fir and spruce) density was more than 20% (Figure 3S.1). Each grid cell was assigned a composition type based on the dominant SBW host species in the forest inventory (see supplemental materials): balsam fir (BF), spruce (SP; i.e. black spruce, white spruce and red spruce), and fir-spruce mixture (FS) (Table 3S.1). In addition, total soil organic C data was obtained from the website of Canadian Soil Information Service (CanSIS) (http://sis.agr.gc.ca/cansis/interpretations/ carbon/index.html) (Tarnocai and Lacelle 1996) and projected to our study area to estimate total soil organic C for each grid cell

(Zhang *et al.*, 2005). We also used the first year of defoliation and subsequent annual defoliation as input for each grid cell in TRIPLEX-Insect simulations. Spruce budworm defoliation data (1969-2017) were obtained from the MFFP (https://www.donneesquebec.ca). All data were loaded into TRIPLEX-Insect for initialization.

The model was run using monthly climate data that included air temperature, precipitation, and relative humidity at each grid cell. Monthly climate data for 2007-2017 (i.e. the current outbreak period), were obtained using BioSIM (Régnière 1996; Régnière and St-Amant 2007) by interpolating data from the four closest weather stations to each location and adjusting for differences in latitude, longitude and elevation. We also obtained earlier (1869-2006) monthly climate data estimated by the Fourth Generation Global Climate Model (CGCM4) from the Environment Canada website (http://climate-modelling.canada.ca).*3.4.2.3. Model parameterization*

The TRIPLEX model has been previously parameterized and calibrated for boreal forests using Canadian growth and yield data (Peng *et al.*, 2002; Zhou *et al.*, 2008; Sun *et al.*, 2008). We also calibrated the parameters corresponding to the TRIPLEX-Insect model (Liu *et al.*, 2018). We assumed 50% average annual defoliation for 11 years duration as input data for calibration of the model parameter (i.e. the index of tree species for defoliation caused mortality for S_{fir}, $S_{fir+spruce}$ and S_{spruce} as 0.375, 0.325 and 0.275 respectively). We then compared our model simulation results with published literature in which defoliation causes 85% mortality in mature (age>60 year) fir stands, 42% in immature (age<60 year) fir stands, 36% in mature fir-spruce mixture stands, and 13% in immature spruce stands at the end of a SBW outbreak (MacLean 1980). Moreover, the index of tree ages (*f*(A)) was calibrated by Liu *et al.*, (2018) as follow Equation (3.3):

$$A = 1.27/(1.75 + exp(-0.001 \times Age)) \qquad (3.3)$$

We ran the TRIPLEX-Insect model twice to compare simulation results with and without SBW defoliation. We then evaluated the impact of SBW infestation as the changes in C fluxes and C stocks.

3.4.2.4. Model validation and uncertainty analysis

We used mortality data surveyed by helicopter by the Société de protection des forêts contre le feu (SOPFEU), to validate mortality predictions obtained with the TRIPLEX-Insect model. Model validation focused on balsam fir, spruce and mixed fir-spruce stands that were over 7m in height that covered 339 grid cells in the North Shore region of Quebec in 2015 and 2016 (Figure 3.2. B).

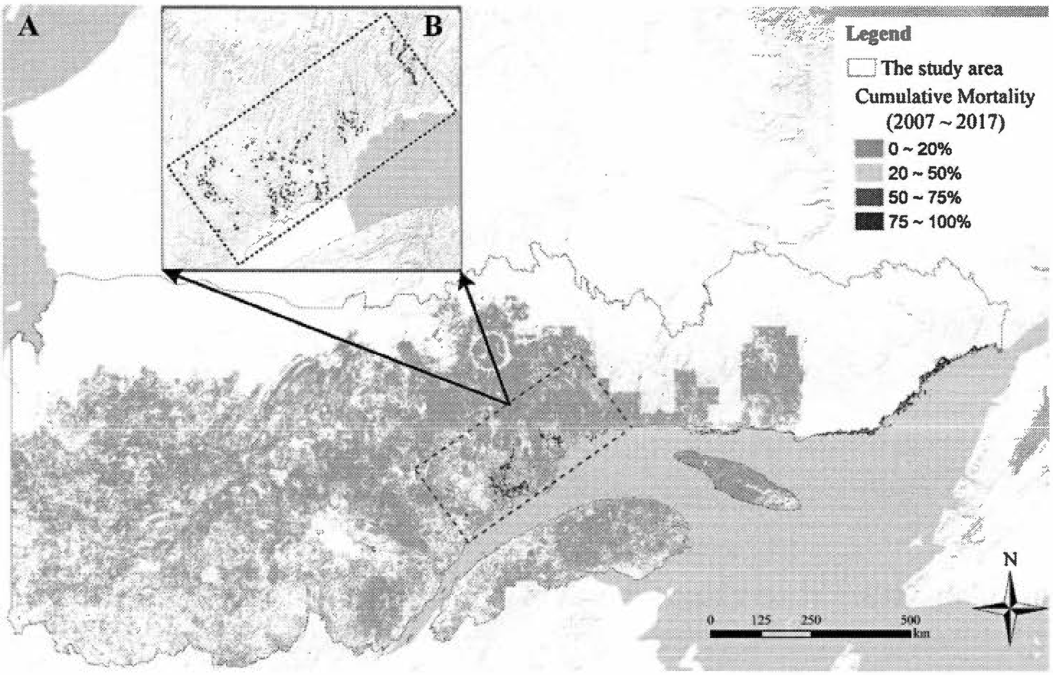

Figure 3. 2. Simulation of SBW caused cumulative mortality (%) in boreal forests of Quebec from 2007- 2017. (B): Mortality was surveyed by helicopter by the Société de protection des forêts contre le feu (SOPFEU) in the North Shore region of Quebec.

Table 3. 1. Ranges for the TRIPLEX-Insect parameters used in the uncertainty calculation of simulated carbon dynamics. Note: BF is fir; FS is mixed fir+spruce; and SP is spruce.

Parameter	**Description**	**Values**	**Reference**
ExtCoef	Radiation extinction coefficient	0.5~0.6	Coops *et al.* (2001)
TaMin	Min temperature (°C) for growth	0~5	Bossel (1996)
GamaF	Leaves turnover per year	0.18~0.3	Gower *et al.* (1997)
GamaR	Fine roots turnover per year	1.4~3.3	Steele *et al.* (1997)
Alpha C	Canopy quantum efficiency	BF=0.1~0.12; FS=0.08~0.1; SP=0.06~0.08	Gower *et al.* 1997
S	the index of tree species for defoliation caused mortality	BF=0.35~0.4; FS=0.3~0.35; SP=0.25~0.3	Assumption

Following Meyer and others' methods (2018), a Monte Carlo simulation was used to estimate the uncertainty on parameters of TRIPLEX-Insect model for large areas simulations. We ran the model 500 times with values of the most sensitive parameters drawn randomly between defined value ranges (Table 3.1). The resulting distributions of TRIPLEX-Insect outputs were summarized as 95th percentiles of C fluxes (i.e. GPP, Ra, NPP, Rh and NEP) and stocks (i.e. aboveground biomass, belowground biomass, soil C and total litterfall).

3.5. Results

3.5.1. Defoliation and Tree Mortality

The validation procedure showed that observed average mortality in the North Shore region of Quebec was 27.03% in 2015 and 21.38% in 2016 while the simulated results were 16.04% and 16.97% in 2015 and 2016, respectively (Table 3.2). These results indicated that TRIPLEX-Insect slightly underestimated the surveyed average mortality in both 2015 and 2016. Across our study areas, simulated results showed cumulative mortality for the period 2007-2017 ranged from 0-20% over 94.48% (i.e. 206,589 km^2) of the study area (see green color in Figure 3.2A). Because there was no or little defoliation in these areas, mortality resulted mainly from natural (senescence) and competitive mortality (NM and CM) in the TRIPLEX-Insect model. We also found that 4.11% (i.e. 8,986 km^2) of the study area had cumulative mortality that ranged between 20% and 50% (see yellow color in Figure 3.2A). Finally, cumulative mortality greater than 50% was simulated in only 1.41% (i.e. 3,090 km^2) of the study area (see red color in Figure 3.2A). In addition, the TRIPLEX-Insect simulation indicated that spruce stands had a lower average cumulative mortality (i.e. 17.75%) than either balsam fir (i.e. 19.91%) or mixed fir-spruce (20.01%) stands during the 2007-2017 SBW outbreak period.

Table 3. 2. Observation and simulation of average mortality of boreal forests (i.e. fir, fir+spruce and spruce) at North Shore region of Québec in 2015 and 2016

	2015	**2016**	**Total**
Areas of validation (km^2)	135	204	339
Observation of average mortality	27.03%	21.38%	23.63%
Simulation of average mortality	16.04%	16.97%	16.60%

Figure 3.1 (bottom panel) shows the spatial distribution of duration of SBW defoliation in Quebec from 2007 to 2017. The duration of defoliation was 4.02 years on average over the 2007-2017 period (Table 3.S1). Annual defoliated areas increased from 1,040 km^2 to 51,851 km^2 during 2007-2017 (Table 3.S2). Figure 3.3 represented the details of the spatial distribution of annual defoliation for 2007-2017. We found that a higher proportion of defoliated areas occurred in balsam fir than either spruce or mixed fir-spruce forests during the SBW outbreak (Table 3.S3). This trend became increasing

apparent as the outbreak progressed from 2007 to 2017 (Table 3.S3). However, fir forests had the lowest mean duration of defoliation (3.75 years; Table 3.S1) and mean cumulative defoliation (236.35%; Table 3.S1) over the 2007-2017study period.

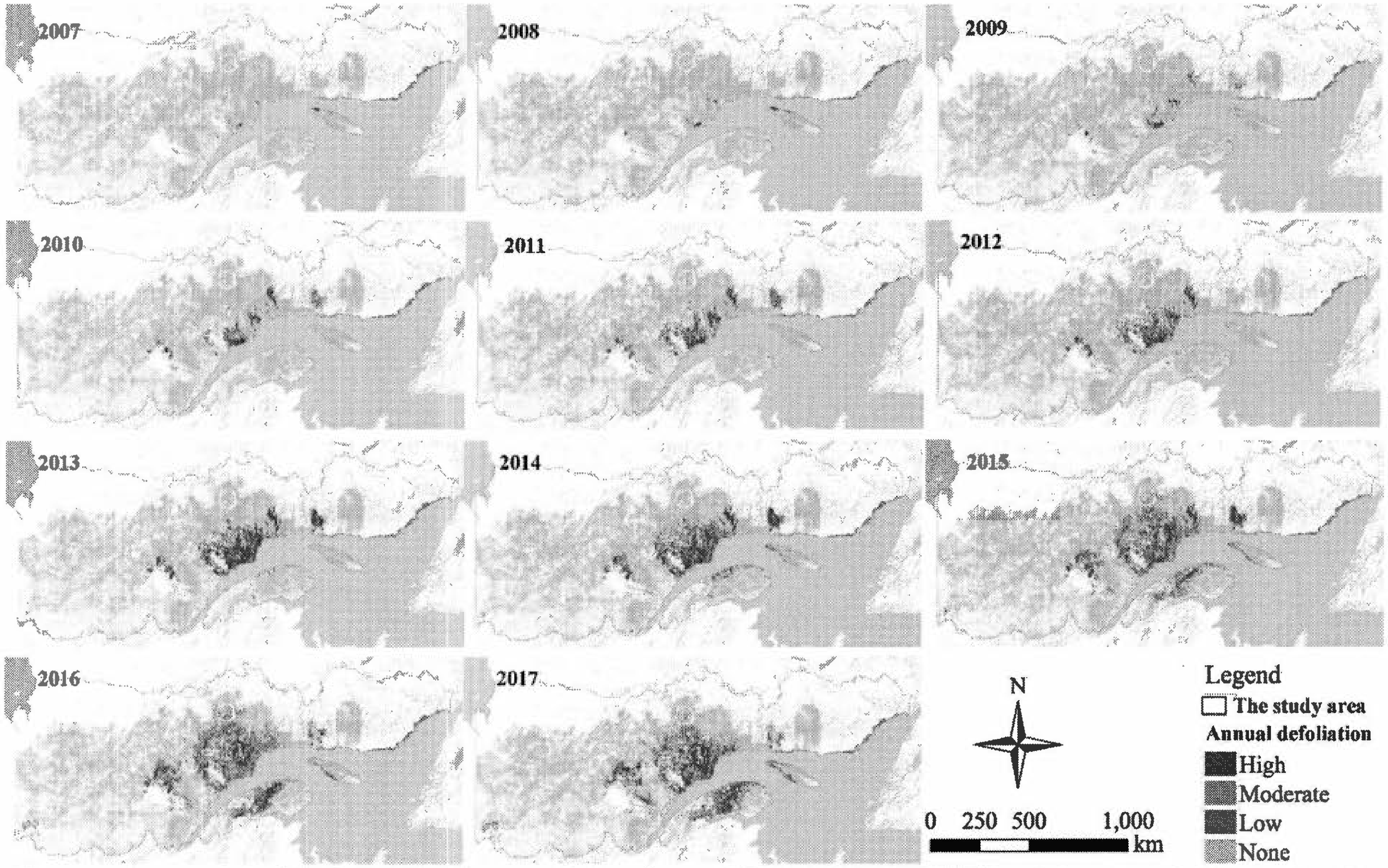

Figure 3. 3. Observed annual defoliation at 1×1km resolution from 2007 to 2017 in SBW host dominated forests (i.e. fir, spruce, and mixed fir+spruce; 218665 km^2) in Québec. None means less than 1% annual defoliation; Light means range from 1% to 35% annual defoliation; Moderate means range from 36% to 70% annual defoliation; Severe means range from 71% to 100% annual defoliation.

3.5.2. Changes in C Fluxes

As the SBW outbreak progressed (Figure 3.2), simulations of average GPP, Ra, NPP and Rh (Figure 3.4) showed clear downward trends for all species in defoliated areas. Comparison of GPP in simulation with SBW disturbances compared to those with no defoliation (control) showed that average GPP declined 321 g C $m^{-2}year^{-1}$ for 2007-2017 in defoliated areas (Figure 3.4A). Indeed, during the SBW outbreak (2007-2017), areas with GPP loss expanded dramatically in Québec (Figure 3.S2). The decrease in average annual GPP over the defoliation period (2007-2017) was the most pronounced in mixed fir-spruce forests followed by spruce and fir forests (Table 3.3). Around 2012, GPP started to diverge between simulations with and without SBW defoliation (Figure 3.4A). By 2017, the maximum reductions were 26.74%, 26.41% and 31.93% for fir, spruce, and mixed fir-spruce forests, respectively (Figure 3.4A). From another perspective, a maximum of 52.94% of fir forests had been defoliated (Table 3.S3) which resulted in -8.20% changes of average GPP per year from 2007-2017 (Table 3.3). We also estimated an average annual change of -0.15% GPP per unit of area of fir forest. For spruce and mixed fir-spruce forests, GPP losses were -0.59% and -0.38%, respectively. Consequently, GPP losses were lower in fir forests than in either spruce or mixed fir-spruce forests during the current outbreak.

Trends in average annual NPP losses were similar to what was simulated with GPP (Figure 3.4A and 4C). Maximum reductions by 2017 were 30.54%, 29.36% and 36.24% for fir, spruce and mixed fir-spruce forests, respectively (Figure 3.4C). Trends in average annual Ra and Rh losses were similar to GPP and NPP. They were, however, greater in Ra compared to Rh (Figure 3.4B and 4D). In addition, unlike GPP, NPP and Ra, simulated Rh following SBW disturbances increased compared to no defoliation in all forest types up to 2013 (Figure 3.4D).

Table 3. 3. Changes correspond to the difference between simulations of scenarios with and without spruce budworm for BF (fir: 16349km^2), FS (fir+spruce: 22007km^2), SP (spruce: 27390km^2) and total forest (65746km^2) in Québec. Legend: NEP—net ecosystem productivity; GPP—gross primary productivity; NPP—net primary productivity; Ra—autotrophic respiration; Rh—heterotrophic respiration; AGB—aboveground tree biomass; BGB—belowground tree biomass; SC—soil organic carbon; TL—total litterfall.

