Recovery of Boreal Forest Carbon Pools Following Stem-Only Harvesting in Quebec, Canada

by

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A thesis submitted in conformity with the requirements
for the degree of Master of Science

Department of Geography
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Abstract

Forêt Montmorency (FM), Quebec, provides an opportunity to use a 77-year chronosequence to evaluate the effects of stem-only harvesting on carbon cycling in a balsam fir-white birch boreal forest. By comparing empirical estimates of 19 carbon pools with those simulated in the Carbon Budget Model (CBM-CFS3), it is possible to assess the accuracy of model assumptions in predicting stand-level carbon dynamics.

Although CBM-CFS3 was able to predict total ecosystem carbon within 10% of the empirical mean at stand maturity, many of the dead organic matter (DOM) pools deviated from field observations, indicating that model initialization of DOM pools did not adequately simulate the 1000 year history of C transfers and stand dynamics prior to the harvesting event. Future modifications to CBM-CFS3 initialization assumptions may be required to more accurately simulate the long-term effects of natural disturbances on carbon pools over time for this forest region.
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<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
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<tbody>
<tr>
<td>AG</td>
<td>Aboveground</td>
</tr>
<tr>
<td>Ae</td>
<td>An A horizon characterized by eluviation of clay, Fe, Al, or organic matter</td>
</tr>
<tr>
<td>BG</td>
<td>Belowground</td>
</tr>
<tr>
<td>C</td>
<td>Carbon</td>
</tr>
<tr>
<td>CBM-CFS3</td>
<td>Carbon Budget Model of the Canadian Forest Sector</td>
</tr>
<tr>
<td>CWD</td>
<td>Coarse woody debris</td>
</tr>
<tr>
<td>DBH</td>
<td>Tree stem diameter at 1.3 m above ground (cm)</td>
</tr>
<tr>
<td>DOM</td>
<td>Dead organic matter</td>
</tr>
<tr>
<td>DWD</td>
<td>Downed woody debris (woody debris and stumps)</td>
</tr>
<tr>
<td>FH</td>
<td>Decomposing organic material beneath the L horizon, where F and H denote “fermentation” and “humus”, respectively</td>
</tr>
<tr>
<td>FWD</td>
<td>Fine woody debris</td>
</tr>
<tr>
<td>FM</td>
<td>Forêt Montmorency</td>
</tr>
<tr>
<td>GHG</td>
<td>Greenhouse gas</td>
</tr>
<tr>
<td>HW</td>
<td>Hardwood</td>
</tr>
<tr>
<td>L</td>
<td>Forest floor horizons containing decomposing foliar litter that is still readily discernable from underlying soil</td>
</tr>
<tr>
<td>LFC</td>
<td>Laurentian Forestry Centre (Canadian Forest Service, Natural Resources Canada),</td>
</tr>
<tr>
<td>LFH</td>
<td>Forest floor horizon, comprised foliar litter and organic material in various stages of decomposition</td>
</tr>
<tr>
<td>NFI</td>
<td>National Forestry Inventory</td>
</tr>
<tr>
<td>SE</td>
<td>Standard error of mean</td>
</tr>
<tr>
<td>SW</td>
<td>Softwood</td>
</tr>
<tr>
<td>SWD</td>
<td>Small woody debris (1 &lt; WD ≤ 10 cm)</td>
</tr>
<tr>
<td>SBW</td>
<td>Spruce budworm</td>
</tr>
<tr>
<td>SOH</td>
<td>Stem-only harvesting</td>
</tr>
<tr>
<td>SOM</td>
<td>Soil organic matter (representing the fine earth fraction of LFH and mineral soil horizons)</td>
</tr>
<tr>
<td>TSD</td>
<td>Time since disturbance, specifically, time since last harvest</td>
</tr>
<tr>
<td>WD</td>
<td>Woody debris</td>
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Chapter 1: Introduction

Understanding the effects of biomass harvesting on carbon cycling in the boreal forest is critical for the development of sustainable forest management policies. In light of global climate change, this area of research has become increasingly important, due to both the magnitude and potential vulnerability of boreal forest carbon stocks. Boreal forests have consistently acted as a strong carbon sink, offsetting roughly 7% of global fossil fuel emissions (Pan et al. 2011). However, in recent decades, increases in natural disturbances and changes in forest management practices have reduced the strength of this sink in Canada by approximately 50% (Pan et al. 2011; Kurz et al. 2013). Integrating bioenergy production into traditional forest harvesting practices represents one strategy for meeting consumer demand while increasing the availability of renewable energy resources and conserving biogenic C stocks. The purpose of my research is to provide a site-specific evaluation of how forest carbon stocks recover from conventional stem-only harvesting, with the ultimate goal of contributing to our understanding of the role of bioenergy systems in reducing greenhouse gas (GHG) emissions.

In this introduction, I will first discuss the potential of boreal forests to contribute to climate change mitigation through management practices that simultaneously preserve biogenic C stocks and facilitate fossil fuel displacement. After establishing the framework for this research, I will highlight the importance of quantifying individual forest carbon pools, and evaluating post-disturbance carbon recovery trends for specific regions. I will then describe the advantages of the chronosequence experimental design used in this field study, in Forêt Montmorency, Quebec. Finally, I will explain the rationale behind the field-model comparison study, which allowed the assumptions and parameters of a lead carbon budgeting model in Canada to be tested with independent field data.

1.1 The role of boreal forests in climate change mitigation

Boreal forests account for 27% of the total global forest, extending over 12.5 ± 1.5 million km$^2$ (Dixon et al. 1994). Cumulatively, boreal forests store approximately 559-703 Pg C, or about 55% of total global forest carbon pool, which is estimated to be 1,146 Pg C (Dixon et al. 1994;
Pimm et al. 2009). The future of this immense carbon pool has become precarious, as it rests within the context of several global-scale issues. The stability of forest C stocks is threatened by population growth, as well as global climate change and the corresponding increases in drought, wildfire, and insect outbreaks (Kurz et al. 2008). Because climate change is expected to have a disproportionately greater effect on northern latitudes, boreal forests are particularly vulnerable to climate-induced stresses and natural disturbances, which may consequently have a greater impact on carbon pools and fluxes in these regions (Laganière et al. 2013; Lamers et al. 2013; Price et al. 2013).

Canada’s managed boreal forests account for approximately 13% of global boreal forest area, and have acted as an C sink of 28 Tg C yr$^{-1}$ from 1990-2008 (Kurz et al. 2013). This sink offsets annual C losses from harvesting, and contributes an additional 11 Tg C yr$^{-1}$ in C storage (Kurz et al. 2013). However, there is already evidence that the carbon sink in boreal forests is weakening, as emissions from increased disturbance and heterotrophic respiration begin to outweigh benefits of increased productivity, creating an ‘asymmetry of risk’ as climate change progresses (Kurz et al. 2013). Climate-induced disturbances are not only jeopardizing the stability of this annual sink, but can also create feedback loops, whereby forest degradation increases terrestrial GHG emissions, which can significantly accelerate global warming and climate change events (Cox et al. 2000).

Human population growth is a fundamental factor contributing global climate change, and it also directly increases forest disturbances through land-use change, fragmentation, and increased harvesting intensity. The way in which boreal forests are utilized to support a growing population, both in terms of ecosystem services and extractable resources, has become increasingly controversial (Price et al. 2013). In order to sustainably meet increasing demands without further exacerbating climate change, forest management practices and priorities need to be re-evaluated (Colombo et al. 2012; Berger et al. 2013). The value of boreal forests in climate change mitigation strategies must be taken into account. Bioenergy systems represent one potential way to meet consumer demand for both energy and traditional forest products, and to do so in a manner that is conducive to long-term carbon sequestration and ecosystem sustainability.
Bioenergy systems could reduce GHG emissions by encouraging forest management practices that increase or maintain forest carbon stocks, increasing carbon storage in harvested wood products, and providing an alternative energy source to help facilitate fossil fuel displacement (Colombo et al. 2012). There are numerous methods for developing bioenergy systems, but the most viable options in Canada might involve utilization of either a) harvesting residues b) salvaged deadwood, or c) mill residues (Dymond et al. 2010). However, utilization of harvesting residues and salvaging standing dead trees would be significantly more intensive, since greater amounts of biomass per hectare would be removed from the site relative to existing stem-only harvesting operations. In contrast, producing biofuel feedstock with mill residues from stem-only harvesting operations would not necessitate increasing biomass utilization intensity.

To be considered ‘sustainable’, existing stem-only harvesting operations would need to be sustainable with regard to numerous environmental factors, including rotation lengths and harvesting intensity, as well as economic and social factors. Sustainable forest management policies have been shown to increase forest C stocks relative to those in unmanaged forests (i.e. not protected from natural disturbances or harvesting), and to maintain this C sequestration for longer time-periods than protected stands, which have been found to saturate within 30 years (Colombo et al. 2012). Similarly, Lamers et al. (2013) found that salvage harvesting after insect outbreaks resulted in greater carbon benefits at both the stand and landscape level relative to protected stands, when the emission offsets from both timber and bioenergy production were accounted for.

In some instances, forest management may also reduce susceptibility to future natural disturbances, which would further contribute to curbing atmospheric carbon emissions (Canadell and Raupach 2008; Lemprière et al. 2013). For example, removing some portion of harvesting residues from the forest floor, or removing deadwood from naturally disturbed stands, reduces fuel loading and can help prevent forest fires (Lippke et al. 2011). Salvage harvesting operations are becoming an important source of bioenergy, particularly on a regional scale, as natural disturbances become more frequent and severe (Dymond et al. 2010). In British Colombia, salvage operations following mountain pine beetle outbreaks already practice residue removal to reduce forest fire risk, but these residues are typically piled on roadsides and either left to decay or burnt, both of which result in substantial GHG emissions from the forestry sector (Lamers et al. 2013). These emissions could be avoided if residues were utilized for bioenergy production,
which, in a long-term mitigation strategy, could further offset forestry carbon emissions through fossil fuel displacement. In this sense, bioenergy harvesting could be both an adaptive and a mitigative solution to climate change.