Average changes	**BF**	**FS**	**SP**	**Total**
GPP per year (2007~2017)	-8.20%	-11.66%	-10.22%	-10.08%
NPP per year (2007~2017)	-8.62%	-12.04%	-10.30%	-10.31%
Ra per year (2007~2017)	-7.90%	-11.41%	-10.15%	-9.93%
Rh per year (2007~2017)	-1.97%	-4.39%	-2.36%	-2.96%
AGB (2017)	-6.67%	-6.67%	-4.44%	-5.96%
BGB (2017)	-7.33%	-7.66%	-5.62%	-6.94%
SC (2017)	-3.59%	-1.62%	-1.55%	-2.15%
TL (2017)	1.18%	4.22%	2.56%	2.68%

The average NEP simulated by TRIPLEX-Insect in defoliated areas was positive for fir (77±18.5g C m^{-2}year^{-1}) but negative for both spruce (i.e. -34±8.2 g C m^{-2}year^{-1}) and mixed fir-spruce (i.e. -59±14 g C m^{-2}year^{-1}) forests in 2016 (Figure 3.4E). However, in 2017, our results showed positive NEP of 152±23 g C m^{-2}year^{-1}, 23±3.5 g C m^{-2}year^{-1} and 2±0.3 g C m^{-2}year^{-1} for fir, spruce and mixed fir-spruce forests, respectively (Figure 3.4E). In addition, simulated results also indicated that forests with SBW defoliation had more areas that were a C source (NEP<0) than areas without SBW disturbances for 2007-2017 (Figure 3.5). 23,017 km^2 or approximately 35% of the defoliated area (65,746 km^2) was a C source in 2017 (Figure 3.5). In contrast, 21,046 km^2 of forested area (i.e. 10% of the whole study area) was converted from a C sink to a source in 2017 (Figure 3.5).

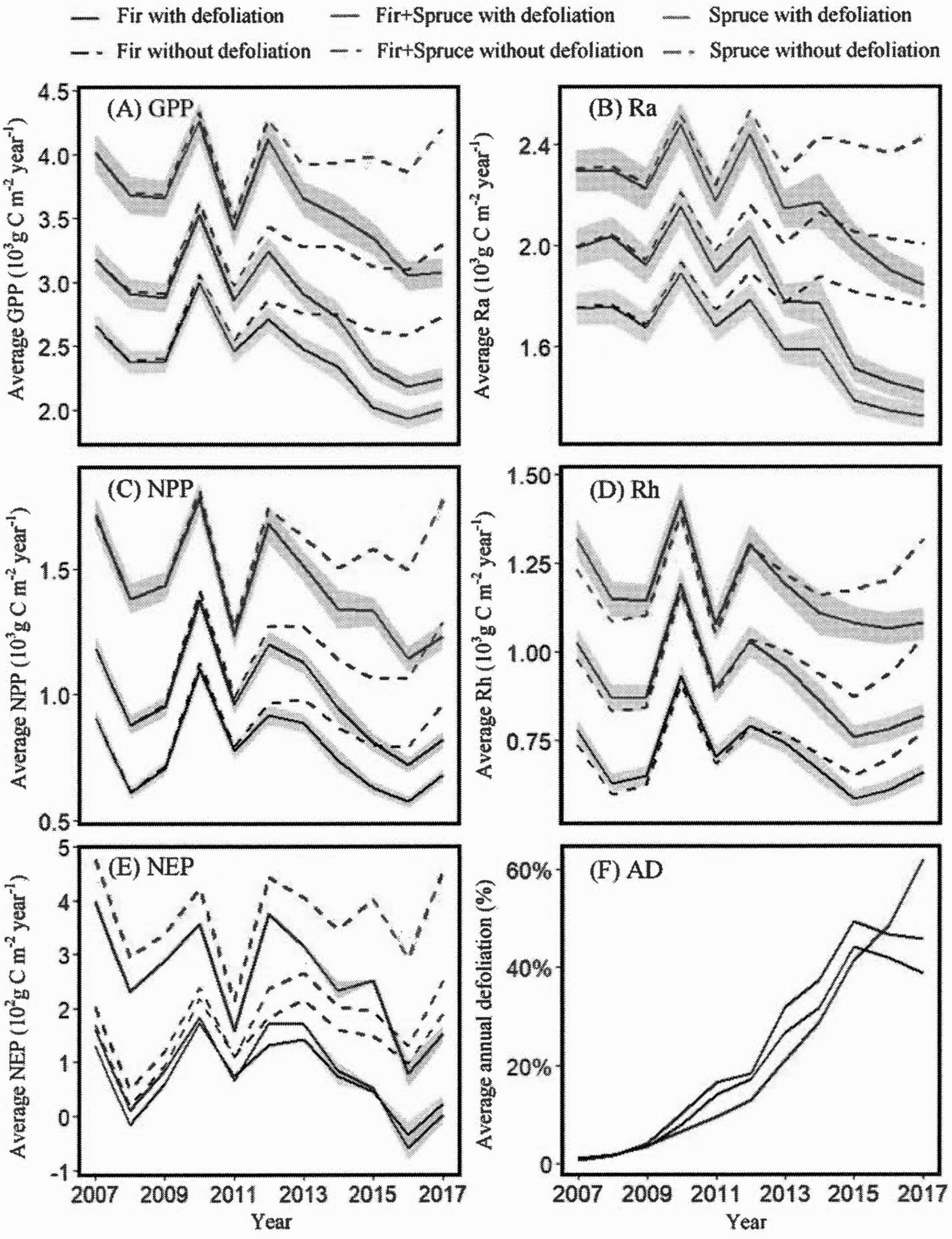

Figure 3. 4. Simulated GPP (A), Ra (B), NPP (C), Rh (D), NEP (E) and observed AD (F) for different species (i.e. fir: 16349 km^2; spruce: 27389 km^2; and mixed

fir+spruce: 22007 km^2) from 2007 to 2017 in Québec. The shaded areas show the standard deviation with uncertainty estimates. Legend: GPP—gross primary productivity; NPP—net primary productivity; Ra—autotrophic respiration; Rh—heterotrophic respiration; NEP—net ecosystem productivity; AD—annual defoliation.

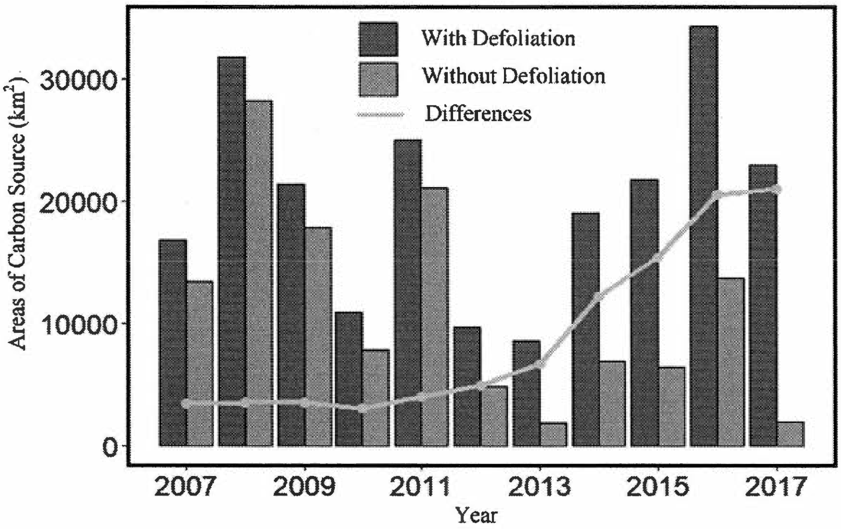

Figure 3. 5. Simulated areas of carbon source with and without SBW defoliation in Quebec from 2007-2017. The blue line is the differences between with and without defoliation.

3.5.3. Changes in C Stocks

Average aboveground biomass (AGB) started to decline in 2013 in both spruce and mixed fir-spruce stands and in 2015 in balsam fir stands (Figure 3.6A). Average belowground biomass (BGB) followed similar trends to that of AGB (Figure 3.6A and 6B). By 2017, average AGB and BGB for all defoliated areas had changed by -5.96% and -6.94%, respectively (Table 3.3). In contrast, average soil organic C (SC) stocks kept increasing for the entire simulation period although at a slower pace with defoliation than without (Figure 3.6C). Regardless of stand composition, average total litterfall biomass (TL) stocks decreased before 2012 (Figure 3.6D). The lowest simulated values of average TL were 6.79±0.33 10^{3}g C m^{-2}, 5.31±0.26 10^{3}g C m^{-2} and

6.34±0.31 10^3g C m^{-2} for balsam fir, spruce, and mixed fir-spruce forests, respectively. After 2012, TL started to increase again until the end of the study (Figure 3.6D). In addition, we found a clear decline in fine root litter (LFR) stock since the start of SBW outbreak (Figure 3.7). The foliage litter (LF) stock was also higher following defoliation than without defoliation during the outbreak period (Figure 3.7). There was a significant increase in fine branch (LB), wood (LW) and coarse root (LCR) litters after 2013 (Figure 3.7).

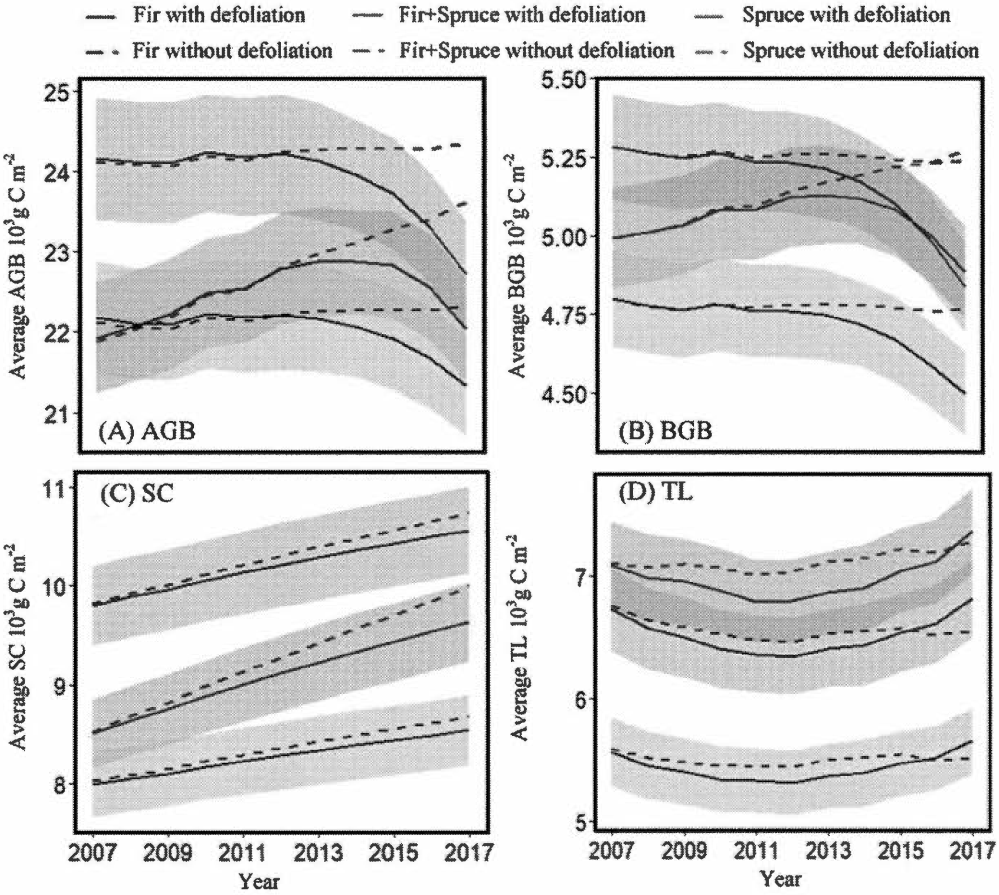

Figure 3. 6. Simulated AGB (A), BGB (B), SC (C) and TL (D) for different species (i.e. fir: 16349 km^2; spruce: 27389 km^2; and mixed fir+spruce: 22007 km^2) from 2007 to 2017 in Québec. The shaded areas show the standard deviation with uncertainty

estimates. Legend: AGB—aboveground tree biomass; BGB—belowground tree biomass; SC—soil organic carbon; TL—total litterfall.

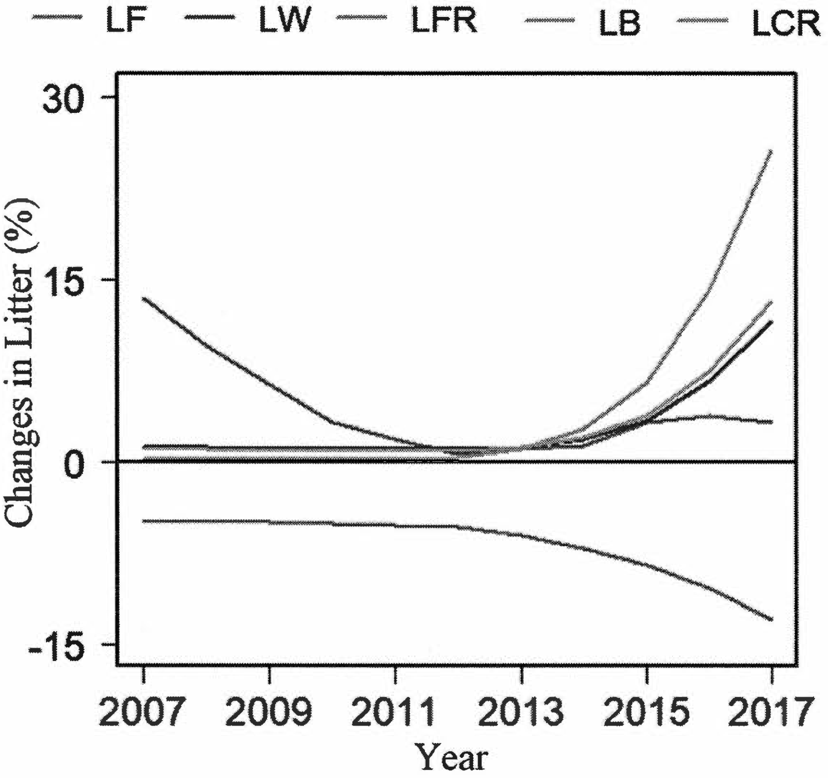

Figure 3. 7. Simulated changes of LF, LB, LW, LCR and LFR with defoliation compare to without defoliation from 2007 to 2017 in defoliated areas (65745 km^2) of Québec. Legend: LF—litter from foliage; LB—litter from fine branch; LW—litter from wood; LCR—litter from coarse root; and LFR—litter from fine root.

3.6. Discussion

In this study, we have demonstrated that the TRIPLEX-Insect model is a useful tool for simulating boreal forest ecosystem response to SBW disturbances at the regional scales, although uncertainties still exist in the structure and parameters of the model (Grimm *et al.*, 2005). In particular: (1) model validation at the regional scale could only be done on mortality since it was the only data observed in the field. Our simulations of mortality were slightly lower than observations from 2015 and 2016 in Quebec. This difference may be the result of a conservative estimation of mortality from cumulative defoliation in Eq.3.2. Moreover, aerial observations of defoliation can also be overestimated because they may include defoliation from insects other than SBW or other factors such as drought or late frost (Meddens *et al.*, 2012; Senf *et al.*, 2017). (2) Some authors have suggested that the impacts of insect dynamics on ecosystem C budgets should be investigated for more accurate modeling of ecosystem response to SBW disturbances in the future (Hicke *et al.*, 2012; Sturtevant *et al.*, 2015; MacLean 2016). We also recognize that the TRIPLEX-Insect model does not consider all SBW dynamics which influence ecosystem C budgets, such as insect respiration processes and decomposition of dead larvae. At the regional scale, these variations in C should be ignored but unfortunately there is currently not enough data to model or simulate these C processes as far as we know. (3) In this study, SBW host species are mostly located in areas with upland soil conditions. Lowland or wetland soil conditions are also characteristic of boreal ecosystems albeit with lower growth rates and thus lower overall carbon stocks. However, in its current state, TRIPLEX-Insect does not account for the effects of these types of soils on C dynamics.

Previous studies suggested that regional C dynamics may be directly affected by the species of defoliating insect, defoliation severity and duration, region, forest types and age (Kurz *et al.*, 2008; Dymond *et al.*, 2010; Ghimire *et al.*, 2015; Landry *et al.*, 2016; MacLean 2016; Liang *et al.*, 2017). In our study area, a higher proportion of defoliated areas occurred in balsam fir forests than either pure spruce or mixed fir-spruce forests thus suggesting a higher vulnerability to SBW (see Table 3.S3). The greater carbon losses in terms of GPP and NPP in mixed stands compared to pure stands of spruce or the most vulnerable host species, balsam fir, is contrary to expectations of a protective effect of biodiversity (Jactel and Brockeroff 2007).

However, there are at least two possible explanations: mixed host stands may increase associational susceptibility by permitting host switching (Bognounou *et al.*, 2017) and in pure stands age may be more important than composition (James *et al.*, 2007). For example, balsam fir was comparatively younger than either pure spruce or mixed fir-spruce forests. This may, at least in part, explain why fir forests did not sustain higher mortality than spruce and mixed fir-spruce stands during the outbreak. Indeed, tree species and tree age are known to be important factors influencing defoliation and mortality (MacLean 1980; Hennigar *et al.*, 2008). Moreover, fir in general has a higher growth rate than spruce particularly when stands are young (Alexander 1987). As younger forests grow more quickly than older forests, they gain more C (Tang *et al.*, 2014), this may explain the lower changes of C fluxes (i.e. GPP, NPP, Ra, Rh and NEP; Table 3.3) estimated by TRIPLEX-Insect for balsam fir than either pure spruce or mixed fir-spruce in defoliated areas during the SBW outbreak. Our results suggest that although there were large losses of C in balsam fir (Figure 3.4), these losses were partially compensated by the younger age and more rapid growth rate of fir stands. This runs contrary to our original hypothesis that fir forests may lose more C than either spruce or mixed fir-spruce forests at the regional scale during the SBW outbreak. This highlights the importance of considering more than just species composition in evaluating vulnerability or resilience.

Average NEP in the TRIPLEX-Insect simulations (123±9.8 g C $m^{-2}year^{-1}$ for defoliated areas of the boreal forest in Quebec) was twice that estimated with CBM-CFS3 model (56.3±51 g C $m^{-2}year^{-1}$) in eastern Canadian Forests (Dymond *et al.*, 2010). There are three possible reasons for this: first, terrestrial ecosystem C fluxes significantly respond to climate (Cao and Woodward 1998; Gang et al., 2017). Our estimates were not only derived from annual defoliation but also included climate conditions, whereas Dymond *et al.*, (2010) did not consider climate effects during the outbreak period. Second, we did not fully estimate C dynamics over the entire outbreak cycle because the current outbreak is not over yet. Third, the extent and severity of the current defoliation are less than what was observed in the previous outbreak in Quebec (Bouchard *et al.*, 2007; Ministère des Ressources naturelles et de la Faune, Government of Québec 2018). As a result, although Dymond *et al.*, (2010) were conservative in their projections of the next SBW outbreak scenario, the extent and severity of the current outbreak are lower than their estimates.

Dead trees continue to contribute to ecosystem respiration whether they are standing or not (Ohtsuka *et al.*, 2007; Moore *et al.*, 2013). Thus, it is important that dead trees be transferred to litterfall pools and incorporated into estimates of ecosystem respiration. Our simulated Rh increased at the beginning of SBW outbreak, but decreased after 2013. Edburg *et al.* (2011) also found a similar result following mountain pine beetle (*Dendroctonus ponderosae*) attack. However, other studies did not report decreases in Rh following insect disturbances (Kurz *et al.*, 2008; Clark *et al.*, 2010; Meyer *et al.*, 2018). Dymond *et al.*, (2010) explained these differences by evoking different mechanisms associated with different insects. For example, SBW causes tree mortality after multiple years of severe defoliation, whereas mountain pine beetle kills the host within a year or two. It is likely that Rh in the TRIPLEX-Insect model is underestimated when mortality is very high. We think that the land-use categorization changed when tree mortality was greater than 95%, and thus TRIPLEX-Insect stopped simulations. In this study, there were approximately 1% (690 km^2) of defoliated areas with mortality greater than 95%. However, we think that these effects can be ignored in large-scale regional simulation.

TRIPLEX-Insect predicts that foliage litter continues to increase, albeit at a slower rate, during the SBW outbreak (Figure 3.7). Conversely, fine root litter decreases at a faster rate as the outbreak progresses. This may be a consequence of NPP being distributed more in foliage than fine roots when defoliation occurred (Eyles *et al.*, 2011; Liu *et al.*, 2018). Before 2012, total litterfall appears to decrease with defoliation for all host species. A possible reason could be that SBW caused tree growth loss resulted in live trees producing less litterfall (Twilley *et al.*, 2017). With increased mortality after continuous defoliation, an increasing number of dead trees were transferred to litterfall pools (Hicke *et al.*, 2012). In total, our simulation showed a trend increasing total litterfall after 2012. Similarly, Grace (1986) reported that total litterfall was not different between defoliated and un-defoliated areas. However, le Mellec and Michalzik (2008) concluded that soil C:N ratios may be greatly increased in defoliated forest areas. Moreover, Chapman *et al.*, (2003) found an increase in litter quality and decomposition with insect herbivory. Overall, quantifying the influence of SBW outbreak on soil C and litterfall pools should be improved through ongoing monitoring of tree mortality, litterfall biomass and C fluxes to the soil.

This study only simulated C dynamics under SBW disturbances for a limited time period (2007-2017). Longer simulations would be needed to evaluate the long-term effects of defoliation scenarios. For example, different management responses (i.e. spray protection, harvest and afforestation strategies) can change forest composition, such as host species and tree ages that will have a further impact on the spread of the SBW epidemic across the landscape (MacLean 1996). Moreover, global changes such as global warming, drought, elevated atmospheric CO_2 concentrations and extreme climates may significantly influence tree productivity, insect population dynamics and host species distribution which certainly need to be further addressed in future work (Fleming and Volney 1995; Zhang *et al.*, 2014; Pureswaran *et al.*, 2015; De Grandpré *et al.*, 2019).

3.7. Conclusions

In this study, TRIPLEX-Insect model performed well in simulating C dynamics at the regional scale. The results demonstrate that there were 21,046 km^2 of defoliated areas were converted from C sinks to sources in 2017. Compared to simulation without defoliation, the average NEP with defoliation from 2007 to 2017 decreased by 91±7.3 g C $m^{-2}year^{-1}$ in defoliated areas of Québec. The spruce budworm outbreaks also led to significant C losses in both aboveground biomass and belowground biomass whereas organic C increased in soil for balsam fir, fir-spruce and spruce forests in Québec from 2007 to 2017. Total litterfall was reduced before 2012, and then increased with increasing mortality caused by spruce budworm disturbances after 2012. Contrary to our hypothesis, balsam fir stands had the least overall carbon losses induced by spruce budworm, which we attributed to their relatively younger age that allowed them to undergo a more rapid growth than spruce and mixed fir-spruce stands.

3.8. Acknowledgements

This study was a part of research project recently funded by the Fonds de recherche du Québec (FQRNT) program and the Natural Sciences and Engineering Research Council of Canada (NSERC) Discover Grant. We wish to thank Ms. Marie-Claude Lambert for supplying the climate data used in this analysis. We also appreciate Mr. Jonathan Boucher from SOPFEU who provided the mortality data for validation in this study.

3.9. Supplementary materials

The estimation of the effects of a SBW outbreak on carbon dynamics followed three steps (Figure S1). First, we defined and produced a forest map based on a forest inventory and defoliation database. Second, we integrated climate data and soil carbon data into the forest map (1×1km resolution). Finally, we simulated the C dynamics in each grid cell (1×1km resolution) from 2007-2017.

3.9.1. Step 1: Production of forest map

(1) Provincial forest inventory plots and geospatial databases were obtained from Le Système d'Information Forestière par Tesselle (SIFORT) (Lord and others 2009; Berger

2015). In this study, the SIFORT database consists of variables from last two forest inventories (1990~now) of the Ministère des Forêts, faune et parcs du Québec (MFFP). These data include an inventory of all forests in the study area at a 300×500m resolution (approximately 14 ha) for each plot.

We divided the tree species into 4 categories based on SIFORT's species code (Lord and others 2009; Berger 2015). The specific classification is as follows:

SS, SAB, SBSB, SBB, SBRX, SBT0 codes were classified as Fir with a code No.1;

SE, SG, ES, CS, SBEN, SBEB, SBEP, ENSB, EPSB, EBSB codes were classified as Fir+Spruce with a code No.2;

EE, EB, EG, EEPL, EEP0, EPH, ENEN, EN, ENRX, EPEPBP, EPEP, ENENBP were classified as Spruce with a code No.3;

and all other species (e.g. non-host species) were removed from the analysis.

(2) Defoliation data for the current spruce budworm outbreak (2007-2017) was obtained from the MFFP (https://www.donneesquebec.ca). Annual defoliation intensity are divided into 4 levels: none (0-5%); light (5-33%); moderate (34-66%); high (67-100%). In this study, we assigned 0% for none and the mean-value for other levels (i.e. light is 19%, moderate is 50%, and high is 83%).

After species classification, we projected and matched defoliation (2007-2017) to the SIFORT data. If the SIFORT plot included more than one defoliation pattern, we estimated the defoliation patterns of plot as the average value.

(3) We produced new forest map at the grid of 1 km^2 resolution. For each grid cell, we combined 6 or 7 SIFORT plots. We kept major tree species for each grid cell by applying the following rules:

a. if the numbers of No.1 >=4, this grid estimated as No.1 host species (i.e. fir);

b. if the numbers of No.3 >=4, this grid estimated as No.3 host species (i.e. spruce);

c. if the numbers of No.2 >=4, or No.1=No.3=3 or 2, this grid estimated as No.2 host species (i.e. fir+spruce).

We also estimated average annual defoliation, tree height, age and density for each major species per 1 km^2 grid. For example, a new grid combined 6 SIFORT cells and had 4 plots with major species. We estimated the density using these 4 densities of plot and dividing by 6.

3.9.2. Step 2: Integration of climate data and soil carbon data

Monthly climate data at a 10×10 km resolution, from 2007-2017 (i.e. the current outbreak period), were obtained using BioSIM (Régnière 1996; Régnière and St-Amant 2007) by interpolating data from the four closest weather stations to each location and adjusting for differences in latitude, longitude and elevation. We also obtained earlier (1869-2006) monthly climate data estimated by the Fourth Generation Global Climate Model (CGCM4) from the Environment Canada website (http://climate-modelling.canada.ca). We integrated monthly temperature, precipitation and relative humidity into the forest map that we developed in step 1.

In addition, Soil organic carbon data was obtained from the website of the Canadian Soil Information Service (CanSIS) (http://sis.agr.gc.ca/cansis/interpretations/carbon/index.html) (Tarnocai and Lacelle 1996). This data includes 15,000 polygons that covers all of terrestrial Canada. We integrated total carbon content per polygon into the forest map that we estimated in step 1 (Zhang and others 2005).

3.9.3. Step 3: Simulation of carbon dynamics

We input all data from the new forest map into the TRIPLEX-Insect model for simulation of carbon dynamics. The model was run twice to compare the changes of carbon dynamic between with and without spruce budworm defoliation.

Table 3S. 1. Observed defoliation for BF (fir), FS (mixed fir+spruce), SP (spruce) and total of fir and spruce forest in Québec. All average value were estimated by total defoliated areas during 2007-2017.

	BF	**FS**	**SP**	**Total**
Average forest age in 2017	67	89	95	83
Total study area (km^2)	29126	58924	130615	218665
Total defoliated area (km^2) during 2007~2017	16349	22007	27390	65746
Observed average defoliation duration between 2007~2017	3.75	4.28	3.98	4.02
Observed average cumulative defoliation during 2007~2017	236.35%	261.86%	288.45%	241.60%

Table 3S. 2. Observed defoliated area and intensity in the total fir and spruce forests in Quebec from 2007 to 2017. The percentage of defoliated areas was estimated by using the total forest area (218665 km2) in this study; the value of average cumulative defoliation and the value of average annual defoliation were estimated using total defoliated areas (65746 km2) from 2007-2017; the value of average current defoliation was estimated using the total current defoliated area. Classes of current defoliated areas are as follows: Low is 1~33%; Moderate is 34~66%; and High is 67~100%.

Year	**Class of current defoliated areas (km^2)**			**Annual defoliated areas (km^2)**	**Annual defoliated areas (%)**	**Average cumulative defoliation**	**Average current defoliation**
	Low	**Moderate**	**High**				
2007	358	467	215	1040	0.476%	0.83%	54.09%
2008	469	758	620	1847	0.845%	2.51%	61.13%
2009	1041	1490	1458	3989	1.824%	6.19%	61.14%
2010	2586	3754	2989	9329	4.266%	14.52%	58.90%
2011	4955	6967	4290	16212	7.414%	28.26%	55.83%
2012	4593	7924	5947	18464	8.444%	44.77%	58.88%
2013	3576	8914	13295	25785	11.792%	71.80%	69.00%
2014	5918	13059	14363	33340	15.247%	104.65%	64.89%
2015	10507	23278	15673	49458	22.618%	149.83%	60.14%
2016	14513	25419	13303	53235	24.345%	194.77%	55.57%
2017	12654	22146	17051	51851	23.713%	241.60%	59.45%

Table 3S. 3. Observed defoliated areas and percentage of current defoliated areas in different species forests (i.e. BF is fir forest; FS is fir-spruce mixture forest; and SP is spruce forest) from 2007 to 2017 in Quebec.

Year	Defoliated areas			Percentage of current defoliated areas in total forests		
	BF	FS	SP	BF	FS	SP
2007	203	299	539	0.70%	0.51%	0.41%
2008	459	568	820	1.58%	0.96%	0.63%
2009	926	1448	1615	3.18%	2.46%	1.24%
2010	1759	3950	3260	6.04%	6.70%	2.50%
2011	2733	6649	6830	9.38%	11.28%	5.23%
2012	3535	6876	8053	12.14%	11.67%	6.17%
2013	5103	9900	10782	17.52%	16.80%	8.25%
2014	7255	12321	13764	24.91%	20.91%	10.54%
2015	11001	17469	20988	37.77%	29.65%	16.07%
2016	12876	17924	22435	44.21%	30.42%	17.18%
2017	15420	16846	19585	52.94%	28.59%	14.99%

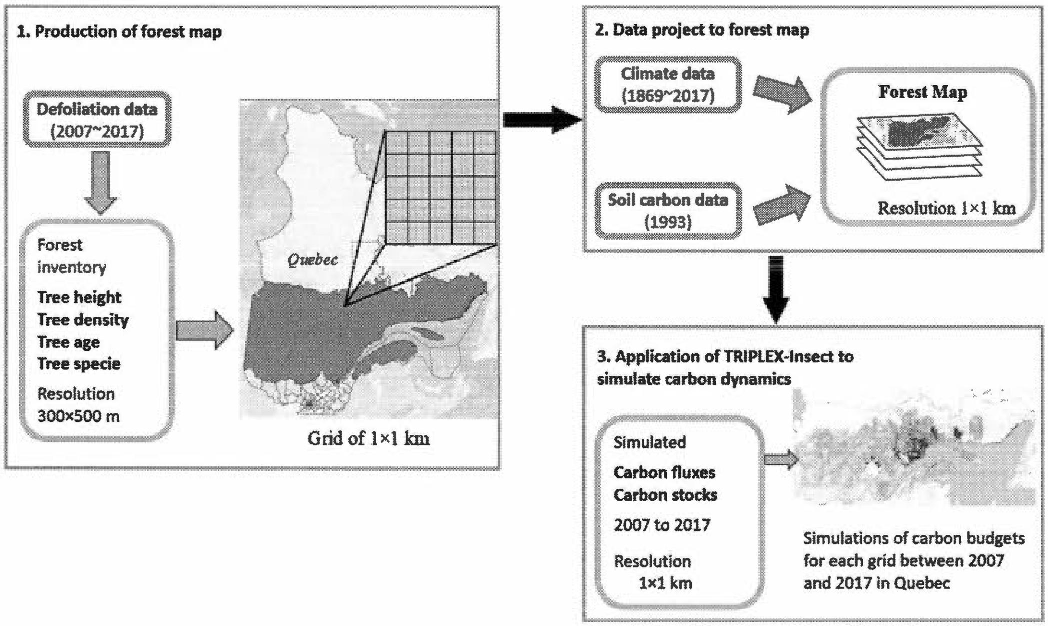

Figure 3S.1. Illustration of the three main steps of the study.