A fundamental challenge in all bioenergy operations lies in determining the amount of biomass that can be sustainably removed, or the ‘ecological potential’ of a forest (Dymond et al. 2010; Aherne et al. 2012). This can be particularly difficult given the range of environmental conditions in forests, as well as the high inter-site variability observed in ecosystem carbon pools (Yanai et al. 2003). More research is needed to determine under what circumstances bioenergy systems can produce the aforementioned carbon benefits, and if it is possible to do so in a manner that is both a) effective in terms of the timing of the mitigation benefits, and b) sustainable with regard to other ecosystem functions and processes.

The degree to which bioenergy systems can be considered to be carbon neutral is still under debate. This is in part due to the possibility that the repayment of carbon debt may not be achieved for several decades following harvest, when the benefits of C storage in wood products and ecosystem sequestration in the next rotation are realized (Dymond et al. 2010; Bernier and Paré 2013; Lamers et al. 2013a). In addition to concerns over the timing of the mitigation benefits, there is still considerable uncertainty as to the ecological repercussions of disrupting the recovery of disturbed stands, particularly with regard to how forest regeneration is impacted by the removal of deadwood and harvesting slash (Lindenmayer 2006). The ability of forest ecosystems to recover to pre-disturbance conditions is contingent upon factors such as nutrient availability and habitat diversity, and the role of decaying biomass in providing these ecosystem functions is critical, particularly following both natural and anthropogenic disturbances (Janisch and Harmon 2002; Thiffault et al. 2006; Aherne et al. 2012).

There are numerous other concerns associated with bioenergy systems that will continue to be addressed in complimentary studies, including economic and social costs. Life-cycle assessments must be conducted in order to evaluate cradle-to-grave C emissions associated with various fuel sources, as well as the impacts of fossil fuel displacement and C storage in harvested wood products (Lippke et al. 2011). Although it is necessary to carefully evaluate the risks of all alternative energy sources, some trade-offs will be inevitable, and it is critical that these trade-offs be evaluated in the context of global climate change. The ecological, economic, and social
consequences of continued fossil fuel dependency are becoming increasingly apparent, and will only worsen if we are not dedicated to finding sustainable methods for renewable energy production.

One of the first steps in evaluating the potential of bioenergy systems for climate change mitigation, is to determine if the desired emission reductions can be achieved without disrupting long-term carbon cycling in forest ecosystems. The purpose of my research is to provide a site-specific analysis of the consequences of harvesting disturbance on carbon cycling in balsam fir – white birch forest ecosystems, in an effort to contribute to our understanding of the role of boreal forests in climate change mitigation. The empirical data collected in this study was from healthy forest stands that were consistently managed with stem-only harvesting, with harvesting residues left on-site. Therefore, conclusions from this research can only be extended to reflect the sustainability (with regard to preserving forest carbon stocks) of bioenergy systems that utilize sawmill or pulp mill residues from these existing harvesting operations.

By combining field and model-based analyses, it is possible to improve our understanding of the ecological response of boreal forests to disturbance at both the stand and landscape level. In order to improve the accuracy with which we predict post-disturbance carbon dynamics, independent field data was used to test hypotheses related to carbon cycling and the validity of model parameters. This carbon-based assessment can help us to determine the vulnerability of forest carbon dynamics to disturbance events, and can complement more holistic assessments regarding the viability of bioenergy systems. Ultimately, this research can contribute to a policy framework that emphasizes the necessity of managing forests to increase mitigation potential without compromising ecosystem sustainability.

1.2 A chronosequence approach to estimating carbon stocks

The field study that was established in Forêt Montmorency (FM) provides an opportunity to use a chronosequence experimental design to quantify carbon pools over time in a boreal forest ecosystem. A chronosequence is a method used to study ecological succession that relies on “space-for-time” substitution (Johnson and Miyanishi 2008). In many instances, it is not logistically feasible to capture trends over time at a single site, given the length of time required to observe changes in vegetative succession. Therefore, the benefit of chronosequence studies is
that a series of sites can be assembled to reflect the passage of time, and the consequential ecological changes, which would be expected for a single site in succession. The primary assumption underlying space-for-time substitution is that sites differ only in age since an initial disturbance, and that they share the same history with regard to both biotic and abiotic environmental conditions.

Although there are clearly some inherent issues with the assumptions associated with chronosequence studies, the experimental design used in FM is considered to be robust both in the length of the time span and the high replication of plots at the two end-points in chronosequence. The chronosequence in FM extends over almost 80 years, and includes a complete rotation period for this forest type. Many of the chronosequence studies conducted to date are either not as long or complete as the chronosequence that was constructed in FM, and/or represent very different forest types (Taylor et al. 2008; Kashian et al. 2013) in FM (Martin et al. 2005; Seedre et al. 2014). This study closely aligns to the research conducted by Moroni et al. (2010a), both in terms of objectives and experimental approach. However, Moroni et al. (2010a) conducted their research in Newfoundland, and the stands sampled only represented three broad age classes.

In addition to the advantages associated with experimental design, the FM is located in a boreal region that is appropriate for evaluating the potential of bioenergy production in boreal forests. Compared to other boreal regions, where conditions are colder, FM has relatively fast growing trees, which contributes to higher biomass and deadwood C stocks (Moroni 2006; Hagemann et al. 2010). From a bioenergy perspective, carbon recovery trends in FM may be of particular interest, since it is situated within a region of Eastern North America where forest ecosystem dynamics have historically been driven by insect disturbances (MacLean and Erdle 1984; Boulanger and Arseneault 2004). In order to assess the repercussions of salvage harvesting operations in this region, it is first necessary to have reliable estimates of carbon stocks (Dymond et al. 2010a). The field study in FM allows us to estimate C stocks over time following stem-only harvesting, as well as the variability associated with each pool. Due to the high natural variability in forests, as well as the fact that the plots in FM are not necessarily representative of other stands in boreal Quebec, this study is intended to serve as an example of how carbon pools recover within one rotation period, as opposed to providing precise C stock estimates at a given
point in time. Understanding these carbon recovery trajectories is arguably one of the most important steps in determining the vulnerability of forest carbon pools to disturbance.

Several other studies have estimated ecosystem carbon in mature boreal forests across North America (Smith et al. 1986; Hoover et al. 2012), and several studies have examined specific carbon pools, such as: deadwood (Moroni 2006; Bond-Lamberty and Gower 2008), or soil (Yanai et al. 2003; Nave et al. 2010; Laganière et al. 2013; Poirier et al. 2014). However, many of these studies do not have the advantage of being able to evaluate trends in carbon pools over time, and to do so for virtually all significant carbon pools in a forest ecosystem. The field study in FM can help us to address fundamental knowledge gaps in our understanding of forest carbon recovery by combining the benefits of 1) a long and complete chronosequence, 2) a robust sampling procedure that allows for quantification of 19 carbon pools, and 3) a study region that has been historically shaped by insect disturbances and is now managed with conventional stem-only harvesting. Therefore, the purpose of this field study is to provide a comprehensive assessment of trends in ecosystem carbon pools following stem-only harvesting disturbance in a balsam fir-white birch boreal forest in Quebec.

1.3 The utility of field-model comparison studies

Scientific models provide the only opportunity to simulate and assess future environmental conditions, and allow for analysis across broader spatial and temporal than is typically feasible through field observations alone (Kurz et al. 2009). By developing a field-model comparison study of carbon pools in FM, I was able to use empirical data to test our theoretical understanding as to how ecosystem C dynamics respond to disturbance, as well as attain model results that may be more representative of average conditions for Eastern boreal forests in Quebec. The level of replication employed in the field study in FM provided insight into the precision of C pool estimates and expressed the wide inter-site variability in forest carbon pools. Because this inherent variability in C pool estimates is not expressed in model simulations, the field-model comparison process created a more appropriate framework for evaluating model results.

The Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) was the most suitable and robust model available for conducting this evaluation, given the location of my field research in Quebec, Canada, as well as the need to individually assess 19 unique carbon pools. CBM-
CFS3 was developed by Werner Kurz and colleagues, and is used for predicting carbon stocks and greenhouse gas emissions at both the stand and landscape level. It implements a Tier-3 (the most complex) approach of the Intergovernmental Panel on Climate Change (IPCC) Good Practice Guidance for reporting carbon stocks and fluxes, and has become a valuable tool in climate change mitigation strategies at a global scale (Kurz et al. 2009). Due to the model’s flexibility in predicting C dynamics across a variety of ecozones and spatial scales, it is particularly important to use independent field studies to evaluate the accuracy of CBM-CFS3 simulations for specific forests.

Several studies have used field data to assess the ability of CBM-CFS3 to predict carbon stocks, some of which have been based on National Forest Inventory (NFI) ground plot data for Canadian managed forests (Stinson et al. 2011; Kurz et al. 2013; Shaw et al. 2014), while others have collected data for specific forest regions (Taylor et al. 2008; Moroni et al. 2010; Hagemann et al. 2010). This study provides the means to validate model predictions for a specific region of boreal Quebec. By comparing field and modelled C stocks, it is possible to determine if the existing model parameters can accurately simulate stand-level ecosystem dynamics in Forêt Montmorency.

1.4 Research Objectives

1. To develop a quantitative understanding of the effects of natural disturbances and stem-only harvesting intensity on carbon pools and dynamics in Forêt Montmorency.

2. To assess the accuracy of the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) in predicting carbon dynamics in post-harvest boreal balsam fir – white birch forest ecosystems.
Chapter 2 : Methods

2.1 Field Methods

2.1.1 Study site

The field study was conducted in Forêt Montmorency, which is located in the Laurentian Highlands, 70 km north of Quebec City, Quebec, Canada. Located within the Laurentide-Onatchiway region of Quebec (B.1a), Forêt Montmorency (FM) is classified as a wet boreal forest, receiving 1583 mm of mean annual precipitation (Rowe 1972; Environment Canada, 2015) (Figure 1). The mean annual temperature (MAT) is 0.36°C, based on climatic normals from 1961 - 2010 (Environment Canada, 2015). Stands are dominated by balsam fir (*Abies balsamea* (L.) Mill.), with occasional white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP). Hardwoods represent less than 5% of basal area in mature stands, and include the following species: white birch (*Betula papyrifera* Marsh.), American mountain-ash (*Sorbus americana* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). The soils in FM are well-drained, and are mainly characterized as Ferro-Humic Podzols (Krasowski et al. 2010) (Figure 2).

Clear-cutting in Forêt Montmorency began in the early 1930s, and has continued on approximately 70-year rotation cycles. Laval University has been managing FM as an experimental research forest since 1964, with the property expanding from 66 km$^2$ to 412 km$^2$ in 2014. Insect outbreaks are the predominant source of natural disturbance in this region, as conditions have not been favourable for natural wildfires to occur at any appreciable frequency over the last 4500 years (Couillard et al. 2013). Spruce budworm (*Choristoneura fumiferana* (Clem.)) epidemics occur at intervals of ~ 40 years in eastern Quebec (Boulanger and Arseneault 2004). Stand mortality typically begins in the 5th year after the start of the outbreak, but may continue for up to 24 years (Gray & MacKinnon 2006; Dymond et al. 2010a). Historically, spruce budworm (SBW) outbreaks in this region have varied in severity, depending on the age of the stand and species composition, but generally are not characterized as stand-replacing events (MacLean and Erdle 1984; Royama 1984). However, in recent years, climate change has made conditions more favourable for hemlock looper (*Lambdina fiscellaria*) epidemics, which are often stand-replacing events (Vallières et al. 2015).
Figure 1. Annual precipitation map for Quebec, with Forêt Montmorency located within the circled region (Gerardin and McKenney, 2001).

Figure 2. Soil profile from a pit in Forêt Montmorency. Photo credit: Jacques Morissette.
2.1.2 Experimental design

A chronosequence experimental design was used to establish plots in FM that have minimal variation in site conditions and disturbance history. Sites were selected to be consistent with regard to elevation, aspect, slope, position on slope, drainage type, and soil properties. All chronosequence sites have been managed with stem-only harvesting over a 77-year time span, beginning in 1933 (Figure 3). The year of harvest was determined through a combination of forestry records, management plans, and aerial photographs. Similarly, these methods were used to ensure that the harvesting intensity and species composition were relatively similar over time, and that sites were not differentially impacted by insect infestations.

**Figure 3.** Chronosequence plots illustrating ecological succession in Forêt Montmorency, with years corresponding to the last harvest, and 1933 representing year-77 of the sequence.
All plots were established using a protocol developed by the Laurentian Forestry Centre (LFC), “Guidelines: Establishing permanent plots for monitoring the environmental effects of forest biomass harvesting” (Thiffault et al. 2011). This protocol is based on the National Forestry Inventory (NFI) ground sampling guidelines, with slight modifications to better suit this region of boreal Quebec (NFI 2008). The chronosequence is comprised of 42 plots, which were all subjected to stem-only harvesting at various points in time. Eighteen of these plots were established in sites with homogenous ecological characteristics, with each plot representing a distinct harvesting year within the chronosequence (Figure 4). An additional 18 plots were established on one hillside, which were all initially harvested in 1943, and therefore represent year-67 in the chronosequence. Six of these 18 plots were re-harvested in 2010 (representing year-0).

**Figure 4.** Experimental design for the chronosequence field study in Forêt Montmorency, Quebec. All samples were collected in 2010.

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<td>Time since disturbance (yrs)</td>
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<td>Plots (n)</td>
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2.1.3 Sampling procedure

Sampling of forest carbon pools was conducted within circular plots (radius 20 m) using the LFC protocol (Thiffault et al. 2011) (see Table 1 for details regarding empirical pool divisions). Two transects were established perpendicular to the center of the main plot, using a table of random numbers to determine the bearing of the first transect. Coarse woody debris was measured over both 40 m transects, and small woody debris was measured in the first and last 5-meter sections of each transect. Woody debris (WD) diameters were measured perpendicular to the intersection point and decomposition class was recorded for both size classes. Buried WD (downed woody debris) was measured if at least 50% of the surface was exposed. Within the main plot, two concentric sub-plots were established to measure large trees (> 9 cm DBH), as well as small trees.
(≤ 9 cm DBH), with plot radius of 11.28 m and 3.99 m, respectively. DBH, species, and state (live or dead) were recorded for all trees, and an average height was determined using measurements from three representative large trees. Heights of broken snags were estimated in order to account for missing volume in the volume-to-biomass conversion equations (Lambert et al. 2005). Stumps were also measured in the smaller sub-plot, and species, decomposition class, height, and top diameter (inside bark) were recorded for each individual.

Soil samples were taken from six stations (20 x 20 cm area) within each plot. Fine woody debris (FWD) and litter were collected from the surface of each quadrat, and FH samples (including fine and coarse roots, buried woody debris, and other organic material) were collected to the depth of the Ae horizon. Ten mineral samples were taken from the quadrats using a 25-cm-long, 5-cm internal diameter soil core. Samples were taken from depths of 0-15 (n=6), 15-35 (n=3), and 35-55 cm (n=1), where 0 cm marks the top of the Ae horizon. Please refer to the LFC protocol for a more detailed description of sampling and data compilation procedures (Thiffault et al. 2011).

2.1.4 Data compilation and laboratory procedures

Field data for trees, stumps, and woody debris included species classifications of “unknown”, “generic HW” and “generic SW”. In order to more accurately estimate C stocks in each pool, a system for allocating unknown and generic species was developed, based on stand composition, which used species-specific decay classes in carbon calculations. Species recorded as ‘unknowns’ were allocated to either HW or SW pools based on the ‘known’ proportion of HW and SW individuals. The same procedure was used for unknown woody debris and stumps.

Stumps were also allocated within appropriate diameter classes for HW and SW pools (4-12 cm for HW, > 12 cm for SW). All unknowns allocated to SW pools (and generic softwoods) were treated as balsam fir, and those allocated to HW pools (and generic hardwoods) were treated as white birch, because these were the leading SW and HW species in the stand.

Aboveground live and dead tree biomass was allocated based on species and DBH into wood, bark, branches, and foliage based NFI biomass equations (Lambert et al. 2005). Biomass of woody debris and stumps was calculated by assigning decay classes to dead wood densities (NFI 2008). FWD and litter samples were dried at 55°C until a stable weight was reached. All carbon
pools, with the exception of FH and mineral soil pools, were determined by multiplying oven-dried biomass by a factor of 0.5 (Lamlom and Savidge, 2003).

FH and mineral samples were passed through a 2 mm sieve, and both the fine earth fraction and coarse material (roots, buried wood, and other organic material) were oven-dried at 55°C for 2 days. Samples of FH and mineral horizons from the 18 plots harvested in 1943 were processed for C analysis using a LECO TruMac CNS combustion analyzer, using the LECO corporation method (2003). Loss on Ignition (LOI) analysis was used to estimate carbon concentration for the remaining chronosequence plots. After determining the correlation between LOI and LECO methods, LOI results for organic and mineral soil were multiplied by a factor of 2 and 0.6595, respectively, to convert LOI values to carbon concentrations.

2.1.5 Statistical Analyses

Carbon stocks (Mg C ha\(^{-1}\)) were quantified over the 77-year (1933-2010) chronosequence, where the explanatory variable was time since disturbance (TSD). TSD was calculated as the sampling year (2010) minus the harvesting year. In this thesis, TSD, or the number of years following stem-only harvest, will be expressed as year-x. Although the chronosequence extended to year-77, the replication at year-0 and year-67 allowed for determination of significant change over the rotation period. Therefore, year-0 and year-67 were used as the end-points to compare C stocks (means and standard error) over the length of the chronosequence (Figure 4). References to C stocks at stand maturity are based on data from year-67, which was a sufficient time span to represent one full rotation cycle.

C stock data was assumed to be normally distributed. Second order polynomial regressions were fitted to assess trends over time, and to estimate coefficients of determination (R\(^2\)) and p-values. Bartlett’s test was used to assess the homogeneity of variances at year-0 and year-67, the results of which informed the two-sample \(t\)-test assumptions (where \(p\)-values ≤ 0.05 signified unequal variance). Welch’s two-sample \(t\)-tests were used to determine if the difference in carbon stock averages at each point in time were statistically significant, and means and standard error at year-0 and year-67 were calculated for each pool. Statistical analyses were conducted using R, version 0.98.501 (R Core Team, 2014).
Table 1. Description of empirical pools based on sampling procedure in LFC protocol. These pools are divided into subtotal pools and compiled into ecosystem pools based on CBM-CFS3 pool definitions (see Table 3 for correspondence between empirical and modelled pools).