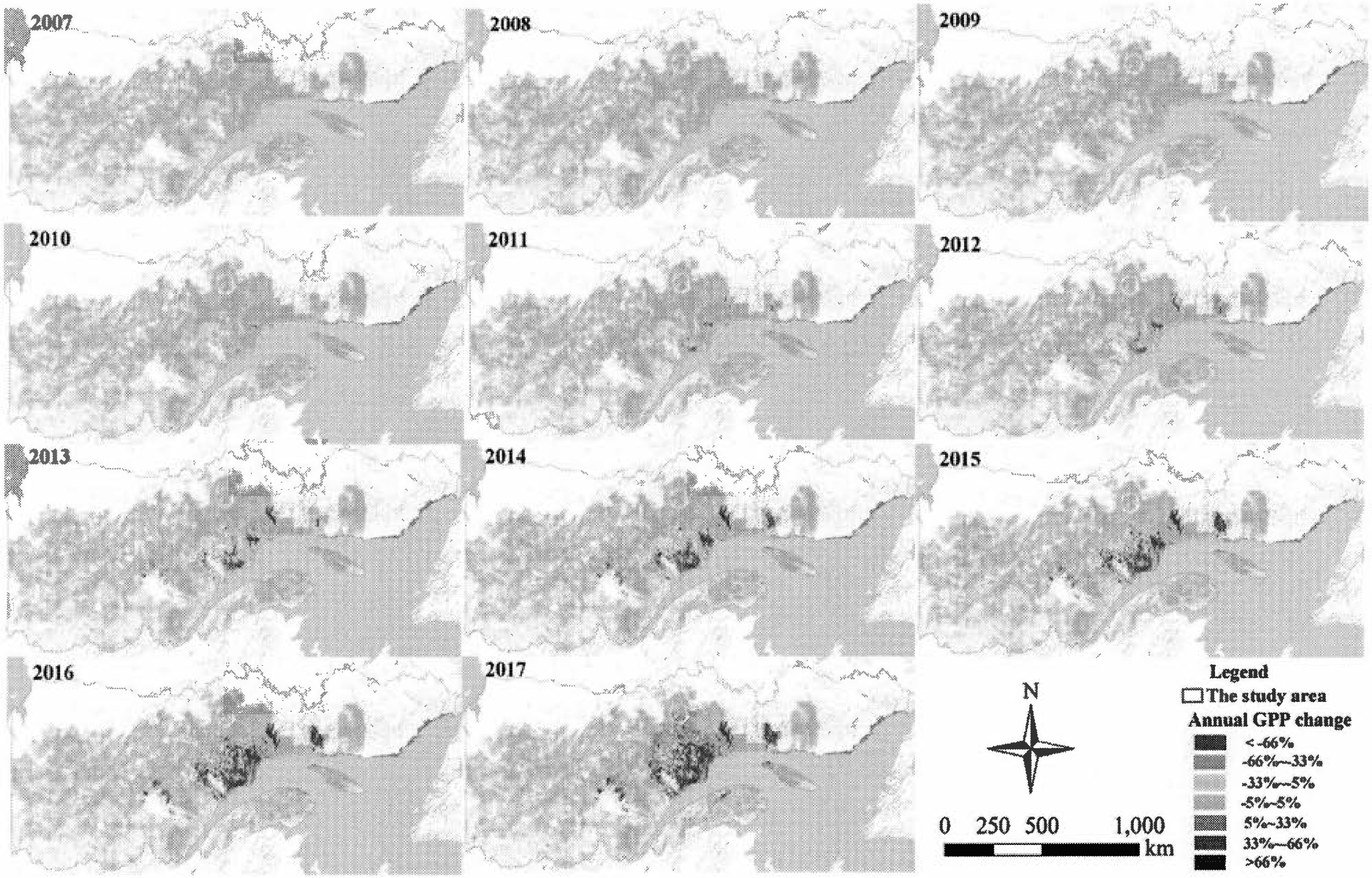

Figure 3S.2. Simulated of GPP changes between with and without defoliation at 1×1km resolution from 2007 to 2017 in dominated forests (i.e. fir, spruce, and mixed fir+spruce; 218665 km2) of Québec.

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CHAPTER IV

AERIAL SPRAYING OF BACTERIAL INSECTICIDES TO CONTROL SPRUCE BUDWORM DEFOLIATION LEADS TO REDUCED CARBON LOSSES

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4.1. Résumé

Les épidémies de tordeuse des bourgeons de l'épinette (TBE) représentent une perturbation naturelle majeure pour la forêt boréale de l'est de l'Amérique du Nord. Durant des épidémies à grande échelle, un épandage aérien d'insecticide bactérien est fréquemment utilisé pour le contrôle de grandes populations de TBE. Bien que l'intention première de cet épandage soit de protéger le volume de bois pour récolte ultérieure, il contribue également au maintien du carbone (C) séquestré par les arbres. Cette étude présente la première analyse quantitative de l'efficacité de l'épandage aérien d'insecticide contre la TBE sur la dynamique du C en sapinière, pessière et peuplement mixte de sapins baumiers et d'épinettes. Dans cette étude, nous avons utilisé le modèle TRIPLEX-Insect pour simuler la dynamique du C avec et sans épandage d'insecticide dans 14 unités d'échantillonnage localisées dans différentes régions au sein de la forêt boréale du Québec. Nous avons observé une plus grande efficacité de l'épandage aérien à réduire la défoliation lorsqu'effectuée dans les premiers stades de l'épidémie plutôt que lors des stades tardifs. Nos résultats démontrent que ce traitement permet une plus grande maintenance de productivité écosystémique nette (PEN) en sapinière qu'en pessière et en peuplement mixte de sapins baumiers et d'épinettes. De façon similaire, les pertes moyennes en biomasse aérienne dues à l'épidémie par la TBE en sapinière ont eu lieu plus lentement lorsque l'épidémie était précédée par un épandage aérien. Ces résultats suggèrent d'une part que l'épandage aérien d'insecticide pourrait être utilisé pour le maintien du C séquestré en forêts de conifères lors d'épidémies par la TBE. Toutefois, ceux-ci montrent également que l'efficacité des programmes d'épandage est affectée par l'identité de l'hôte et par le stade de l'épidémie.

4.2. Abstract

Spruce budworm (SBW) outbreaks are a major natural disturbance in boreal forests of eastern North America. During large-scale infestations, aerial spraying of bacterial insecticide are used to suppress locally high SBW populations. While the primary goal of spraying is the protection of wood volume for later harvest, it should also maintaining carbon stored in trees. This study provides the first quantitative analysis of the efficacy of aerial spraying against SBW on carbon dynamics in balsam fir, spruce and mixed fir-spruce forests. In this study, we used the TRIPLEX-Insect model to simulate carbon dynamics with and without spray applications in 14 sites of the boreal forest located in various regions of Quebec. We found that the efficacy of aerial spraying on reducing annual defoliation was greater in earlier stage of the outbreak than in later stage. Our results showed that more net ecosystem productivity (NEP) is maintained in fir than in either spruce or mixed fir-spruce forests following spraying. Similarly, average losses in aboveground biomass due to the SBW following spraying occurred more slowly than without spraying in fir forests. Our findings suggest that aerial spraying could be used to maintain carbon in conifer forests during SBW disturbances, but that the efficacy of spray programs is affected by host species and stage of the SBW outbreak.

4.3. Introduction

Pest outbreaks can have considerable effects on forest carbon (C) budgets, because they destroy photosynthetic tissues, reduce tree growth and increase tree mortality (Kurz *et al*., 2008; Dymond *et al*., 2010; Zelin *et al*., 2018). In temperate and boreal regions where outbreaks are predicted to increase in frequency and severity as a result of climate change (Bentz *et al*., 2010; Régnière *et al*., 2012; Seidl *et al*., 2018), so forests will release more C to the atmosphere (Dymond *et al*., 2010). For example, in eastern North America, there is increasing evidence that severe defoliation by the spruce budworm (*Choristoneura fumiferana,* SBW) has progressed further north in recent outbreaks affecting forests that were previously not defoliated by this insect (Bouchard and Pothier 2010; Navarro *et al*. 2018; De Grandpré *et al*. 2018). As the severity of future SBW outbreaks is predicted to increase, finding ways to mitigate forest damage will also contribute to reducing C emissions (Dymond *et al*. 2010).

Over the last four decades, Bacillus thuringiensis ssp. Kurstaki (Btk) has been widely used as biological insecticide for protecting forests affected by insect defoliators such as SBW, gypsy moth (*Lymantria dispar* (Linnaeus)) and hemlock looper (*Lambdina fiscellaria fiscellaria* (Guenée)) (Bauce *et al*., 2004; van Frakenhuyzen *et al*., 2016). For example, from 2006 to 2016, over 2 million ha of forests were aerially sprayed with insecticides in Canada, 82.02% of which was Btk (Canadian Council of Forest Minister 2018). While action thresholds for BtK application vary provincially, spraying often occurs only after substantial defoliation is detected. For example, in Québec, aerial spraying protection is applied after one year of moderate to severe SBW defoliation (Hardy and Dorais 1976; Bauce *et al*., 2006; Fuentealba *et al*., 2019). The main objective of Btk application is to maintain 50% or more of current-year foliage on trees and thereby reduce timber losses during outbreaks (Carisey *et al*., 2004; Fuentealba *et al*., 2015). Fuentealba *et al* (2019) reported that without Btk protection coniferous forests loose much of their residual photosynthetic capacity (RPC). However, it is still unknown how much C could be maintained in forest by aerial spraying programs during a SBW outbreak.

Forest vulnerability to defoliation by the SBW depends on host species and their assemblages. Balsam fir (*Abies balsamea* (L.) Mill.) is the most vulnerable host of the SBW, however, spruce (*Picea sp.*) species can also be severely defoliated (Hennigar *et al.*, 2008; Gray, 2013; Nealis 2015; Candau *et al.*, 2018). The insect is a specialist herbivore which feeds upon current year foliage of balsam fir and spruce genus (MacLean 1980). Bognounou *et al.*, 2017 showed that balsam fir stands were more severely defoliated than other stand types, and black spruce (*Picea mariana*) suffered more defoliation when in a mixture with balsam fir than in monospecific stands. Furthermore, black spruce was more vulnerable to defoliation with increasing proportion of fir as neighbours in the earlier stage of an outbreak but not in later stages (Bognounou *et al.*, 2017).

Populations of SBW in eastern Canada oscillate at supra-regional scales with a periodicity of 30-40 years (Burleigh *et al.*, 2002). During outbreaks, defoliation may last locally for 5 to 8 years (Boulanger and Arseneault 2004). Tree mortality usually occurs after 4 to 7 years of severe SBW defoliation but growth reductions are typically observed following 2 years of severe SBW defoliation (Blais 1958, 1981; MacLean 2016). Reduced tree growth and increased tree mortality resulting from SBW defoliation has significant impacts on forest carbon budgets over vast areas (Dymond *et al.*, 2010; Hicke *et al.*, 2012; Liu *et al.*, 2018, 2019). In the absence of empirical data on C fluxes, process-based models can be used to evaluate the impact of an outbreak on C dynamics.

TRIPLEX-Insect is a process-based model which was developed to quantify forest C sequestration in response to SBW disturbances at stand and regional scale (Liu *et al.*, 2018). It uses monthly climate conditions to simulate both short- and long-term forest C dynamics (e.g. gross primary productivity, net primary productivity, net ecosystem productivity, etc.) under SBW disturbances (Liu *et al.*, 2018). The model can also be applied to test different scenarios of SBW outbreak mitigation such as assessing the impacts of spraying Btk on C dynamics in the boreal forest of Québec. In this study, we used spatially explicit annual defoliation sequences, aerial spraying data and the TRIPLEX-Insect model to determine how much C could be maintained by reducing defoliation through aerial spraying during a SBW outbreak. We also compared the effects of reducing defoliation by aerial spraying of Btk on C dynamics for three different forest compositions (i.e. pure fir, pure spruce, and a mixture of both species). Finally, we evaluated the effect of timing of spraying (earlier vs later in the outbreak) on C dynamics. The results of these analyses could be useful to forest managers and protection agencies in needs to evaluate the impacts of outbreak mitigation scenarios on C budgets.

4.4. Methods

4.4.1. Study Area

Québec's commercial boreal forest, which covers 683,001 km^2, is dominated by balsam fir and black spruce (Figure 4.1). Other species that can be regionally abundant are birch (*Betula papyrifera* Ehrh.) trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) (De Grandpré *et al.*, 2009). Historically, most of the forests in the balsam fir forest domain suffered SBW defoliation of various severities during the 1970s and 1980s (https://mffp.gouv.qc.ca/forets/fimaq/insectes/pdf/tord-1967.pdf, accessed Mar. 19, 2019). Since the start of the current infestation, the area defoliated by the SBW has increased from 2319 ha in 2006 to 8.2 million ha in 2018 (Ministère des Forêts de la Faune et des Parcs du Québec 2018).

Table 4.1. Observed number of cells* and average age of sites on Québec before spray for earlier spray sites (Group 1 in 2010) and later spray sites (Group 2 in 2015).

Sample ID	Year	Number of stands		Average Age (years)	
		Will Spray	Not Spray	Will Spray	Not Spray
S1	2010	87	107	61	64
S2		204	207	78	83
S3		127	284	98	95
S4		92	202	102	99
S5		183	151	58	62
S6		246	176	57	56
Total		939	1127		
Mean				72.08	80.5
S7	2015	53	132	52	55
S8		173	124	51	48
S9		227	116	60	60
S10		173	132	67	67
S11		215	148	80	83
S12		144	200	57	58
S13		126	211	102	104
S14		87	96	120	118
Total		1198	1159		
Mean				71.36	71.93

*---- each cell is 1 km^2 in the map of study areas which we built.

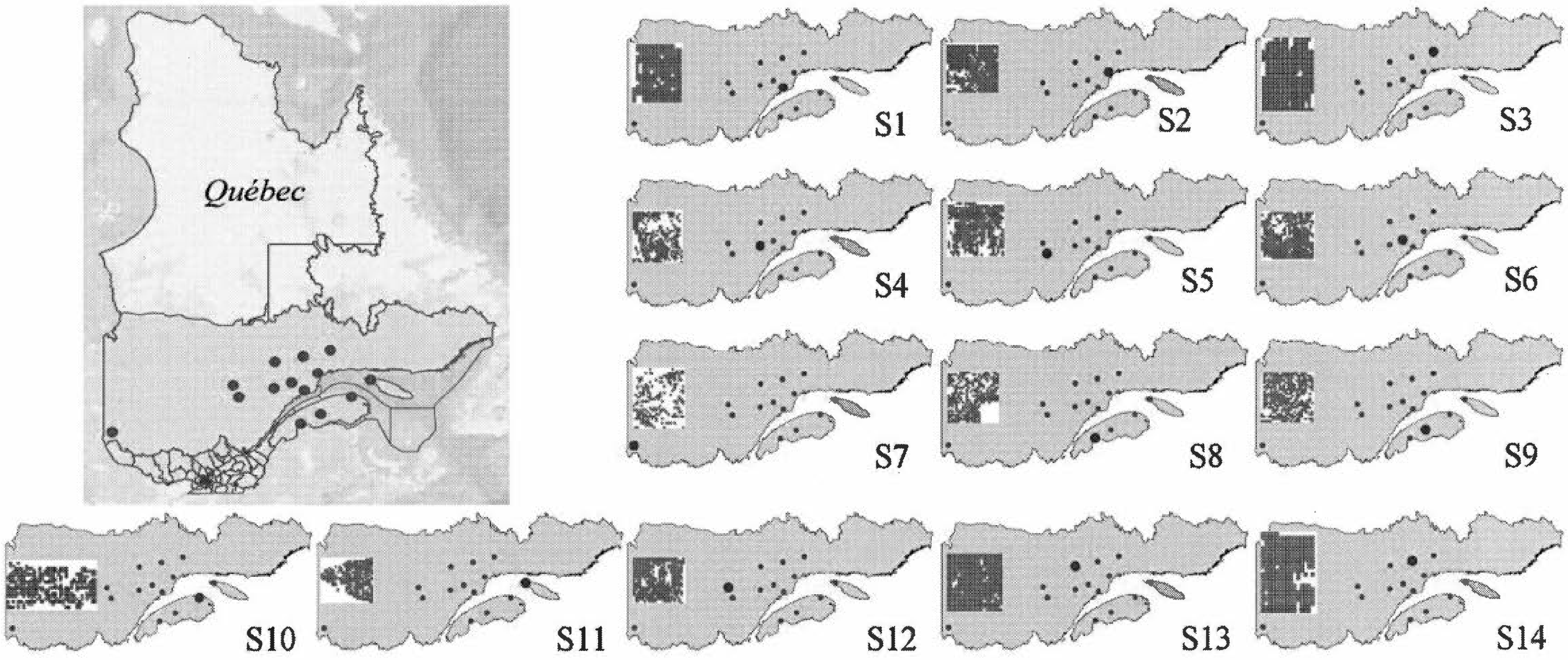

Figure 4. 1. Map showing the study areas, the locations of the 14 sample stands (i.e. S1-14) and the distribution of grid cells for each sample unit in Québec.

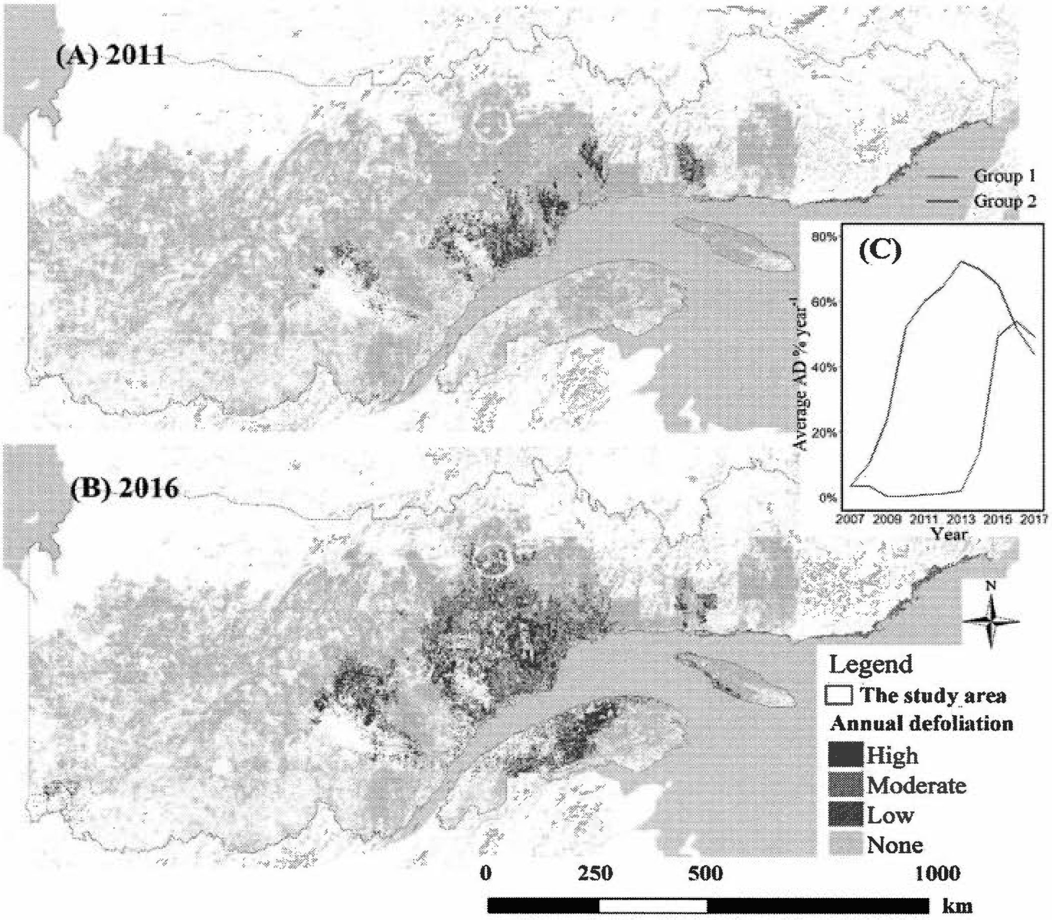

Figure 4. 2. Observed the average defoliation intensity in 2011 (A) and 2016 (B) in study areas of Québec; and observation of average AD (i.e. annual defoliation) for Group 1 and Group 2 from 2007-2017 (C).