<table>
<thead>
<tr>
<th>Empirical Pools</th>
<th>Subtotal pools</th>
<th>Ecosystem pools</th>
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</thead>
<tbody>
<tr>
<td>Large live trees&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>Stemwood (large stems + bark)</td>
<td>AG</td>
</tr>
<tr>
<td>(height ≥ 1.3 m, DBH ≥ 9 cm)</td>
<td>Other wood (large and small tree branches, small stems + bark)</td>
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<tr>
<td>Small trees&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>Foliage (large and small tree foliage)</td>
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<tr>
<td>(height ≥ 1.3 m, DBH &lt; 9 cm)</td>
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<tr>
<td>Coarse roots&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
<td>BG</td>
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<tr>
<td>Fine roots&lt;sup&gt;c&lt;/sup&gt;</td>
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<tr>
<td>Large snags&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>Snag stemwood (large stems + bark)</td>
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<tr>
<td>(height ≥ 1.3 m, DBH ≥ 9 cm)</td>
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<td></td>
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<tr>
<td>Small snags&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>Snag other wood (branches, &amp; small stems + bark)</td>
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<tr>
<td>(height ≥ 1.3 m, DBH &lt; 9 cm)</td>
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<tr>
<td>Stumps&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>(Height &lt; 1.3 m, diameter ≥ 4 cm)</td>
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<tr>
<td>Coarse woody debris (10 cm)</td>
<td>Woody debris</td>
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<tr>
<td>Small woody debris (1.1 – 10 cm)</td>
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<td>Fine woody debris (≤ 1 cm)</td>
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<tr>
<td>L horizon (foliar litter)</td>
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<tr>
<td>FH horizon</td>
<td>Coarse FH fraction&lt;sup&gt;d&lt;/sup&gt;</td>
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<tr>
<td>Mineral horizon (fine earth fraction)</td>
<td>Fine FH fraction &lt;sup&gt;;&lt;/sup&gt; Fine fraction &lt;sup&gt;;&lt;/sup&gt; Fine SOM</td>
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<tr>
<td>Dead fine and coarse roots in mineral</td>
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<tr>
<td>horizon</td>
<td>Not measured&lt;sup&gt;e&lt;/sup&gt;</td>
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<sup>a</sup> All live biomass and dead standing wood were also divided by species (HW and SW)

<sup>b</sup> Subtotal pools (stems, branches, foliage and bark) were divided using equations from Lambert et al. (2005)

<sup>c</sup> Coarse and fine live roots were not measured in the field, but quantified using empirical aboveground biomass estimates in the Li et al. (2003) equations

<sup>d</sup> Coarse FH fraction was sampled empirically, but was not included in and compiled ecosystem pools or the comparison analysis, as it is not modelled in CBM-CFS3

<sup>e</sup> The LFC protocol was not adequate for sampling dead roots, and therefore these pools are excluded from ecosystem total estimate
2.2 Model Evaluation Methods

2.2.1 Overview

The Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) is a stand and landscape-level model designed to predict forest dynamics and carbon cycling following both natural and anthropogenic disturbances (Kurz et al. 2009). The CBM-CFS3 tracks carbon stocks and stock changes in annual time-steps, using empirical yield curves, forecast and historical disturbance events, stand dynamics, and spatially referenced forest inventory data. This information was integrated and imported into the model in files formatted for the CBM Standard Import Tool, including files representing age classes, disturbance types, classifiers and values, forest inventory, growth and yield curves, transition rules, and disturbance events.

The growth rate in live tree biomass pools was estimated by user-specified growth and yield curves, which predict gross merchantable volume over time (Kurz et al. 2009). Merchantable volume was converted to aboveground and belowground biomass using equations developed by Boudewyn et al. (2007) and Li et al. (2003), respectively. The model uses a soil carbon pool initialization process called MAKELIST to bring all soil DOM pools to equilibrium before simulation through a series of iterations of growth and mortality of the inventory. This process employs the user-provided inventory data, growth and yield curves, regional climate data, decay parameters, historic disturbance information, a natural stand-replacing disturbance interval specific to the chosen spatial unit (a combination of administrative boundary (province or territory), and terrestrial ecozone), and disturbance matrices. Disturbance matrices dictate the carbon transfers associated with each disturbance type and spatial unit (Kurz et al. 2009). For a detailed description of model assumptions and parameters, and import data requirements, refer to Kurz et al. (2009) and Kull et al. (2014).

2.2.2 CBM-CFS3 simulations

CBM-CFS3 simulations were designed to reflect forest dynamics and disturbance history as accurately as possible for Forêt Montmorency (FM), in order to compare field and modelled trends for 10 live biomass pools and 9 DOM pools. The method described below is specific to the CBM-CFS3 simulation used in this study, which is considered to be the most accurate representation of historical stand dynamics in FM.
Biomass pools

Yield curves for balsam fir and white birch, the dominant softwood and hardwood species in FM, were constructed from yield tables provided in Pothier and Savard (1998), which were modeled using data from across Quebec. It was assumed that trees in Forêt Montmorency were an average of 1 m in height immediately after harvest, due to the advanced regeneration in balsam fir stands in this region (David Pothier, personal communication). This assumption allowed for the comparison of empirical data, based on time since disturbance, with the curves from Pothier and Savard (1998), which use age at one meter in height as the independent variable. The balsam fir yield curves used to represent FM were selected from several station quality indices (SQI) based on empirical dominant height (m) measurements from FM chronosequence plots. In each chronosequence plot, three heights were recorded from live trees that were representative of the stand, in terms of height and DBH. In order to calculate dominant height, these empirical heights, as well as DBH measurements, were used in the following equation:

\[
H_d = 1.3 + \left[ \frac{\bar{D}_4}{\left( \frac{\bar{D}}{H-1.3} \right) + \beta_2 (D_4 - \bar{D})} \right]
\]

Where \( H_d \) is dominant height, \( D_4 \) is the average DBH of the four largest trees per plot, \( \bar{D} \) is the average DBH of all trees per plot, \( H \) is the average height per plot and \( \beta_2 \) is the coefficient for balsam fir (0.03735).

Dominant height was then used to determine the appropriate SQI for stands at age 50. An SQI of 16.5 m was selected, as it was the mid-point between the two yield curves that contained the majority of dominant heights measurements (Appendix 1, Figure 1A). Relative density was classified as ‘medium’, using the following equation:

\[
\rho_r = \frac{N_0}{\left[ \frac{D_{qt}}{10^{b_2}} \right]^{\frac{1}{\beta_2}}}
\]

Where \( \rho_r \) is relative density, \( N_0 \) is basal area per hectare, \( D_{qt} \) is the quadratic mean DBH per plot and \( \beta_1 \) and \( \beta_2 \) are the coefficients for balsam fir (2.790335 and 0.04599).

An average SQI (16.5 m) and ‘medium’ stand density were selected to determine the white birch yield curve, due to a lack of empirical data. Both yield curves were reduced from the original fully stocked volumes to reflect the species composition of mature stands (calculated by mean
basal area as 95.2 % softwood, 4.8% hardwood). Balsam fir yield curves (assuming fully stocked volume) are shown in Appendix 1, Figure 1B. Refer to Pothier and Savard (1998) for more details regarding yield curve calculations.

**Dead organic matter pools**

Carbon is transferred from living biomass to DOM pools through litterfall, tree mortality, and disturbance events (Kurz et al. 2009). Background turnover rates are based on user-specified spatial unit (Quebec -Boreal Shield East for this study). This spatial unit uses a mean annual temperature of 0.36 °C, which is the same as the average temperature recorded from the weather station at Forêt Montmorency from 1961-2010 (Environment Canada, 2015). Temperature influences decomposition rates for the selected spatial unit, but model parameters are not sensitive to precipitation, or the effects of climate change on forest C stocks, and relevant empirical climate data was consequentially not incorporated into the simulation (Kurz et al. 2009).

CBM-CFS3 uses a MAKELIST initialization process that requires the historical disturbance type for each stand in the inventory to be stand-replacing. Disturbance events occur at the interval associated with the spatial unit selected (every 125 years for the Boreal Shield East ecozone) (Kull et al. 2014). For the past 4500 years, conditions in FM have been too humid for natural wildfires, and SBW outbreaks are generally not stand-replacing (Couillard et al. 2013; Royama 1984). Therefore, employing the MAKELIST initialization process may not be an appropriate means of developing soil carbon pools. Instead, a pseudo-initialization modeling scenario was set up for the SBW simulation that employed modified non-stand-replacing disturbance types and matrices that better represented the partial disturbances caused by insect outbreaks.

The pseudo-initialization modeling scenario began with a nonforest stand with a default soil carbon value for the selected nonforest soil type (Podzol) being converted to forest via an afforestation event. The stand was then grown for 1,000 years on a single balsam fir yield curve that combined the volume of both balsam fir and white birch components. During this period, spruce budworm outbreaks were scheduled to occur every 40 years, the average interval for outbreaks in Quebec (Boulanger and Arsenault 2004). For the purposes of this simulation, the outbreaks were modeled to have stand mortality occur over a 5-year period. An alternating-impact pattern was also modeled for SBW-induced mortality, in order to reflect the decrease in
average stand age following an outbreak in a mature stand. Impact levels were based on estimated average mortality for mature stands (85%) and immature stands (37.5%) in Quebec (MacLean 1980). Disturbances matrices transferred carbon out of all softwood living biomass pools over the 5-year period, in equal increments (i.e., 17% or 7.5% per year). Transition rules were used to reset the age of the stand after the last year of each outbreak. Resetting the age was necessary in order to prevent the stand from ageing beyond the end of its growth curve in the model (causing biomass to plateau), and to better reflect changes to growth increment of the remaining trees following the removal of those killed by the spruce budworm. Determining the reset age after the fifth year of an outbreak was done through an iterative modeling process that essentially reset the age by matching the post-disturbance biomass level with a corresponding amount of biomass in an earlier time step (year).