4.4.2. Data Collection and Sampling

Québec provincial forest inventory plots and geospatial databases (1990-now) were obtained from Le Système d'Information Forestière par Tesselle (SIFORT) (Lord *et al.*, 2009; Berger 2015). We selected sites in which the density of any of the three SBW's host species (i.e. balsam fir, spruce, and mixed fir-spruce) was greater than 20%. In Québec, annual aerial surveys are used to map areas of SBW defoliation and classify them in 3 classes of severity (light 0-30%, moderate 30-70% and severe >70%) based on the percentage of current foliage loss. Annual defoliation data from 2007 to 2017 in our study areas were obtained from the Québec Ministry of Forests, Wildlife and Parks (MFFP) (https://www.donneesquebec.ca).

Monthly climate data for 2007-2017 were obtained using BioSIM (Régnière 1996; Régnière and St-Amant 2007) to interpolate the data of the four closest weather stations from each location while adjusting for latitude, longitude and elevation. In addition, we obtained aerial spraying data in 2011 and 2016 from the Société de Protection des Forêts contre les Insectes et Maladies (SOPFIM) (http://www.sopfim.qc.ca). In order to maximize Btk's efficacy, aerial spraying was scheduled during the third to fourth instar larvae stages of the SBW (about mid-June). When SBW populations were very high, a second and third spray were carried out 5 and 10 days later, respectively (Fuentealba *et al.*, 2015). Forest inventories, defoliation surveys, aerial spraying programs as well as monthly climate data were transformed to the same cartographic projection and spatially aligned.

We selected 14 sites located in various regions of Québec (Figure 4.1). Each site included 200-400 sprayed and non-sprayed 1 km^2 grid cells (Table 4.1). Spraying occurred in only one year in each sprayed cell. Sites were further divided into two groups. Group 1 (hereafter called 'earlier') was sprayed in 2011. Although the current SBW outbreak began at 2006 in Québec (Ministère des Forêts de la Faune et des Parcs du Québec 2018), 16212 km^2 or 7.414% of the study areas had been defoliated by the time that the earlier group had been sprayed (Figure 4.2A). Before 2013, the most of cells in Group 2 (hereafter called 'later') had not been detected SBW defoliation (Figure 4.2C). Actually, the later group was sprayed in 2016. By the time Group 2 was sprayed, 53235 km^2 (24.345%) of the study area had been defoliated (Figure 4.2B). To reduce the effects of tree ages on the simulation of C dynamics, we chose sites with similar forest age in each site. In Group 1, the mean age is 72 years for the sprayed areas and 80 years for the areas without treatment, respectively in 2010 (Table 4.1). In Group 2, the mean age is 71 years (with spray) and 72 years (without spray) respectively in 2016 (Table 4.1). The sites were classified into 3 categories based on their host tree composition: balsam fir (i.e. more than 74% of balsam fir), spruce (i.e. more than 74% of black spruce, white spruce or red spruce), and fir-spruce mixture (i.e. 21~74% balsam fir or spruce) (Table 4.2).

Table 4. 2. Observed number of cells* and average age of fir, spruce and mixed fir+spruce forests before spray for earlier spray sites (Group 1 in 2010) and later spray sites (Group 2 in 2015).

	Species	**Year**	**Number of cells**		**Average Age (years)**	
			Will Spray	Not Spray	Will Spray	Not Spray
Group 1	Fir	2010	216	103	64	62
	Fir+Spruce		465	398	69	74
	Spruce		258	626	84	87
Group 2	Fir	2015	588	433	61	58
	Fir+Spruce		310	300	88	90
	Spruce		300	426	76	81

*---- each cell is 1 km^2 in the map of study areas which we built.

4.4.3. TRIPLEX-Insect Model

The TRIPLEX-Insect model (Liu *et al.*, 2018) has been adapted to simulate C dynamics in forests affected by the spruce budworm. TRIPLEX-Insect is driven by monthly climate which includes monthly mean temperature, monthly precipitation and monthly mean relative humidity. Forest net primary productivity (NPP) is estimated using Eq. (4.1):

$$\mathrm{NPP} = GPP - Ra \tag{4.1}$$

where Ra is autotrophic respiration which is estimated using air temperature, component C pools and nitrogen (N) (Zhou *et al.*, 2008; Wang *et al.*, 2011). GPP is estimated as a function of monthly photosynthetically active radiation (PAR), monthly air temperature, the percentage of frost days in a month, forest age, soil water content as well as the leaf area index, respectively (Peng *et al.*, 2002). Net ecosystem productivity (NEP) is the difference between ecosystem respiration, which is sum of Ra and heterotrophic respiration (Rh), and GPP. Rh is estimated by subtracting root respiration from soil respiration, expressed as the exponential function of temperature and Q10 (Zhou *et al.*, 2008).

Observation of annual defoliation (AD) is an input parameter in the TRIPLEX-Insect model. It is used to calculate both leaf biomass loss due to defoliation and defoliation caused mortality (DM; % year^{-1}) (Liu *et al.*, 2018). DM is estimated as a function of the species of tree (fir is more vulnerable than spruce e.g. Hennigar *et al.*, 2008), annual and cumulative defoliation (Blais 1958) as well as tree age (MacLean 1980). In addition, we did not consider new natural regeneration in this study, because SBW caused little to no seed production during an outbreak (Schooley 1978).

The set of parameters in each component such as GPP, NPP, and soil C and N, are derived from both previous studies (Peng *et al.*, 2002; Zhou *et al.*, 2006; Sun *et al.*, 2008; Liu *et al.*, 2018) in this study (Table 4.S1). We used observation of mortality data, which includes balsam fir, spruce and mixed fir-spruce forests, to validate model at both stand (Liu *et al.*, 2018) and regional scales (Liu *et al.*, 2019) in the North Shore region of Québec. The TRIPLEX-Insect model has been calibrated and validated under SBW defoliation conditions against the observed data in previous studies (Liu *et al.* 2018). More details about the TRIPLEX-Insect model can be found in Liu *et al*, (2018).

4.4.4. Comparative Analysis

The delayed effects of spray on defoliation, carbon fluxes or stocks, 1-3 years (i.e. the period for which foliage protection is considered efficacious, Fuentealba *et al.*, 2018) after the application was compared to the immediate effect numerically by calculating the delayed effect X_{DSn} on variable X as follows:

$$X_{DS_n} = \left[\sum_{i=1}^{p}\left(\overline{X}_{DSi\,spray} - \overline{X}_{DSi\,no\,spray}\right)_{n>0} - \left(\overline{X}_{DSi\,spray} - \overline{X}_{DSi\,no\,spray}\right)_{n=-1}\right]/p \qquad (3)$$

Where X is annual defoliation, carbon fluxes or stocks (e.g. GPP, NEP, aboveground biomass etc.). *n* is the number of years after spraying, *i* is the site index, p is the total number of sites. $\overline{X}_{DSi\ spray}$ and $\overline{X}_{DSi\ no\ spray}$ are the means of X over all the sprayed cells and non-sprayed cells in site i, respectively.

The immediate and delayed effects of spray on GPP, NPP, NEP and AD were also analyzed statistically using analyses of covariance (ANCOVA) with sites (6 levels), year (4 levels) and stand age (continuous 2nd order polynomial) as covariates. The delayed effects of spray up to 3 years after the application were thus captured in the interactions between spray and year. All analyses were performed with R version 3.5.1 (R core team 2018).

4.5. Results

4.5.1. Efficacy of Btk Application on Defoliation Reduction

As expected, we found that aerial spraying of Btk significantly reduced annual defoliation (AD) for both earlier and later spray groups (Figure 4.3F). However, the efficacy of spraying was stronger in the earlier spray group (AD_{DS1} = -16.14%) than in the areas sprayed later in the development of the outbreak (AD_{DS1} = -5.78%). Fir forests that were not sprayed had the highest AD in both earlier (82%) and later groups (69.23%) in the year following spraying (Figure 4.4F). Fir forests also had the lowest average AD_{DS1} for both earlier (-24.44%) and later sprayed areas (-23.62%) in one year after application of Btk whereas AD was higher in either spruce or mixed (i.e. fir-spruce) forests. Mixed forests had the highest average AD_{DS1} (5.49%; Table 4.3) in the year following spraying in the later sprayed areas.

Statistically, the results of the ANCOVA confirmed that the immediate effects of spraying on AD are significant for all 3 classes of species composition (Table 4.S2). The effect is more pronounced in pure fir than in pure spruce or mixed stands (-20.29% vs -4.84% and –11.35%, respectively). Delayed effects of spraying on AD are more complex: there is no significant delayed effect in pure fir forests, the effects are significant 1 and 3 years after application in pure spruce forests (-6.47% and -4.87% respectively). In mixed stands the effect is significant 1 year after the application in mixed stands (-5.33%) as well as 2 years after the application but in this case the effect is positive (+5.70%).

Table 4. 3. Simulation of average AD_{DSn} (% year^{-1}), GPP_{DSn} (10^{2}g C m^{-2} year^{-1}), NPP_{DSn} (10^{2}g C m^{-2} year^{-1}), Ra_{DSn} (10^{2}g C m^{-2} year^{-1}), NEP_{DSn} (10^{2}g C m^{-2} year^{-1}), Rh_{DSn} (10^{2}g C m^{-2} year^{-1}), VOL_{DSn} (m^{3} ha^{-1}), AGB_{DSn} (10^{6}g C ha^{-1}) and BGB_{DSn} (10^{6}g C ha^{-1}) for fir, spruce, mixed fir+spruce and total forests in Group 1 (from before to 1, 2, or 3 years after spraying) and Group 2 (from before to the years following spraying). Note: GPP—gross primary productivity; NPP—net primary productivity; Ra—autotrophic respiration; NEP—net ecosystem productivity; Rh—heterotrophic respiration; VOL— merchantable volume; AGB—aboveground biomass; BGB—belowground biomass. DSn is the value compare the differences between before and after spray protection for forests with and without aerial spray. n is the number of years after spraying.

	Species	**n**	**AD_{DSn}**	**GPP_{DSn}**	**NPP_{DSn}**	**Ra_{DSn}**	**NEP_{DSn}**	**Rh_{DSn}**	**VOL_{DSn}**	**AGB_{DSn}**	**BGB_{DSn}**
Group 1	Fir	1	-24.44%	2.60	0.92	1.68	0.70	0.23	-0.73	1.57	-0.16
		2	-15.89%	5.81	2.77	3.03	1.73	1.05	-1.50	1.93	-0.12
		3	-19.91%	6.23	2.96	3.27	1.81	1.15	-1.87	1.53	-0.31
	Spruce	1	-12.76%	1.32	0.52	0.81	0.34	0.17	0.05	0.58	0.03
		2	-10.08%	1.71	0.88	0.84	0.52	0.36	-0.01	0.54	0.05
		3	-11.12%	2.55	1.25	1.29	0.65	0.60	0.51	0.72	0.05
	Fir+Spruce	1	-11.21%	2.56	1.02	1.53	0.48	0.55	0.96	2.23	0.12
		2	-0.55%	3.33	1.87	1.47	0.85	1.02	1.92	1.94	0.27
		3	-2.45%	2.25	1.13	1.12	0.36	0.77	2.71	2.36	0.42
	Total	1	-16.14%	2.16	0.82	1.34	0.51	0.32	0.09	1.46	0.00
		2	-8.84%	3.62	1.84	1.78	1.03	0.81	0.14	1.47	0.07
		3	-11.16%	3.68	1.78	1.90	0.94	0.84	0.45	1.54	0.05
Group 2	Fir	1	-23.62%	4.71	2.24	2.47	1.21	1.03	0.85	1.62	0.10
	Spruce		0.79%	-0.12	0.08	-0.20	0.18	-0.10	-0.53	-0.52	-0.07
	Fir+Spruce		5.49%	-0.73	-0.30	-0.43	-0.09	-0.22	0.17	-0.36	0.03
	Totel		-7.69%	1.28	0.67	0.61	0.42	0.24	0.16	0.25	0.02

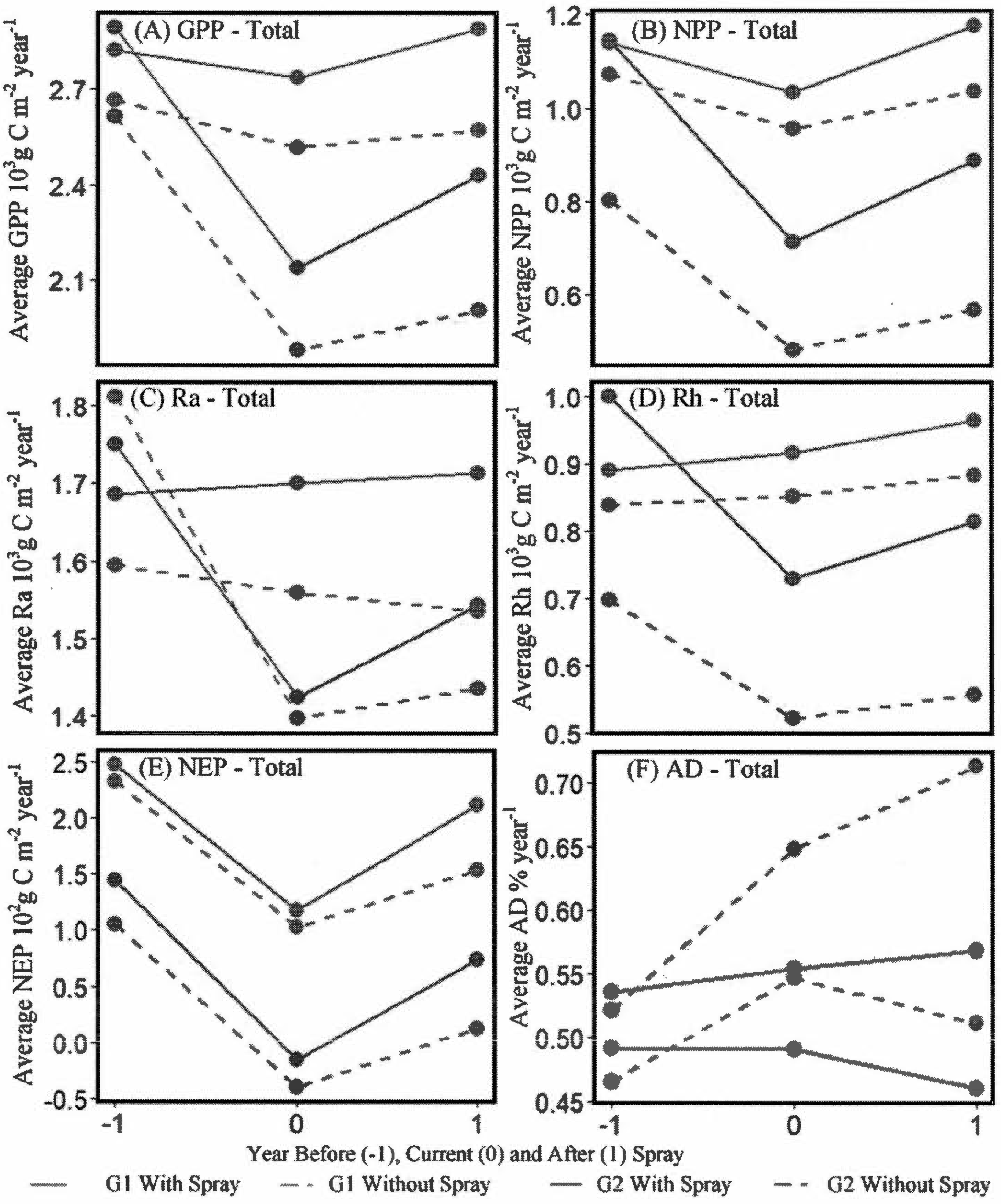

Figure 4 3. Simulations of average annual GPP (A), NPP (B), Ra (C), Rh (D) and NEP (E), and observations of average AD (F) with and without spray for all forests in Group 1 (red lines) and Group 2 (blue lines) in the year before, the current year and the year after spraying. Legend: GPP—gross primary productivity (10^3g C m^{-2} year^{-1}); NPP—net primary productivity (10^3g C m^{-2} year^{-1}); Ra—autotrophic respiration (10^3g C m^{-2} year^{-1}); Rh—heterotrophic respiration (10^3g C m^{-2} year^{-1}); NEP—net ecosystem productivity (10^2g C m^{-2} year^{-1}); AD—annual defoliation (%).