After the 1,000 year “pseudo-initialization” period, the stand was harvested using a modified “97% Quebec clear-cut” disturbance, which best represented the intensity of stem-only harvesting in FM. It was also determined that this harvesting intensity would have been used throughout the chronosequence, despite changes in harvesting methods (Ken Armson, personal communication). The original physical transfer parameters in the matrix were modified as shown in Table 2.

The modified parameters were based on empirical data before and after the 2010 harvest. Data from the “merchantable stem wood + bark” pool aligned closely with the Quebec 97% standard (97.24 % harvested), which is why this disturbance was chosen as the baseline disturbance. Following this harvesting disturbance, the stand was transitioned to age zero, and began to grow using two component curves, one for hardwood (white birch), and one for softwood (balsam fir). Results for the stand from that point onwards could then be filtered by component species.

2.2.3 Compilation of carbon pools for field and model comparison

Definitions of CBM-CFS3 and empirical carbon pools (based on NFI ground sampling guidelines) were not always consistent, so “comparison C pools” were compiled to assess the relationships between measured and modelled C estimates (Table 3). Aboveground biomass (AG) pools were directly comparable, as both modelled and measured pools define merchantable stemwood and snags as DBH ≥ 9 cm. Empirical AG biomass was allocated into component pools
using Lambert et al. (2005) tree-level DBH equations, which were scaled-up to the stand-level in CBM-CFS3 using Boudewyn et al. (2007) equations. In order to compare CBM-CFS3 DOM pools with empirical pools, the dead coarse roots had to be removed from the “aboveground fast” pool, because it was not possible to quantify dead roots using the NFI sampling protocol. Dead coarse roots were excluded from modelled estimates by subtracting the “belowground fast” pool from “aboveground fast”, which was possible as dead coarse roots in both the FH and mineral horizons were modelled using the same parameters (Shaw et al. 2014). This allowed for comparison with the compiled downed woody debris empirical pool. Dead fine roots were not observed in the L horizon, and for the purposes of this comparison, the L horizon pool is assumed to only include foliar litter. Dead fine roots in the mineral soil were also not quantifiable, and the belowground very fast pool was therefore removed from CBM-CFS3 data.

2.2.4 Statistical Analyses

Modelled carbon stocks were compared to the empirical averages at year-0 and -67 to assess the degree to which pools were over/underestimated, and determine if predictions fell within ± 2 SEs of the observed average carbon stocks (Mg C ha⁻¹). Similarity in carbon pool trends was assessed by evaluating the degree to which CBM-CFS3 simulations fell within the 95% confidence intervals of the second order polynomial regressions. In this study, the differences in estimates were determined by dividing the mean difference (modelled minus empirical), by the empirical mean, in order to express model under/over-estimation as a percentage of empirical observations. Using this convention, negative mean differences indicate model underestimation.
Table 2. Original and modified (in parentheses) C transfer parameters used for 97% Quebec clear-cut in CBM-CFS3 simulation. See Kurz et al. (2009) for details regarding decay rates and background transfer parameters, and Table 3 for a description of modelled pools.

<table>
<thead>
<tr>
<th>CBM-CFS3 pool</th>
<th>Transferred C (% Mg C ha(^{-1}))</th>
<th>Pool receiving transfer</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW stemwood</td>
<td>0 (3)</td>
<td>SW stemwood Medium Forest products</td>
</tr>
<tr>
<td></td>
<td>3 (6)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>97 (91)</td>
<td></td>
</tr>
<tr>
<td>SW other wood</td>
<td>0 (3)</td>
<td>SW other wood SW AG fast</td>
</tr>
<tr>
<td></td>
<td>100 (97)</td>
<td></td>
</tr>
<tr>
<td>SW foliage</td>
<td>0 (3)</td>
<td>SW foliage SW AG very fast</td>
</tr>
<tr>
<td></td>
<td>100 (97)</td>
<td></td>
</tr>
<tr>
<td>SW fine roots</td>
<td>0 (3)</td>
<td>SW fine roots SW AG very fast</td>
</tr>
<tr>
<td></td>
<td>50 (48.5)</td>
<td>SW BG very fast</td>
</tr>
<tr>
<td></td>
<td>50 (48.5)</td>
<td></td>
</tr>
<tr>
<td>SW coarse roots</td>
<td>0 (3)</td>
<td>SW coarse roots SW AG fast</td>
</tr>
<tr>
<td></td>
<td>50 (48.5)</td>
<td>SW BG fast</td>
</tr>
<tr>
<td></td>
<td>50 (48.5)</td>
<td></td>
</tr>
<tr>
<td>HW stemwood</td>
<td>0 (39)</td>
<td>HW stemwood Medium Forest products</td>
</tr>
<tr>
<td></td>
<td>3 (61)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>97 (0)</td>
<td></td>
</tr>
<tr>
<td>HW other wood</td>
<td>0 (39)</td>
<td>HW other wood Medium</td>
</tr>
<tr>
<td></td>
<td>100 (61)</td>
<td></td>
</tr>
<tr>
<td>HW foliage</td>
<td>0 (39)</td>
<td>HW foliage HW AG very fast</td>
</tr>
<tr>
<td></td>
<td>100 (61)</td>
<td></td>
</tr>
<tr>
<td>HW fine roots</td>
<td>0 (39)</td>
<td>HW fine roots HW AG very fast</td>
</tr>
<tr>
<td></td>
<td>50 (30.5)</td>
<td>HW BG very fast</td>
</tr>
<tr>
<td></td>
<td>50 (30.5)</td>
<td></td>
</tr>
<tr>
<td>HW coarse roots</td>
<td>0 (39)</td>
<td>HW coarse roots HW AG fast</td>
</tr>
<tr>
<td></td>
<td>50 (30.5)</td>
<td>HW BG fast</td>
</tr>
<tr>
<td></td>
<td>50 (30.5)</td>
<td></td>
</tr>
<tr>
<td>Snag stems (SW and HW)</td>
<td>0 (13)</td>
<td>Snag stems Medium</td>
</tr>
<tr>
<td></td>
<td>100 (87)</td>
<td></td>
</tr>
<tr>
<td>Snag branches (SW and HW)</td>
<td>0 (13)</td>
<td>Snag branches (SW and HW) AG fast</td>
</tr>
<tr>
<td></td>
<td>100 (87)</td>
<td>(SW and HW)</td>
</tr>
</tbody>
</table>
Table 3. Correspondence between CBM-CFS3 modelled C pools and empirical C pools, with “Ecosystem C pools” representing pools used in the field and model comparison study.

<table>
<thead>
<tr>
<th>Ecosystem C pool</th>
<th>CBM-CFS3 C pool</th>
<th>Empirical C pools</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Live biomass</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stemwood</td>
<td>Merchantable + bark (SW or HW)</td>
<td>Large live trees (stem + bark) (^ab)</td>
</tr>
<tr>
<td>Other wood</td>
<td>Other wood + bark (SW or HW)</td>
<td>Large live tree branches + small live trees (stem + branches + bark) (^b)</td>
</tr>
<tr>
<td>Foliage</td>
<td>Foliage (SW or HW)</td>
<td>Large tree foliage + small tree foliage (^ab)</td>
</tr>
<tr>
<td>Fine roots</td>
<td>Fine roots (SW or HW) (^c)</td>
<td>Live fine roots (^b)</td>
</tr>
<tr>
<td>Coarse roots</td>
<td>Coarse roots (SW or HW) (^c)</td>
<td>Live coarse roots (^b)</td>
</tr>
<tr>
<td><strong>Standing dead wood</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snag stemwood</td>
<td>Snag stems DOM (SW or HW) (^b)</td>
<td>Large snags (stem + bark) (^ab)</td>
</tr>
<tr>
<td>Snag other wood</td>
<td>Snag branches DOM (SW or HW) (^b)</td>
<td>Branches &amp; small snag stemwood + bark (^b)</td>
</tr>
<tr>
<td><strong>Woody debris</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CWD</td>
<td>Medium DOM</td>
<td>CWD (&lt; 10 cm)</td>
</tr>
<tr>
<td>SWD, FWD &amp; stumps</td>
<td>Aboveground fast DOM</td>
<td>SWD (1.1 – 10 cm), FWD (&lt; 1 cm), &amp; stumps</td>
</tr>
<tr>
<td><strong>LFH and Mineral horizons</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>Aboveground very fast DOM</td>
<td>L horizon (foliar litter)</td>
</tr>
<tr>
<td>FH</td>
<td>Aboveground slow DOM</td>
<td>Fine FH fraction</td>
</tr>
<tr>
<td>Mineral soil</td>
<td>Belowground slow DOM (^c)</td>
<td>Fine fraction</td>
</tr>
<tr>
<td>Dead fine roots (not measured)</td>
<td>Belowground very fast DOM</td>
<td>Not measured (^f)</td>
</tr>
<tr>
<td>Dead coarse roots (&quot;&quot;&quot;)</td>
<td>Belowground fast DOM</td>
<td>Not measured (^f)</td>
</tr>
</tbody>
</table>

Empirical pools are based on NFI ground sampling guidelines; please refer to field methods for more detail on pool classification.

\(^ab\) Merchantability in CBM-CFS3 is defined as stemwood with DBH ≥ 9 cm, which is consistent with NFI criteria (refer to field methods for plot sampling procedures).

\(^b\) Empirical aboveground biomass was divided into component pools using Lambert et al. (2005) equations.

\(^c\) CBM-CFS3 aboveground biomass was divided into component pools using Boudewyn et al. (2007) equations.

\(^d\) Comparison method where Li et al. (2003) equations were used to derive live root pools from empirical total aboveground biomass data. This method is used for comparison with CBM-CFS3 biomass pools only.

\(^e\) CBM-CFS3 measures carbon in the mineral soil to a depth of 1 m, while empirical measurements only sampled to a depth of 55 cm.