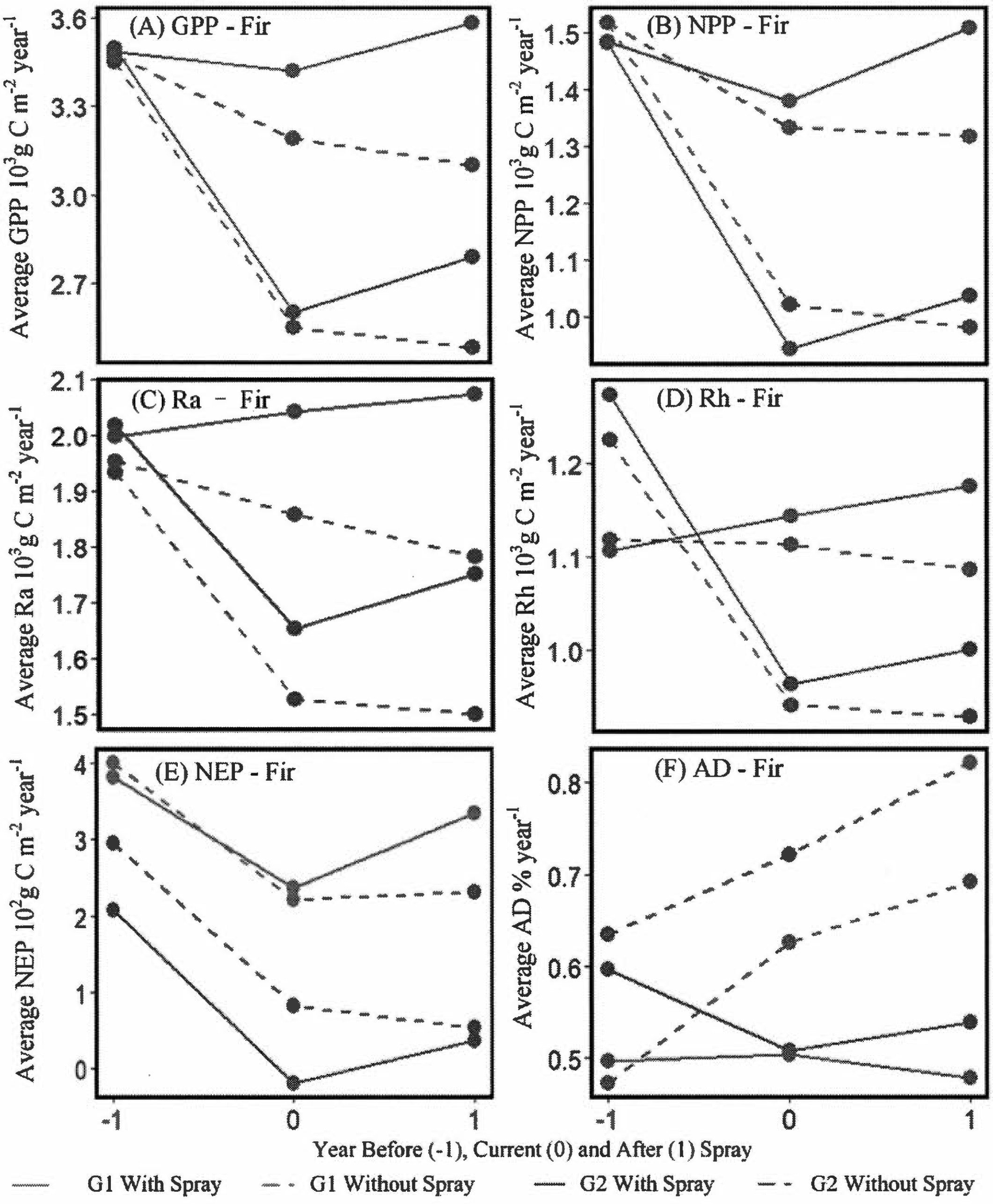

Figure 4. 4. Simulations of average annual GPP (A), NPP (B), Ra (C), Rh (D) and NEP (E), and observations of average AD (F) with and without spray for fir forests in Group 1 (red lines) and Group 2 (blue lines) in the year before, the current year and the year after spraying. Legend: GPP—gross primary productivity (10^3g C m^{-2} $year^{-1}$); NPP—net primary productivity (10^3g C m^{-2} $year^{-1}$); Ra—autotrophic respiration (10^3g C m^{-2} $year^{-1}$); Rh—heterotrophic respiration (10^3g C m^{-2} $year^{-1}$); NEP—net ecosystem productivity (10^2g C m^{-2} $year^{-1}$); AD—annual defoliation (%).

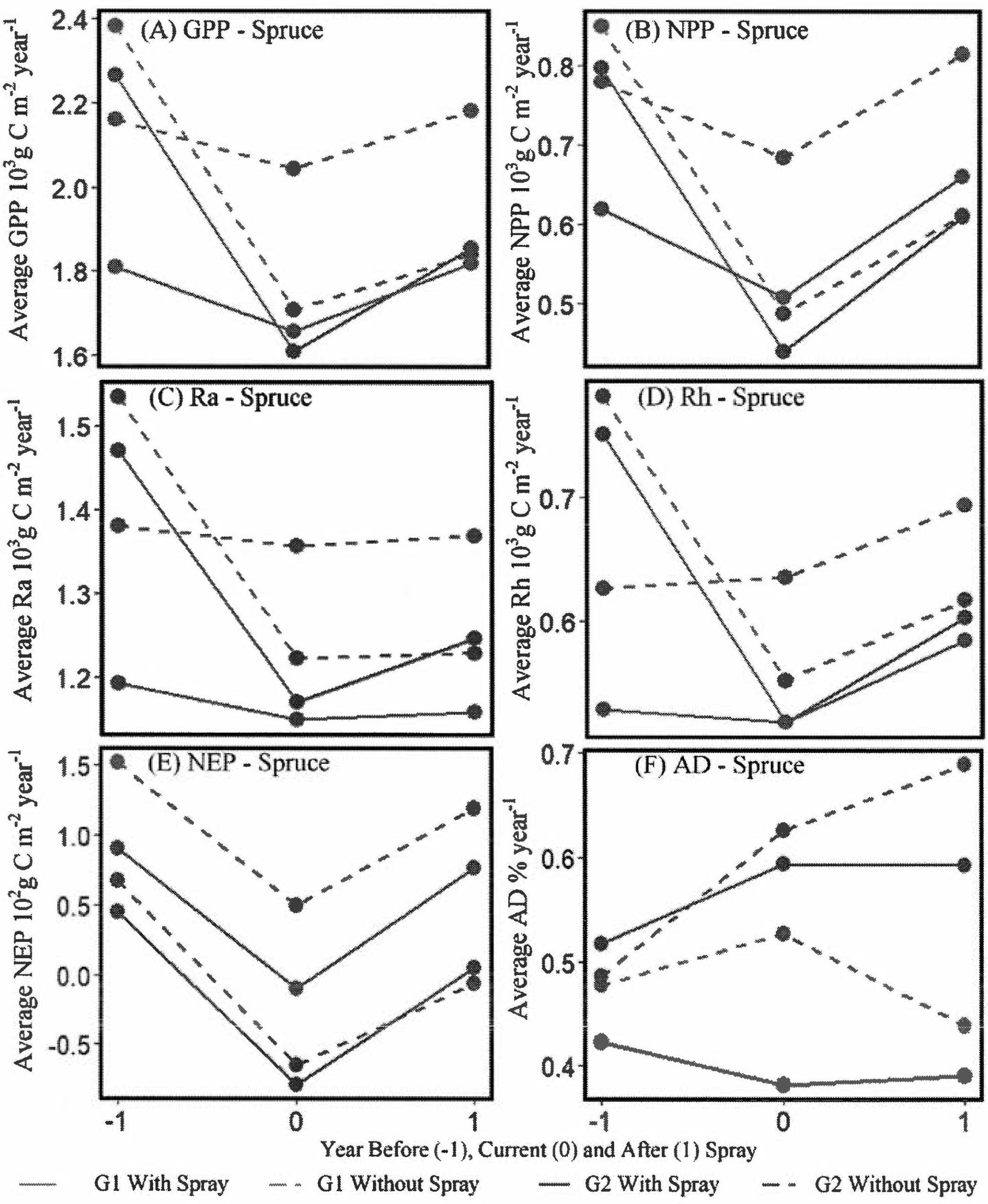

Figure 4. 5. Simulations of average annual GPP (A), NPP (B), Ra (C), Rh (D) and NEP (E), and observation of average AD (F) with and without spraying for spruce forests in Group 1 (red lines) and Group 2 (blue lines) in the year before, the current year and the year after spraying. Legend: GPP—gross primary productivity (10^{3}g C m^{-2} year^{-1}); NPP—net primary productivity (10^{3}g C m^{-2} year^{-1}); Ra—autotrophic respiration (10^{3}g C m^{-2} year^{-1}); Rh—heterotrophic respiration (10^{3}g C m^{-2} year^{-1}); NEP—net ecosystem productivity (10^{2}g C m^{-2} year^{-1}); AD—annual defoliation (%).

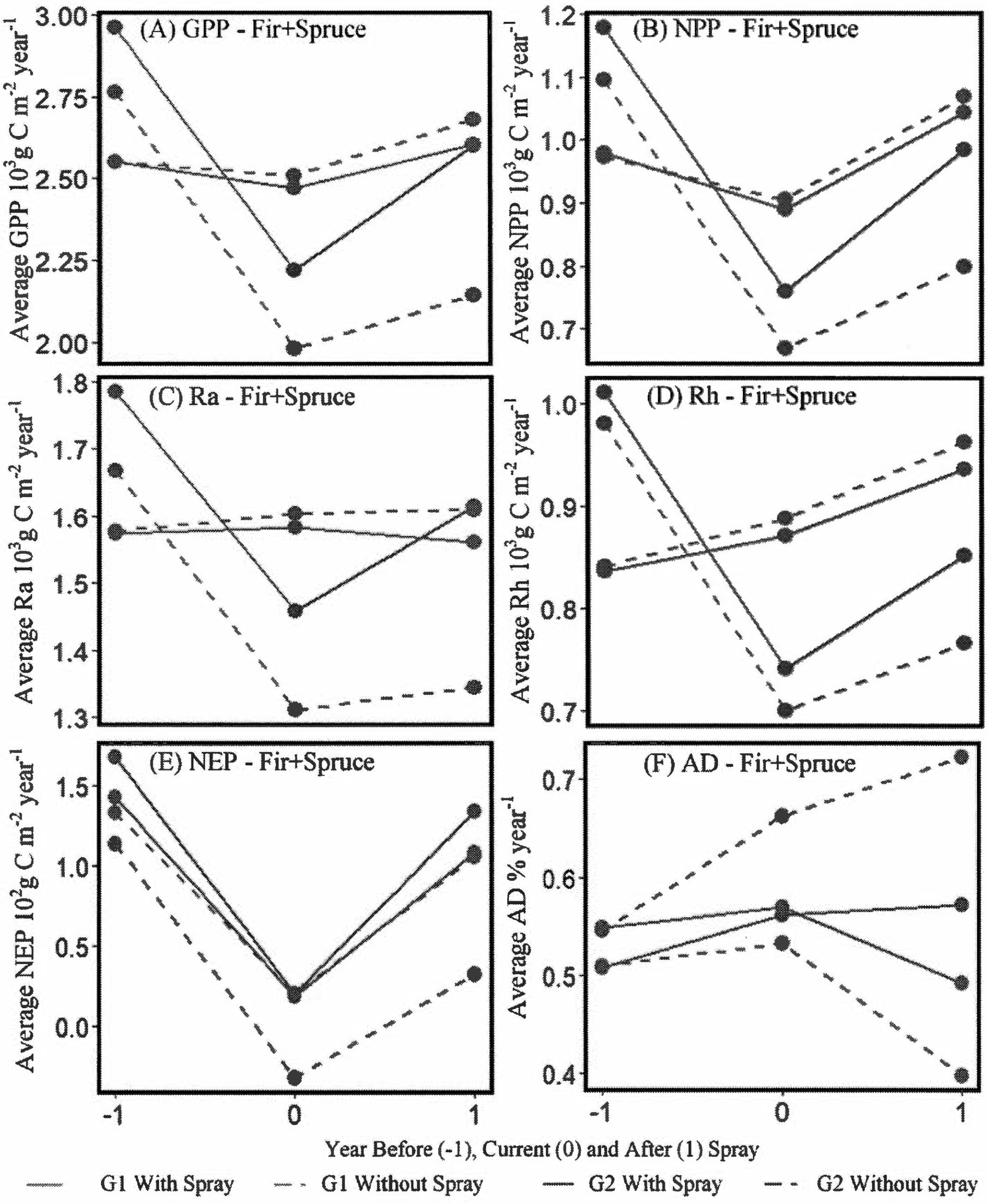

Figure 4. 6. Simulations of average annual GPP (A), NPP (B), Ra (C), Rh (D) and NEP (E), and observation of average AD (F) with and without spray for mixed fir+spruce forests in Group 1 (red lines) and Group 2 (blue lines) in the year before, the current year and the year after spraying. Legend: GPP—gross primary productivity (10^3g C m^{-2} year^{-1}); NPP—net primary productivity (10^3g C m^{-2} year^{-1}); Ra—autotrophic respiration (10^3g C m^{-2} year^{-1}); Rh—heterotrophic respiration (10^3g C m^{-2} year^{-1}); NEP—net ecosystem productivity (10^2g C m^{-2} year^{-1}); AD—annual defoliation (%).

4.5.2. The Effect of Aerial Spraying on Carbon Fluxes

Average total GPP decreased more quickly from the year before spraying to the year of spraying in the areas sprayed earlier compared to later in both sites that were sprayed and those that were not (red lines vs blue lines in Figure 4.3A). However, average total GPP_{DS1} was higher in the earlier sprayed forests (2.16 10^2g C m^{-2} $year^{-1}$) compared to those sprayed later in an outbreak (1.28 10^2g C m^{-2} $year^{-1}$, Table 4.3). Consequently, average total GPP increased more quickly from the year of spraying to the year after spraying in the earlier sprayed sites than in those sprayed later (Figure 4.3A). Simulations of GPP in fir forests increased following spraying, but decreased or were maintained in forests that were not treated for both earlier and later treated sites (Figure 4.4A). The maximum average GPP_{DS1} was 4.71 10^2g C m^{-2} $year^{-1}$ for fir forests sprayed later in the outbreak (Table 4.3). While the minimum average GPP_{DS1} was -0.73 10^2g C m^{-2} $year^{-1}$ for mixed forests, in the 2016 (i.e. later sprayed, Table 4.3).

The results of the ANCOVA show that spraying had no immediate effect on GPP regardless of species composition. The effects of spraying were delayed until 2 and 3 years after the application in pure fir (+5.80 and +6.25 10^2g C m^{-2} $year^{-1}$ respectively) and pure spruce stands (+1.51 and +2.34 10^2g C m^{-2} $year^{-1}$ respectively), and after 1-3 years in mixed stands (+2.02, +2.83 and +1.73 10^2g C m^{-2} $year^{-1}$ respectively, Table 4.S3).

Simulations of average of total NPP and NEP showed similar trends to GPP (Figure 4.3A, 4.3B and 4.3E). The maximum average total NPP_{DS1} was 2.24 (10^2g C m^{-2} $year^{-1}$) for fir forests in the later sprayed areas (Table 4.3). The average of total NEP_{DS1} was 0.51 (10^2g C m^{-2} $year^{-1}$) (early sprayed forests) and 0.43 (10^2g C m^{-2} $year^{-1}$) (later sprayed forests), respectively, in the year following spraying (Table 4.3). Moreover, the TRIPLEX-Insect model simulated positive NEP_{DS1} for all species in both early and later spraying periods except for later sprayed mixed fir+spruce forests (Table 4.3). We found that more carbon was maintained in fir than either spruce or mixed (i.e. fir+spruce) forests in the year following spraying. The average NEP_{DS1} for fir forests was 0.7 (10^2g C m^{-2} $year^{-1}$) (early sprayed forests) and 1.21 (10^2g C m^{-2} $year^{-1}$) (later sprayed forests), respectively, in the year following spraying (Table 4.3). In addition, the average Ra and Rh increased in fir forests with spraying but decreased in fir forests without spray treatment (Figure 4.4C and 4.4D). However, there were no significant changes between sites that were sprayed and not sprayed in both spruce and mixed fir-spruce forests (Figure 4.5C, 4.5D, 4.6C and 4.6D).The maximum average Ra_{DS1} and Rh_{DS1} were 2.47 (10^2g C m^{-2} $year^{-1}$) and 1.03 (10^2g C m^{-2} $year^{-1}$), respectively, for fir forests in later sprayed areas in the year following spraying (Table 4.3). Statistically, the effects of spraying on NPP were positive and significant 2-3 years after Btk application in pure fir and spruce stands and after 1-3 years in mixed stands (Table 4.S4).The effects on NEP were positive and significant 2-3 years after application in pure fir and after 1-3 years in pure spruce and mixed stands (Table 4.S5).