\(^f\) Coarse and fine roots in the mineral soil were not quantified in empirical sampling procedure, and belowground fast and very fast pools were therefore removed from modelled total DOM and total ecosystem estimate.
Chapter 3: Results

Estimates of empirical and modelled carbon pools

3.1 Overview

Carbon pools in FM were quantified in chronosequence plots, and evaluated both in terms of C stocks following harvest and at stand maturity, as well as C dynamics over time. The main ecosystem pools -- live biomass, dead standing wood, woody debris & stumps, and soil -- accounted for 34, 4, 3, and 59% of total ecosystem carbon in year-67, respectively (Figure 5). The largest C stocks in year-67 were found in the soil pool (average of 163.16 Mg C ha\(^{-1}\)) and live biomass pool (94.79 Mg C ha\(^{-1}\)) (Table 4).

![Ecosystem carbon pools in Forêt Montmorency](image)

**Figure 5.** Carbon stocks for the main ecosystem carbon pools (top to bottom: live tree biomass, standing deadwood, downed woody debris, and soil), stacked to reflect total ecosystem carbon over the 77-year chronosequence in FM. Pool proportions are based on empirical second order polynomial regression equations.
Table 4. Mean (SE) of C stocks (Mg C ha\(^{-1}\)) in year-0 and year-67 of the stem-only harvesting chronosequence. Asterisks denotes significance of two sample T-test results, 95% CI (*\(p < 0.1\), **\(p < 0.05\), ***\(p < 0.01\), and ****\(p < 0.001\)).

<table>
<thead>
<tr>
<th>C Pool</th>
<th>Year-0</th>
<th>Year-67</th>
<th>p-value</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stemwood (HW)</td>
<td>1.27 (0.25)</td>
<td>3.13 (0.75)</td>
<td>0.001</td>
<td>****</td>
</tr>
<tr>
<td>Stemwood (SW)</td>
<td>0.15 (0.10)</td>
<td>51.76 (4.13)</td>
<td>7.74e-14</td>
<td>****</td>
</tr>
<tr>
<td>Other wood (HW)</td>
<td>0.73 (0.33)</td>
<td>2.03 (0.57)</td>
<td>0.043</td>
<td>**</td>
</tr>
<tr>
<td>Other wood (SW)</td>
<td>0.21 (0.12)</td>
<td>10.21 (0.54)</td>
<td>2.58e-13</td>
<td>****</td>
</tr>
<tr>
<td>Foliage (HW)</td>
<td>0.16 (0.05)</td>
<td>0.40 (0.05)</td>
<td>0.017</td>
<td>**</td>
</tr>
<tr>
<td>Foliage (SW)</td>
<td>0.09 (0.05)</td>
<td>8.45 (0.30)</td>
<td>6.74e-16</td>
<td>****</td>
</tr>
<tr>
<td><strong>AG biomass</strong></td>
<td>2.60 (0.71)</td>
<td>75.87 (2.83)</td>
<td>5.13e-16</td>
<td>****</td>
</tr>
<tr>
<td>Fine roots (HW)</td>
<td>0.65 (0.09)</td>
<td>0.99 (0.08)</td>
<td>0.028</td>
<td>**</td>
</tr>
<tr>
<td>Fine roots (SW)</td>
<td>0.04 (0.02)</td>
<td>1.97 (0.02)</td>
<td>2.20e-16</td>
<td>****</td>
</tr>
<tr>
<td>Coarse roots (HW)</td>
<td>1.21 (0.21)</td>
<td>2.32 (0.23)</td>
<td>0.015</td>
<td>**</td>
</tr>
<tr>
<td>Coarse roots (SW)</td>
<td>0.06 (0.03)</td>
<td>13.64 (0.62)</td>
<td>5.83e-14</td>
<td>****</td>
</tr>
<tr>
<td><strong>BG biomass</strong></td>
<td>1.96 (1.17)</td>
<td>18.92 (0.33)</td>
<td>2.20e-16</td>
<td>****</td>
</tr>
<tr>
<td><strong>Live biomass</strong></td>
<td>4.56 (1.04)</td>
<td>94.79 (3.49)</td>
<td>2.76e-16</td>
<td>****</td>
</tr>
<tr>
<td>Snag stemwood (HW)</td>
<td>0.91 (0.38)</td>
<td>1.23 (0.22)</td>
<td>0.481</td>
<td>-</td>
</tr>
<tr>
<td>Snag stemwood (SW)</td>
<td>0.68 (0.22)</td>
<td>5.27 (0.94)</td>
<td>0.000</td>
<td>****</td>
</tr>
<tr>
<td>Snag other wood (HW)</td>
<td>0.38 (0.15)</td>
<td>1.63 (0.42)</td>
<td>0.011</td>
<td>**</td>
</tr>
<tr>
<td>Snag other wood (SW)</td>
<td>0.71 (0.28)</td>
<td>3.70 (0.54)</td>
<td>0.076</td>
<td>*</td>
</tr>
<tr>
<td><strong>Dead standing wood</strong></td>
<td>2.68 (0.52)</td>
<td>11.82 (1.44)</td>
<td>6.87e-06</td>
<td>****</td>
</tr>
<tr>
<td>Coarse woody debris ((&gt; 10 \text{ cm}))</td>
<td>4.26 (1.12)</td>
<td>1.43 (0.40)</td>
<td>0.006</td>
<td>***</td>
</tr>
<tr>
<td>Small woody debris ((1 &lt; \text{ SWD} \leq 10 \text{ cm}))</td>
<td>13.08 (0.52)</td>
<td>5.22 (0.38)</td>
<td>3.02e-10</td>
<td>****</td>
</tr>
<tr>
<td>Fine woody debris ((\leq 1 \text{ cm}))</td>
<td>4.36 (0.38)</td>
<td>0.57 (0.06)</td>
<td>0.000</td>
<td>****</td>
</tr>
<tr>
<td>Stumps (HW)</td>
<td>0.06 (0.04)</td>
<td>0.01 (0.01)</td>
<td>0.364</td>
<td>-</td>
</tr>
<tr>
<td>Stumps (SW)</td>
<td>1.31 (0.41)</td>
<td>0.24 (0.05)</td>
<td>6.12e-05</td>
<td>****</td>
</tr>
<tr>
<td><strong>Downed woody debris</strong></td>
<td>23.06 (1.36)</td>
<td>7.37 (0.44)</td>
<td>5.87e-11</td>
<td>****</td>
</tr>
<tr>
<td>L horizon</td>
<td>8.02 (1.45)</td>
<td>3.60 (0.26)</td>
<td>0.027</td>
<td>**</td>
</tr>
<tr>
<td>FH soil</td>
<td>NA</td>
<td>28.58 (1.33)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>LFH horizon</td>
<td>NA</td>
<td>32.18 (1.34)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>Mineral</td>
<td>NA</td>
<td>130.98 (9.23)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>LFH and mineral horizons</td>
<td>NA</td>
<td>163.16 (9.04)</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td><strong>Total ecosystem</strong></td>
<td>NA</td>
<td>278.51 (7.99)</td>
<td>NA</td>
<td></td>
</tr>
</tbody>
</table>

Hardwood (HW), Softwood (SW), above (AG) and belowground (BG), Main ecosystem pools are bolded

\(^{a}\) Belowground biomass was calculated using equations from Li et al. (2003) based on empirical AG biomass data

\(^{b}\) Debris classes are based on CBM-CFS3 definitions, as opposed to NFI definitions

\(^{c}\) Soil pools cannot be compared in T-tests, as plots were not re-sampled in year 0

\(^{d}\) Total ecosystem carbon is based on plots with complete data sets (n=12)
Empirical C stocks were compared with modelled predictions in order to evaluate agreement between estimates both in terms of initial and final C amounts, and trends over time. C dynamics following SOH were clearly portrayed by combining both HW and SW species components (Figures 5-11), since hardwoods represent a relatively minor contribution to C stocks (accounting for less than 5% of species composition in FM). Individual graphs of HW and SW C pools can be found in Appendix 1, Figures 2-7. In all graphs, chronosequence observations (filled circles) are fitted with 2nd order polynomial regressions (solid line), and 95% confidence intervals (dashed line). Modelled output (open circles) from the CBM-CFS3 simulation is plotted when applicable.

3.2 Total ecosystem carbon

Total ecosystem carbon increased significantly over the chronosequence ($p < 0.05$), reaching 278.51 Mg C ha$^{-1}$ by year-67 (Figure 6). CBM-CFS3 underestimated the total ecosystem carbon pool by only 7% at stand maturity, with estimates varying by 20 Mg C ha$^{-1}$ (Table 5). However, the model simulations fall outside of the 95% confidence interval from year-10 to 73. While empirical total ecosystem data showed a significant increase over time ($p < 0.05$), the predicted pool declines for nearly a decade after harvest. CBM-CFS3 predicted that total ecosystem carbon recovered to over 95% of pre-harvest levels by the end of the 77-year simulation. Although empirical pre-harvest carbon pools are unknown, the increase in total ecosystem carbon, as well as the relative agreement with modelled results, suggest that carbon pools recovered following stem-only harvesting in this rotation period.
Figure 6. Total ecosystem carbon in FM, based on complete plot data for the 19 C pools. Modelled output includes an additional 20 years of pre-harvest data, before the simulation began in year-0. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Table 5. Mean (SE) of C stocks (Mg C ha\(^{-1}\)) in year-0 and year-67 of the SOH chronosequence and CBM-CFS3 SBW simulation. See Table 3 for definitions of comparison pools.