4.5.3. The Effect of Aerial Spraying on Wood Volume and Carbon Stocks

Our results showed that average wood volume (VOL) decreased the year after spraying in the earlier sprayed fir sites but increased slightly in the later sprayed sites (Figure 4.7A). Indeed, our simulations also showed that average NEP_{DSn} in fir forests was positive and increasing after spraying with Btk, but that average VOL_{DSn} was negative and decreasing for the same period in the simulations (Table 4.3). Average VOL_{DS1} in fir stands was -0.73 m^3 ha^{-1} (earlier sprayed forests) and 0.85 m^3 ha^{-1} (later sprayed forests). Moreover, both average VOL_{DS2} and VOL_{DS3} decreased in the earlier sprayed forests. In contrast, for mixed fir-spruce forests, average VOL_{DSn} (i.e. n is 1, 2, and 3) increased from 0.96 to 2.71 m^3 ha^{-1} over the same period of simulation (Table 4.3).

We found that average aboveground biomass (AGB) in forests protected by spraying decreased more slowly than in untreated forests for all species in the earlier sprayed forests. Defoliation reduced average AGB in the year following spraying for all host species (red lines in Figures 7B, 7E, and 7H), however AGB_{DS1} remained positive in the earlier sprayed forests (Table 4.3). Average total AGB_{DS1} was 1.46 10^6g C m^{-2} in forests treated earlier in the outbreak and 0.25 10^6g C m^{-2} in forests treated later in the outbreak. Average AGB_{DS1} in fir stands was 1.57

(earlier sprayed areas) and 1.62 10^6g C m^{-2} (later sprayed areas), in the year following spraying (Table 4.3). Conversely, simulated positive AGB_{DS1} was only positive (i.e. 2.23 10^6g C m^{-2} in mixed forests and 0.58 10^6g C m^{-2} in spruce forests) in the earlier sprayed forests but negative (i.e. -0.36 10^6g C m^{-2} in mixed fir-spruce and -0.52 10^6g C m^{-2} in spruce) in the later sprayed sites at the end of the simulation period (Figure 4.7B). The simulated average belowground biomass (BGB) followed a similar trend to that of AGB in both the earlier and later sprayed forests (Figure 4.7C). Although average BGB_{DSn} changed little, it followed a trend similar to VOL_{DSn} in all forest compositions (Table 4.3). Average BGB_{DSn} observed in the earlier sprayed forests decreased from -0.16 to -0.31 10^6g C m^{-2} for fir (Table 4.3).

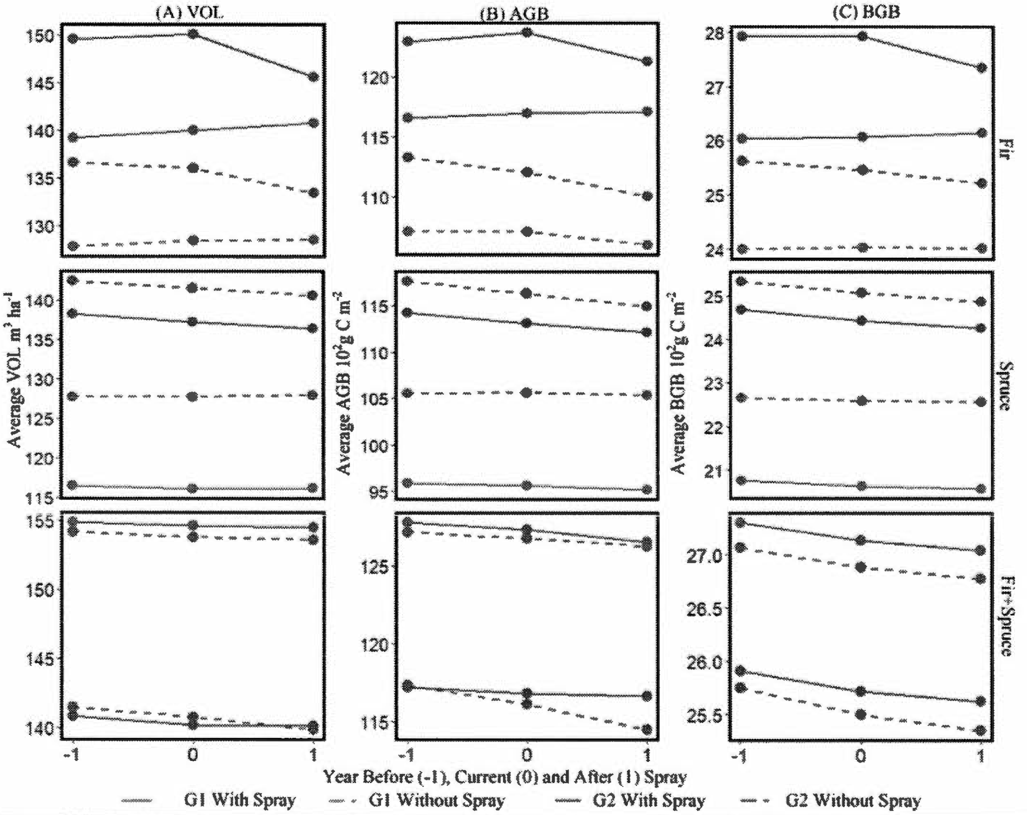

Figure 4. 7. Simulations of average total VOL (A), AGB (B) and BGB (C) with and without spray for fir, spruce and mixed fir-spruce in the year before, the current year and the year after spraying. Legend: VOL— merchantable volume (m^3 ha^{-1}); AGB—aboveground biomass (10^2g C m^{-2}); BGB—belowground biomass (10^2g C m^{-2}).

4.6. Discussion

Estimates of annual or cumulative defoliation may not adequately describe the effects of damage on forest growth or carbon losses (Cooke and Régnière 1999; van Frankenhuyzen *et al.*, 2007). Fuentealba *et al.* (2019) suggested that residual photosynthetic capacity (RPC) can be used to better estimate the effects of damage by SBW than measures of defoliation in short term studies. Because there are less effects of SBW population dynamics as shown by low RPC dynamics among years (Hardy and Dorais 1976). Although we did not observe a direct relationship between AD and NEP, we found a clear inverse relationship between AD_{DS1} and NEP_{DS1} for all forest types whether sprayed earlier or later in the outbreak (Table 4.3).Therefore, we used both AD_{DS1} (i.e. how much defoliation be controlled) and NEP_{DS1} (i.e. a proxy for carbon loss) to evaluate the efficacy of aerial spraying in this study. Our simulated results showed that aerial spraying can maintain forest carbon during a SBW outbreak, however the efficacy of these application is conditioned by host species, frequency of spraying, and stage of the outbreak (MacLean 2016; Fuentealba *et al.*, 2019).

4.6.1. Different species impact the efficacy of Aerial Spraying

Btk application reduced both defoliation and carbon losses to a greater extent better in balsam fir stands than in either spruce or mixed fir-spruce in this study. This is in part due to the fact that spruce (both black and white spruce) are generally more resistant to SBW defoliation than balsam fir (Hennigar *et al.*, 2008). This resistance is often attributed to phenological asynchrony between budburst in spruce and SBW emergence. While Kumbaşlı *et al.* (2011) reported that secondary plant metabolites in spruce also inhibit digestion of foliage by SBW. In our study, balsam fir was defoliated more quickly than either spruce or mixed fir-spruce in unprotected areas for both earlier and later sprayed forests for the simulation period. However AD differed less between forests that were sprayed and those that were not sprayed in both spruce and mixed fir-spruce compared to balsam fir forests. In experimental manipulations of spraying operations, Fuentealba *et al.* (2019) found similar trends where treatments were more effective in fir stands but offered little advantage in black spruce stands. This is also consistent with results from the spruce budworm decision support system (SBWDSS) (Chang *et al.,* 2012).

4.6.2. Different stages of outbreak impact the efficacy of Aerial Spraying

In our study, spraying earlier in the outbreak was more effective than spraying later. Different stages of an outbreak represent a gradient in the density of eggs and larvae which is strongly related to subsequent defoliation (Ostaff *et al.*, 2006; MacLean 2016). Earlier in the outbreak across a given range of areas, there will be fewer eggs and less larvae and likely fewer sources for colonization of stands by immigrating females. Later stages in the outbreak, in contrast, will have higher densities of eggs and larvae and likely have increased chances of immigration from fecund females. Bognounou et al (2017), in a longitudinal study showed that defoliation and stand vulnerability increased as the number of years of an outbreak increased. After treatment, SBW may migrate over from surrounding areas that were not sprayed but which had higher SBW populations in 2016 than did surrounding areas in the 2011 spraying. The importance of SBW migration on efficacy of treatments has been previously reported (Carter and Lavigne 1993). Our results suggest that large-scale aerial spraying in the earlier stage of an outbreak is more beneficial to reducing carbon losses than later stage of outbreak in boreal forest of Québec.

4.6.3. Different frequency of spraying impact the efficacy of Aerial Spraying

It is clear that the efficacy of aerial spraying decreased over time due to increasing SBW populations and immigration from neighboring sites (Rauchfuss *et al.*, 2011; Dupont *et al.*, 2018). In this study, due to data limitation, we only simulated 5 consecutive years of C dynamics (i.e. from one year before to three years after spraying) for the earlier sprayed sites and for three years (i.e. from one year before to one years after spraying) for the later sprayed sites. The MFFP aerial observations show that both AD_{DS2} and AD_{DS3} were higher than AD_{DS1} for all species in sites sprayed earlier in the outbreak (Table 4.3). This suggests that the efficacy of aerial spraying for controlling defoliation decreased two years after treatment. However, this is in contrast to NEP for all forest compositions as the results in (Table 4.3) show that the effect of Btk protection on NEP can be maintained 2-3 years after spraying for the earlier sprayed forests. However, for the later sprayed areas, more observation are needed to evaluate the effect of aerial spraying on NEP through time. Fuentealba *et al.* (2019) reported similar results, suggesting that different Btk applications (i.e. every 2 or 3 years) could provide enough protection to maintain residual photosynthetic capacity (above the 50% threshold) for Québec's forests.

4.7. Conclusions

Our simulations demonstrate that the aerial spraying with Btk provides good foliage protection and help maintain forest carbon in boreal forests of Quebec. In this study, aerial spraying reduced annual defoliation by 23.62-24.44% and increased net ecosystem productivity from 0.7 to 1.21 10^2g C m^{-2} $year^{-1}$ in fir forests. Spray efficacy and carbon protection were greater in fir than either spruce or mixed fir+spruce forests in the year following spraying. Although we found that average aboveground biomass decreased in both sprayed and unsprayed forests, biomass losss occurred more slowly in the fir forests that were sprayed. These benefits were most pronounced one-year after the Btk treatment but weakened two years after spraying for the forest compositions studied. Maintaining carbon during outbreaks benefits could also be enhanced by forest regeneration of non-host or secondary host species and additional mortality of SBW by natural enemies (i.e. predators and parasitoids) and pathogens which are currently not implemented within the TRIPLEX-Insect model. We suggest that exploring possible additive benefits of these factors on C dynamics should be considered and included in the TRIPLEX-Insect model in the future.

4.8. Acknowledgements

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4.9. Supplementary materials

Table 4S. 1. Values of key parameters used in simulations of the TRIPLEX-Insect model. Note: BF refers to fir; FS refers to fir+spruce; and SP refers to spruce.

Parameter	Description	Values	Reference
PAR			
Absorb	Atmospheric absorption factor	0.15	Bossel (1996)
Cloud	Time faction of cloud days	0.4	Bossel (1996)
PAR factor	Sloar radiation fraction	0.47	Bossel (1996)
GPP			
BlCond	Canopy boundary layer conductance (ml $m^{-2}s^{-1}$)	0.2	Coops et al. (2001)
MaxCond	Max canopy conductance (ml $m^{-2}s^{-1}$)	0.02	Coops et al. (2001)
StomCond	Stomata conductance (ml $m^{-2}s^{-1}$)	0.006	Coops et al. (2001)
ExtCoef	Radiation extinction coefficient	0.5	Coops et al. (2001)
TaMin	Min temperature (°C) for growth	0~5	Bossel (1996)
TaMax	Max temperature (°C) for growth	30	Bossel (1996)
Topt	Optimum temperature (°C) for growth	12	Bossel (1996)
N factor	Nitrogen factor for tree growth	0.2	Parton et al. (1993)
Na	Effect of age to GPP	3	Landsberg and Waring (1997)
Sla	Specific leaf area (m^2kg^{-1} of carbon)	6	Kimball et al. (1997)
NPP			
GamaF	Leaves turnover per year	0.18~0.3	Gower et al. (1997)
GamaR	Fine roots turnover per year	1.4~3.3	Steele et al. (1997)
Soil C and N			
Lnr	Lignin-nitrogen ratio	0.26	Parton et al. (1993)
Ls	Lignin for leaf, fine root, coarse root, branch, and wood	0.215,0.215, 0.235,0.255, 0.255	Parton et al. (1993)
Species			
CSP	Wood carbon density (Mg m^{-3})	0.21	Newcomer et al. (2000)
CD	Crown to stem diameter ratio	25	Bossel (1996)
Alpha C	Canopy quantum efficiency	BF=0.1~0.12; FS=0.08~0.1; SP=0.06~0.08	Gower et al. 1997
S	the index of tree species for defoliation caused mortality	BF=0.35~0.4; FS=0.3~0.35; SP=0.25~0.3	Assumption

Table 4S. 2. Regression results for AD

Predictor	*Fir*		*Spruce*		*Fir+Spruce*	
	b	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]
(Intercept)	87.66**	[73.78, 101.53]	61.59**	[50.01, 73.17]	75.47**	[65.71, 85.22]
Sites2	0.39	[-3.10, 3.88]	1.48	[-2.18, 5.14]	-7.52**	[-10.82, -4.21]
Sites3	-7.22	[-18.39, 3.94]	-19.30**	[-23.16, -15.44]	-21.73**	[-25.07, -18.39]
Sites4	1.99	[-2.59, 6.57]	3.78	[-0.30, 7.87]	-6.51**	[-10.39, -2.64]
Sites5	-18.32**	[-21.21, -15.43]	-21.37**	[-25.36, -17.38]	-15.77**	[-19.02, -12.53]
Sites6	-5.86*	[-10.77, -0.94]	-8.84**	[-12.78, -4.89]	-6.61**	[-9.40, -3.83]
Age	-0.35	[-0.75, 0.04]	0.34**	[0.08, 0.60]	-0.02	[-0.26, 0.22]
Age^2	0.00*	[0.00, 0.01]	-0.002**	[-0.00, -0.00]	0.0005	[-0.00, 0.00]
Year2012	9.94**	[4.88, 15.01]	6.44**	[3.86, 9.01]	5.90**	[2.78, 9.03]
Year2013	13.78**	[8.71, 18.85]	11.34**	[8.77, 13.92]	9.91**	[6.78, 13.03]
Year2014	14.32**	[9.25, 19.39]	10.26**	[7.68, 12.84]	6.83**	[3.70, 9.95]
Spray	-20.29**	[-24.73, -15.85]	-4.84**	[-8.23, -1.45]	-11.35**	[-14.38, -8.32]
Year2012:Spray	-5.07	[-11.23, 1.09]	-6.47**	[-11.24, -1.70]	-5.33*	[-9.59, -1.08]
Year2013:Spray	3.46	[-2.70, 9.62]	-3.81	[-8.58, 0.96]	5.70**	[1.44, 9.95]
Year2014:Spray	-0.58	[-6.73, 5.58]	-4.87*	[-9.64, -0.10]	3.95	[-0.31, 8.21]
	R^2 = .437**		R^2 = .195**		R^2 = .157**	
	95% CI[.39,.47]		95% CI[.17,.21]		95% CI[.13,.17]	

Note. A significant b-weight indicates the semi-partial correlation is also significant. b represents unstandardized regression weights. LL and UL indicate the lower and upper limits of a confidence interval, respectively.
* indicates p < .05. ** indicates p < .01.