<table>
<thead>
<tr>
<th>Comparison Pool</th>
<th>Measured (Year-0)</th>
<th>Modelled (Year-0)</th>
<th>% Difference(^a)</th>
<th>Measured (Year-67)</th>
<th>Modelled (Year-67)</th>
<th>% Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stemwood (HW)</td>
<td>1.27 (0.25)</td>
<td>0.00</td>
<td>-100</td>
<td>3.13 (0.75)</td>
<td>1.72</td>
<td>-45</td>
</tr>
<tr>
<td>Stemwood (SW)</td>
<td>0.15 (0.10)</td>
<td>1.49</td>
<td>893</td>
<td>51.76 (4.13)</td>
<td>44.81</td>
<td>-13</td>
</tr>
<tr>
<td>Other wood (HW)</td>
<td>0.73 (0.33)</td>
<td>0.00</td>
<td>-100</td>
<td>2.03 (0.57)</td>
<td>0.66</td>
<td>-67</td>
</tr>
<tr>
<td>Other wood (SW)</td>
<td>0.21 (0.12)</td>
<td>0.31</td>
<td>48</td>
<td>10.21 (0.54)</td>
<td>15.75</td>
<td>54</td>
</tr>
<tr>
<td>Foliage (HW)</td>
<td>0.16 (0.05)</td>
<td>0.00</td>
<td>-100</td>
<td>0.40 (0.05)</td>
<td>0.13</td>
<td>-68</td>
</tr>
<tr>
<td>Foliage (SW)</td>
<td>0.09 (0.05)</td>
<td>0.17</td>
<td>89</td>
<td>8.45 (0.30)</td>
<td>5.98</td>
<td>-29</td>
</tr>
<tr>
<td><strong>AG biomass</strong></td>
<td><strong>2.60 (0.71)</strong></td>
<td><strong>1.97</strong></td>
<td><strong>-24</strong></td>
<td><strong>75.87 (2.83)</strong></td>
<td><strong>69.04</strong></td>
<td><strong>-9</strong></td>
</tr>
<tr>
<td>Fine roots (HW)</td>
<td>0.65 (0.09)</td>
<td>0.01</td>
<td>-98</td>
<td>0.99 (0.08)</td>
<td>0.25</td>
<td>-75</td>
</tr>
<tr>
<td>Fine roots (SW)</td>
<td>0.04 (0.02)</td>
<td>0.18</td>
<td>350</td>
<td>1.97 (0.02)</td>
<td>1.75</td>
<td>-11</td>
</tr>
<tr>
<td>Coarse roots (HW)</td>
<td>1.21 (0.21)</td>
<td>0.01</td>
<td>-99</td>
<td>2.32 (0.23)</td>
<td>1.87</td>
<td>-19</td>
</tr>
<tr>
<td>Coarse roots (SW)</td>
<td>0.06 (0.03)</td>
<td>0.26</td>
<td>333</td>
<td>13.64 (0.62)</td>
<td>13.02</td>
<td>-5</td>
</tr>
<tr>
<td><strong>BG biomass</strong></td>
<td><strong>1.96 (1.17)</strong></td>
<td><strong>0.46</strong></td>
<td><strong>-77</strong></td>
<td><strong>18.92 (0.33)</strong></td>
<td><strong>16.89</strong></td>
<td><strong>-11</strong></td>
</tr>
<tr>
<td><strong>Total biomass</strong>(^b)</td>
<td><strong>4.56 (1.04)</strong></td>
<td><strong>2.43</strong></td>
<td><strong>-47</strong></td>
<td><strong>94.79 (3.49)</strong></td>
<td><strong>85.94</strong></td>
<td><strong>-9</strong></td>
</tr>
<tr>
<td>Snag stemwood (HW)</td>
<td>0.91 (0.38)</td>
<td>0.00</td>
<td>-100</td>
<td>1.23 (0.22)</td>
<td>0.14</td>
<td>-89</td>
</tr>
<tr>
<td>Snag stemwood (SW)</td>
<td>0.68 (0.22)</td>
<td>1.66</td>
<td>144</td>
<td>5.27 (0.94)</td>
<td>3.92</td>
<td>-26</td>
</tr>
<tr>
<td><strong>Total snag stemwood</strong></td>
<td><strong>1.60 (0.37)</strong></td>
<td><strong>1.66</strong></td>
<td><strong>4</strong></td>
<td><strong>6.50 (0.97)</strong></td>
<td><strong>4.06</strong></td>
<td><strong>-38</strong></td>
</tr>
<tr>
<td>Snag other wood (HW)</td>
<td>0.38 (0.15)</td>
<td>0.00</td>
<td>-100</td>
<td>1.63 (0.42)</td>
<td>0.04</td>
<td>-98</td>
</tr>
<tr>
<td>Snag other wood (SW)</td>
<td>0.71 (0.28)</td>
<td>0.06</td>
<td>-92</td>
<td>3.7 (0.54)</td>
<td>1.11</td>
<td>-70</td>
</tr>
<tr>
<td><strong>Total snag other wood</strong></td>
<td><strong>1.08 (0.31)</strong></td>
<td><strong>0.06</strong></td>
<td><strong>-94</strong></td>
<td><strong>5.32 (0.84)</strong></td>
<td><strong>1.15</strong></td>
<td><strong>-78</strong></td>
</tr>
<tr>
<td><strong>Total dead standing</strong></td>
<td><strong>2.68 (0.52)</strong></td>
<td><strong>1.72</strong></td>
<td><strong>-36</strong></td>
<td><strong>11.82 (1.44)</strong></td>
<td><strong>5.21</strong></td>
<td><strong>-56</strong></td>
</tr>
<tr>
<td><strong>CWD ( &gt; 10 cm)</strong>(^c)</td>
<td><strong>4.26 (1.12)</strong></td>
<td><strong>47.58</strong></td>
<td><strong>1017</strong></td>
<td><strong>1.43 (0.40)</strong></td>
<td><strong>15.86</strong></td>
<td><strong>1009</strong></td>
</tr>
<tr>
<td><strong>SWD, FWD &amp; stumps</strong></td>
<td><strong>18.80 (0.76)</strong></td>
<td><strong>10.15</strong></td>
<td><strong>-46</strong></td>
<td><strong>5.45 (0.41)</strong></td>
<td><strong>7.10</strong></td>
<td><strong>30</strong></td>
</tr>
<tr>
<td><strong>Total DWD</strong></td>
<td><strong>23.06 (1.36)</strong></td>
<td><strong>57.73</strong></td>
<td><strong>150</strong></td>
<td><strong>7.37 (0.44)</strong></td>
<td><strong>22.95</strong></td>
<td><strong>211</strong></td>
</tr>
<tr>
<td><strong>L horizon</strong></td>
<td><strong>8.02 (1.45)</strong></td>
<td><strong>9.83</strong></td>
<td><strong>23</strong></td>
<td><strong>3.60 (0.26)</strong></td>
<td><strong>8.21</strong></td>
<td><strong>128</strong></td>
</tr>
<tr>
<td><strong>FH soil</strong>(^d)</td>
<td>NA</td>
<td>34.64</td>
<td>NA</td>
<td>28.58 (1.33)</td>
<td>33.42</td>
<td>17</td>
</tr>
<tr>
<td><strong>LFI horizon</strong>(^d)</td>
<td>NA</td>
<td>44.46</td>
<td>NA</td>
<td>32.18 (1.34)</td>
<td>41.63</td>
<td>29</td>
</tr>
<tr>
<td><strong>Mineral</strong></td>
<td>NA</td>
<td>104.65</td>
<td>NA</td>
<td>130.98 (9.23)</td>
<td>102.94</td>
<td>-21</td>
</tr>
<tr>
<td><strong>Fine fraction (FH + mineral)</strong></td>
<td>NA</td>
<td>139.29</td>
<td>NA</td>
<td>159.56 (9.06)</td>
<td>136.36</td>
<td>-15</td>
</tr>
<tr>
<td><strong>LFIH and mineral horizons</strong>(^d)</td>
<td>NA</td>
<td>149.11</td>
<td>NA</td>
<td>163.16 (9.04)</td>
<td>144.57</td>
<td>-11</td>
</tr>
<tr>
<td><strong>Total ecosystem</strong>(^e)</td>
<td>NA</td>
<td>211.00</td>
<td>NA</td>
<td>278.51 (7.99)</td>
<td>258.67</td>
<td>-7</td>
</tr>
</tbody>
</table>

Hardwood (HW), softwood (SW), aboveground (AG), belowground (BG), downed woody debris (DWD), coarse, small, and fine woody debris (CWD), (SWD) & (FWD).

\(^a\) Differences are expressed as a percentage of empirical averages. Negative values indicate underestimation of C pools.

\(^b\) Total biomass was calculated using belowground biomass estimates derived from equations in Li et al. (2003).

\(^c\) Woody debris classes are based on CBM-CFS3 definitions, as opposed to NFI definitions.

\(^d\) Soil pools cannot be compared in t-tests, as plots were not re-sampled in year-0.

\(^e\) References to FH horizon include only the fine FH fraction.

\(^f\) Ecosystem totals based on plots with complete data.
3.3 Live biomass
Empirical estimates of live tree biomass pools, both above and belowground, all showed significant increases with forest age, with trends following truncated sigmoidal curves (Figure 7A-H). Total biomass plateaued near the end of the chronosequence at an average of 94.79 Mg C ha\(^{-1}\) in year-67 (Figure 7A). Softwood biomass pools (stemwood, other wood, foliage, and coarse & fine roots) also showed truncated sigmoidal increase, seeing as softwoods represent 94.8% of stand basal area (Appendix 1, Figure 3). Hardwood biomass pools increased for the first half of the chronosequence, after which they appeared to decrease. Despite downward concave shapes, the hardwood C pools still showed a statistically significant increase from year-0 to year-67 (Appendix 1, Figure 2; Table 5).