Table 4S. 3. Regression results for GPP

Predictor	*Fir*		*Spruce*		*Fir+Spruce*	
	b	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]
(Intercept)	4.15	[-2.35, 10.64]	3.61*	[0.51, 6.71]	-0.59	[-3.69, 2.51]
Sites2	1.80*	[0.17, 3.44]	-1.70**	[-2.68, -0.72]	3.27**	[2.22, 4.32]
Sites3	2.02	[-3.20, 7.25]	-0.91	[-1.94, 0.12]	2.96**	[1.89, 4.02]
Sites4	11.43**	[9.29, 13.58]	7.37**	[6.28, 8.46]	14.40**	[13.17, 15.63]
Sites5	14.14**	[12.79, 15.50]	12.02**	[10.96, 13.09]	12.78**	[11.75, 13.81]
Sites6	9.87**	[7.57, 12.17]	6.37**	[5.31, 7.42]	8.17**	[7.29, 9.06]
Age	0.51**	[0.33, 0.70]	0.24**	[0.17, 0.31]	0.46**	[0.38, 0.53]
Age^2	-0.004**	[-0.01, -0.00]	-0.001**	[-0.00, -0.00]	-0.003**	[-0.00, -0.00]
Year2012	-0.65	[-3.02, 1.72]	1.29**	[0.61, 1.98]	1.66**	[0.67, 2.66]
Year2013	-7.99**	[-10.36, -5.61]	-3.27**	[-3.96, -2.58]	-4.32**	[-5.31, -3.32]
Year2014	-11.27**	[-13.64, -8.89]	-7.24**	[-7.93, -6.55]	-7.37**	[-8.37, -6.38]
Spray	-0.63	[-2.71, 1.45]	0.10	[-0.81, 1.00]	0.94	[-0.02, 1.90]
Year2012:Spray	2.57	[-0.31, 5.45]	1.13	[-0.15, 2.40]	2.02**	[0.67, 3.37]
Year2013:Spray	5.80**	[2.92, 8.68]	1.51*	[0.24, 2.79]	2.83**	[1.47, 4.18]
Year2014:Spray	6.25**	[3.36, 9.13]	2.34**	[1.06, 3.61]	1.73*	[0.38, 3.08]
	R^2 = .471**		R^2 = .441**		R^2 = .432**	
	95% CI[.43,.50]		95% CI[.42,.46]		95% CI[.41,.45]	

Note. A significant b-weight indicates the semi-partial correlation is also significant. b represents unstandardized regression weights. LL and UL indicate the lower and upper limits of a confidence interval, respectively.

* indicates p < .05. ** indicates p < .01.

Table 4S. 4. Regression results for NPP

Predictor	*Fir*		*Spruce*		*Fir+Spruce*	
	b	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]
(Intercept)	9.72**	[6.55, 12.89]	7.37**	[6.06, 8.69]	6.39**	[4.92, 7.86]
Sites2	0.88*	[0.09, 1.68]	-0.74**	[-1.16, -0.33]	1.49**	[0.99, 1.99]
Sites3	0.78	[-1.78, 3.33]	-0.59**	[-1.03, -0.16]	1.41**	[0.91, 1.91]
Sites4	5.82**	[4.77, 6.87]	3.37**	[2.90, 3.83]	7.49**	[6.90, 8.07]
Sites5	6.32**	[5.66, 6.98]	4.94**	[4.49, 5.40]	5.71**	[5.22, 6.20]
Sites6	4.51**	[3.39, 5.64]	2.80**	[2.35, 3.25]	3.68**	[3.26, 4.10]
Age	-0.02	[-0.11, 0.07]	-0.09**	[-0.12, -0.06]	-0.01	[-0.05, 0.02]
Age^2	-0.0004	[-0.00, 0.00]	0.0004**	[0.00, 0.00]	-0.0002*	[-0.00, -0.00]
Year2012	-0.33	[-1.49, 0.83]	1.24**	[0.95, 1.53]	1.35**	[0.88, 1.82]
Year2013	-3.33**	[-4.48, -2.17]	-0.39**	[-0.68, -0.09]	-1.07**	[-1.54, -0.60]
Year2014	-5.31**	[-6.47, -4.15]	-2.50**	[-2.79, -2.21]	-3.07**	[-3.54, -2.60]
Spray	-0.89	[-1.90, 0.13]	-0.08	[-0.46, 0.31]	0.24	[-0.21, 0.70]
Year2012:Spray	1.31	[-0.10, 2.71]	0.45	[-0.09, 1.00]	0.87**	[0.22, 1.51]
Year2013:Spray	3.16**	[1.75, 4.56]	0.82**	[0.28, 1.36]	1.73**	[1.09, 2.37]
Year2014:Spray	3.35**	[1.94, 4.75]	1.20**	[0.65, 1.74]	1.01**	[0.37, 1.66]
	R^2 = .447** 95% CI[.40,.48]		R^2 = .498** 95% CI[.48,.52]		R^2 = .458** 95% CI[.43,.48]	

Note. A significant b-weight indicates the semi-partial correlation is also significant. b represents unstandardized regression weights. LL and UL indicate the lower and upper limits of a confidence interval, respectively.

* indicates $p < .05$. ** indicates $p < .01$.

Table 4S. 5. Regression results for NEP

Predictor	*Fir*		*Spruce*		*Fir+Spruce*	
	b	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]	*b*	*b* 95% CI [LL, UL]
(Intercept)	7.43**	[5.63, 9.23]	4.58**	[3.96, 5.19]	5.01**	[4.32, 5.71]
Sites2	0.27	[-0.18, 0.72]	-0.26**	[-0.46, -0.07]	0.65**	[0.42, 0.89]
Sites3	0.78	[-0.66, 2.23]	0.35**	[0.15, 0.55]	1.49**	[1.25, 1.73]
Sites4	4.10**	[3.50, 4.69]	1.12**	[0.91, 1.34]	2.58**	[2.31, 2.86]
Sites5	2.55**	[2.17, 2.92]	2.14**	[1.93, 2.35]	2.36**	[2.13, 2.59]
Sites6	2.34**	[1.70, 2.97]	1.36**	[1.15, 1.57]	1.65**	[1.45, 1.85]
Age	-0.16**	[-0.21, -0.11]	-0.11**	[-0.13, -0.10]	-0.12**	[-0.13, -0.10]
Age^2	0.0003*	[0.00, 0.00]	0.0004**	[0.00, 0.00]	0.0003**	[0.00, 0.00]
Year2012	-0.18	[-0.83, 0.48]	0.61**	[0.47, 0.75]	0.71**	[0.49, 0.93]
Year2013	-1.45**	[-2.10, -0.79]	0.03	[-0.11, 0.16]	-0.21	[-0.43, 0.01]
Year2014	-2.36**	[-3.01, -1.70]	-0.91**	[-1.04, -0.77]	-1.04**	[-1.26, -0.82]
Spray	-0.53	[-1.10, 0.05]	-0.06	[-0.24, 0.12]	0.14	[-0.08, 0.35]
Year2012:Spray	0.80	[-0.00, 1.59]	0.25*	[0.00, 0.51]	0.46**	[0.15, 0.76]
Year2013:Spray	1.82**	[1.03, 2.62]	0.43**	[0.18, 0.68]	0.85**	[0.55, 1.15]
Year2014:Spray	1.91**	[1.11, 2.71]	0.56**	[0.31, 0.82]	0.38*	[0.08, 0.68]
	R^2 = .501** 95% CI[.46,.53]		R^2 = .538** 95% CI[.52,.56]		R^2 = .553** 95% CI[.53,.57]	

Note. A significant b-weight indicates the semi-partial correlation is also significant. b represents unstandardized regression weights. LL and UL indicate the lower and upper limits of a confidence interval, respectively.

* indicates $p < .05$. ** indicates $p < .01$.

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CHAPTER V

GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

5.1. Summary of findings

Currently, forest management requires more accurate quantification of the carbon budget under insect disturbances. This PhD work has successfully developed the TRIPLEX-Insect model, a new process-based model, for the simulation and analysis of the impact of spruce budworm disturbance on carbon dynamics of boreal forests in Canada (Chapters II, III and IV). The TRIPLEX-Insect model provides a novel method to integrate the relationship between insect defoliation and tree mortality, this model was validated against tree mortality and current annual volume increment data at the stand level (Chapter II). Then I simulated changes in forest carbon fluxes and stocks between scenarios with and without spruce budworm defoliation using the newly developed model in a large region of boreal forests of Québec (Chapter III). Finally, I applied this model to evaluate and analyze how much net ecosystem productivity could be increased by aerial spray protection during a spruce budworm outbreak (Chapter IV).

5.1.1. The model development and validation

In Chapter II, the TRIPLEX-Insect model was developed by quantifying the relationship among insect defoliation, defoliation caused mortality and compensatory mechanisms. The implementation of insect defoliation caused mortality and compensatory mechanism algorithms as designed in this research are an important step in improving the applicability of an ecological model for forest resource management and pest control initiatives. Despite the uncertainties that exist in the TRIPLEX-Insect model structure and parameters (see section 5.2), the model validation improves the credibility of the model in estimating carbon dynamics in balsam fir and spruce forests under infestation disturbances. In addition, the TRIPLEX-Insect model provides a useful and flexible tool to evaluate and analyze how to implement aerial spray protection in order to minimise insect defoliation and reduce forest carbon losses during spruce budworm outbreaks.

5.1.2. The effect of spruce budworm outbreak on forest carbon dynamics

The results of a sensitivity experiment indicated that the capacity of a forest for carbon sequestration is highly related to tree age, defoliation intensity and duration of defoliation in balsam fir stands. Tree age also affects the capacity of recovery in forest ecosystems following spruce budworm outbreaks. Young trees not only have greater resistance and lower defoliation during spruce budworm attacks, but they also have faster growth and recovery. Furthermore, longer duration outbreaks and higher levels of defoliation caused higher tree mortality, thus controlling the duration and intensity of defoliation can improve the forest's capacity for carbon sequestration recovery. In addition, the simulations showed gross primary productivity to be more sensitive than autotrophic respiration to defoliation intensity during periods of spruce budworm outbreak for both mature and immature balsam fir stands.

Spruce budworm outbreaks always decrease carbon fluxes at both the stand and the regional scale in simulations for all host species (i.e. balsam fir, spruce and mixed fir+spruce forests) (Figure 2.4 and 3.4). The results also showed that insect disturbances have negative effects on aboveground and belowground biomass carbon pools but positive effects on soil organic carbon pools in boreal forests of Québec (Figure 2.5 and 3.7). My first hypothesis that carbon budgets may have a negative feedback on fir and spruce forests under spruce budworm disturbances, is strongly supported by my findings. However, total litterfall carbon pools have a positive feedback on boreal forests when tree mortality was increased by spruce budworm defoliation.

Findings from this study suggest that balsam fir forests may lose less carbon than either spruce or mixed fir+spruce forests during the 2007 to 2017 spruce budworm outbreak in Québec. These findings are contrary to my second hypothesis that balsam fir will maintain less carbon than either spruce or mixed fir+spruce forests under spruce budworm disturbances. Although balsam fir is the species most vulnerable to spruce budworm attacks, its younger age and quick regeneration allowed fir forests to regrow faster than either spruce or mixed fir+spruce forests. Thus this study suggests that when evaluating vulnerability or resilience we should consider a combination of factors rather than just species composition.

5.1.3. The effect of aerial spraying on forest carbon under spruce budworm disturbances

Forest management such as aerial spraying with biotic insecticide (e.g. *Bacillus thuringiensis* ssp. Kurstaki, Btk) can control annual defoliation, as well as reduce carbon losses under spruce budworm outbreaks (Figure 4.3). In this study, the TRIPLEX-Insect model simulation results indicate that the efficacy of aerial spraying application may be effected by multiple factors such as host species, number of years after spraying, stage of the outbreak and local climate condition. These findings support my third hypothesis that aerial spraying could help reduce forest carbon losses during a spruce budworm outbreak. Additionally, balsam fir forests respond better to spraying with Btk than either spruce or mixed fir+spruce forests. This is because NEP increased more quickly and the aboveground biomass decreased more slowly in balsam fir forests than in either spruce or mixed fir+spruce forests after spraying protection (Figure 4.4, 4.5 and 4.6).

5.2. Model limitations and future works

My PhD focused on quantitatively understanding the role of spruce budworm disturbance on forest carbon dynamics by developing a new process-based model (TRIPLEX-Insect). Antecedent assumptions and simplified ecological processes may limit most process-based modeling approaches and developments. The Triplex-Insect model is not immune to these critiques, and may be limited in its ability to simulate responses to future climate change due to it not including insect population dynamics. This could also limit its ability to evaluate compensatory mechanisms or feedbacks, for example if climate change, as speculated by Pureswaran *et al.*, (2015) increases the vulnerability of black spruce stands, but nutrient leaching reduces stand productivity.

5.2.1. Insect Population dynamics

It has been suggested that a first step in predicting insect outbreak temporal and spatial patterns is understanding insect population dynamics as this will determine the amount of defoliation (MacLean 2016). However, insect population factors, such as predators, regeneration rate, parasitoids, survival rate for different stages of the life cycle, etc, are difficult to observe and model due to randomness and complexity (Gray and MacKinnon 2006; Zhao *et al.*, 2014). TRIPLEX-Insect model directly uses annual defoliation as an input parameter, thus skipping the simulation of the insect population dynamics. Because of this, the model can only simulate historical and current spruce budworm outbreaks, but cannot predict future defoliation patterns. Currently, scenario testing (Kurz *et al.*, 2008; Dymond *et al.*, 2010; Arora *et al.*, 2016) and probabilistic predictions (Fleming and Volney 1995; Candau and Fleming 2011) are the most commonly used approaches for forecasting the effects of spruce budworm defoliation under future conditions. The TRIPLEX-Insect model can be used to evaluate different defoliation scenarios to carbon dynamics following future spruce budworm outbreaks. This is a strength of the model that I have developed compared to many other approaches in the literature (Kurz *et al.*, 2009; Foster 2011). In addition, the model also considers some spruce budworm dynamics that impact ecosystem carbon budgets, such as insect respiration processes and decomposition of dead insects. These processes cannot be ignored for model simulations over large areas.

5.2.2. Compensatory mechanisms

Growth reductions due to spruce budworm outbreaks are well known (Piene 1980; Ostaff and MacLean 1995; Hennigar *et al.*, 2008) but mid-term and long-term carbon dynamics depend also on forest recovery. However, the mechanisms of growth recovery are still not very clear and poorly understood following insect defoliation. Therefore, although this study considered three different compensatory mechanisms in the TRIPLEX-Insect model, the validation results probably still underestimate the current annual volume increment (Figure 2.2B). This result is mainly limited by existing approaches and the availability of field observed data that I used in this study. Therefore, if there is enough observational data available, parameter optimization will be an achievable step to improve the model simulations (Li *et al.*, 2015). In addition, more accurate model simulations may also need to consider more reasonable compensatory mechanisms, such as the effect of defoliation on plant water balance (Oosthuizen and Snyman 2003). Foliage biomass losses may lead to reduce plant stomata and evapotranspiration, which also increases the difficulty of moisture acquisition (Stephens *et al.*, 2018).

5.2.3. The impacts of climate changes

It is well known that climate change is projected to have enormous effects on forest carbon sequestration (i.e. photosynthesis, respiration and evapotranspiration processes), especially in the Canadian boreal forest (Warren and Lemmen 2014; Navarro *et al.*, 2018). However spruce budworm population dynamics are also influenced by local climate conditions. Changes in temperature will shift insect feeding, survival, dispersal, regeneration and development rates, which will ultimately impact spruce budworm outbreaks characteristics (e.g. duration and intensity) (Régnière *et al.*, 2012a; Boulanger *et al.*, 2016). Moreover, drought may stress trees making them more vulnerable to insect herbivory (De Grandpré *et al.*, 2018). Based on evidence of more frequency of insect activity and increasing of tree mortality after drought, the intrinsic link between drought and pest is widely accepted (Mattson & Haack, 1987; Volney and Fleming 2000; Régnière *et al.*, 2012b). However, recent empirical evidence suggests that responses are not always as expected (Itter *et al.*, 2018). I have demonstrated that the TRIPLEX-Insect model can simulate the effects of climate change or spruce budworm disturbance on forest carbon dynamics under historic climate change conditions. Once better population dynamic models are developed for defoliation these could be coupled with this model to more accurately predict ecosystem response to interactions between climate change and spruce budworm disturbances under future climate change conditions.

5.3. Concluding remarks

My PhD study has led to the development of a new process-based model (TRIPLEX-Insect) for the simulation and analysis of the impacts of spruce budworm disturbance on tree mortality and carbon dynamics of boreal forests in Québec. This work has helped us to better understand how insect outbreaks interact with multiple factors such as forest age, composition and forest management strategy (i.e. aerial spraying) to influence carbon dynamics. Furthermore, the TRIPLEX-Insect model has improved our estimations of forest carbon losses under insect attacks at both stand and regional scales, which could help forest managers to reduce the potential risk of boreal forests converting from carbon sinks to sources following spruce budworm outbreaks.

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