The CBM-CFS3 simulation predicted total live tree biomass C stocks to be 85.94 Mg C ha\(^{-1}\) in year-67, which was within 10% of the empirical mean (Table 5). CBM-CFS3 simulations of living biomass followed a sigmoidal curve shape, with a clear lag in stand development after harvest (Figure 7A-H). This lag may be partially attributable to the curve-smoothing algorithm in CBM-CFS3, which was used to fill in ages 0-20 in the imported yield curves. Data was unavailable in these years, as the observed stands were too young to reach a merchantable volume (Pothier and Savard 1998). Therefore, although curve shapes closely align after approximately one decade, the 10-year delay in modelled stand growth is probably contributing to systematic under-prediction of biomass C stocks. Modelled total biomass fell outside of the 95% CI from year-5 to 71 in the chronosequence (Figure 7A). All biomass pools were underestimated by CBM-CFS3 in year-67, with the exception of the SW other wood pool, which exceeded the empirical mean by a factor of 1.5 (Appendix 1, Figure 2B). Modelled predictions for all biomass pool after harvest were lower than empirical means, with CBM-CFS3 C stocks amounting to just over half of the observed total biomass in (year-0) (Table 5).

3.4 Standing dead wood
Dead standing wood represented relatively minor (4%) C pools in FM, but increased significantly as the stand reached maturity (2.68 to 11.82 Mg C ha\(^{-1}\)) (Table 4). Dead standing
Figure 7 (A-D). (A) Total live tree biomass, including stemwood, bark, branches, foliage, coarse roots, and fine roots. (B) Stemwood, bark, branches and foliage. (C) Stemwood & bark of trees ≥ 9 cm DBH. (D) Stemwood & bark of trees < 9 cm DBH, and branches of all trees. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 7 (E-H). (E) Foliage from large and small live trees. (F) Total belowground carbon, divided into (G) coarse and (H) fine root pools, which were calculated using Li et al. (2003) equations based on empirical estimates of total aboveground biomass. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
wood was divided into two sub-pools: 1) “Snag stemwood” (Large trees - stemwood + bark) and 2) “Snag other wood” (small trees - stemwood, bark, branches & large tree branches). The HW stemwood pool showed little variation over time (Appendix 1, 4A). The HW other wood followed a downward concave shape similar to that of live biomass HW pools (Appendix 1, Figure 2), which suggests that this pool was initially influenced by regenerating pioneer species, which were eventually out-competed by softwoods. Both SW snag stemwood and other wood increased significantly over time, with the latter increasing after an initial drop in C stocks after harvest (Appendix 1, Figure 5A-B).

Modelled estimates of total dead standing wood were underestimated by 56% in year-67. The modelled C stocks also were less than the empirical mean after harvest (by 36%), and fell outside the 95% CI after year-29 of the chronosequence (Table 5, Figure 8A). Despite the difference in predicted and observed C stocks, both curves follow a similar shape for the first half of the chronosequence, at which point they begin to diverge, with the slope of the empirical curve showing a more consistent increase.

Snag stemwood predictions were closely aligned; falling within the 95% CI until year-59, and the SW snag stemwood was within ± 2 SE of the empirical mean at year-67 (Figure 8B; Table 5). Divergences were more pronounced in the snag other wood pool, with modelled predictions only falling within the 95% confidence level for the first 12 years (Figure 8C). By year-67, empirical C stocks were almost 5 times greater than modelled. The snag other wood pool was also more dynamic in FM, compared to the relatively stable modelled predictions, which only varied by 1.1 Mg C ha⁻¹ over the course of the simulation. While the observed HW snag other wood pool peaked in the middle of the chronosequence, the SW pool decreased shortly after harvest, before exceeding post-harvest levels as the stand matured (Appendix 1, Figure 4B, 5B). This initial decrease in dead standing wood in FM, which is likely attributable to decay from higher post-harvest levels, was not apparent in CBM-CFS3 simulations. CBM-CFS3 predicted the SW snag other wood pool with weak sigmoid curve, which was within the 95% CI until year-52. However, the slopes within this period were opposite, indicating that the parameters driving modelled C transfers in the snag other wood pool were based on a different theoretical construct than is operating at FM.
**Figure 8A.** Total standing dead wood, including stemwood, branches and bark from large (≥ 9 cm DBH) and small (< 9 cm DBH) trees.

**Figure 8 (B & C).** (B) Snag stemwood & bark from large trees (≥ 9 cm DBH). (C) Snag stemwood and bark from small trees (< 9 cm DBH), and snag branches. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
3.5 Downed woody debris

Downed woody debris (DWD) was also a relatively minor pool (3%) in terms of total ecosystem C stocks observed in FM. Total DWD dropped from 23.06 to 7.37 Mg C ha\(^{-1}\) over the course of the chronosequence (Table 4). SWD was the largest of the three classes of WD in year-67, exceeding C stocks in CWD and FWD by a factor of 3.7 and 9.2 (Table 4). All DWD pools tended to follow upward concave curves (Figure 9A-G), with high inputs of debris at the beginning of the chronosequence, followed by gradual decay, and eventually increasing again (after about four decades), with natural stand mortality. It was possible to divide WD (> 3 cm) into HW and SW pools (Appendix 1, Figure 6), and results indicated that although both pools declined following harvest, only SW began to recover as the stand reaches maturity. HW stumps did not change significantly over time, but softwood stumps declined significantly after harvest, with signs of recovery after six decades with natural stand development (Appendix 1, Figure 7).

Measured and modelled C stocks showed the greatest divergences in DWD pools (Figure 9A-G). CBM-CFS3 predictions overestimated the mean of total DWD in year-0 and year-67, by a factor of 2.4 and 3.1, respectively (Table 5). Modelled CWD accounted for 82% of the modelled total DWD in year-0, and was predicted to be over 11 times greater than empirical CWD mean, which represented the largest discrepancy between measured and modeled pools in the CBM-CFS3 comparison. Although the empirical CWD pool began to increase in the 5\(^{th}\) decade of chronosequence (a trend which was not captured by the model within the simulation period), the model prediction still overestimated C stocks by the same proportion (Figure 9C).

Empirical and modelled estimates for SWD, FWD & stumps pool (aboveground fast DOM) were more closely aligned than those of CWD, both in terms of initial and final C stocks, and curve shape (Figure 9D). Unlike CWD, which fell outside of the 95% CI for the entire simulation, the predicted aboveground fast pool was within the CI from year-21 to 29, and again after year-70. In year-0, the CBM-CFS3 underestimated aboveground fast C stocks by 46%, but by year-67, the pool was overestimated by 30% (Table 5). This indicates that while C transfers to aboveground fast DOM allowed the pool to begin to recover within the simulated period, the trends in recovery were not coinciding. Even though this pool showed more agreement in terms of initial C stocks and transfers over time, the modelled predictions only fell within the 95% CI.
Figure 9 (A-D). Downed woody debris & L horizon. (A) Small woody debris (>1 cm, ≤ 10 cm). (B) Fine woody debris (≤ 1 cm), collected at soil stations, above L horizon. (C) Stumps (height < 1.3 m, top diameter ≥ 4 cm, measured inside bark). (D) L horizon, foliar litter above FH soil horizon. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 9 (E-H). (E) Small woody debris (>1 cm, ≤10 cm). (F) Fine woody debris (≤1 cm), collected at soil stations, above L horizon. (G) Stumps (height < 1.3 m, top diameter ≥4 cm, measured inside bark). (H) L horizon, foliar litter above FH soil horizon. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
from year-20 to 28 and after year-70. This suggests that the slight recovery in modelled aboveground fast pool was not sufficient to compensate for the more pronounced drop in observed pool, which occurred before inputs are renewed with natural stand death.

3.6 LFH and mineral soil horizons

The total soil pool (LFH and mineral soil horizons) reached an average of 163.13 Mg C ha\(^{-1}\) by year-67 (Table 4). Modelled estimates of the total soil pool gradually approached the empirical mean (reaching 89% by year-67) but for the majority of the simulation (between year-5 and 72) it fell outside of the 95% CI (Figure 10A). While the empirical pool decreased slightly, the trend was not significant over time \( (p = 0.194) \). The modeled pool was also relatively stable, although there was a predicted drop in C stocks for the first decade following harvest, which was eventually recovered towards the end of the simulation period.

Of the empirical soil C pools, only the L horizon showed a significant trend over time, increasing in the second half of the chronosequence, similar to trends observed in DWD pools (Figure 9H). CBM-CFS3 predictions for the L horizon fell within the 95% CI between year-2 and 5, and again between year-15 and 21, but by year-67, the model overestimated the pool by a factor of 2.3. The FH horizon showed the least variation over time of all carbon pools sampled \( (R^2 = 0.008) \) (Figure 10D). Modelled predictions of the FH and LFH pools were also relatively stable, although the CBM-CFS3 simulation showed a slight accumulation of C in the FH horizon after harvest (Figure 10C,D). Modelled estimates of the FH horizon were within the 95% CI for the majority of simulation period, but the model consistently overestimated C stocks (by 17% in year-67). In contrast, CBM-CFS3 predictions of the mineral pool were less accurate in terms of the magnitude of the C stocks, which were underestimated by 21% in year-67 (Figure 10B). The mineral soil pool showed the most variability of all empirical pools, with a range of almost 110 Mg C ha\(^{-1}\) in year-67. In CBM-CFS3, and the modelled mineral soil pool was actually predicted to be one of the most stable pools over time, varying by less than 2 Mg C ha\(^{-1}\) over the course of the simulation period.
Figure 10 (A-D). (A) Total soil, including the LFH horizon and mineral horizon. B) Mineral soil, measured to 55 cm below the Ae horizon. C) LFH horizon, including the foliar litter overlaying organic material in the FH soil horizon. (D) FH horizon. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
By excluding mineral soil pool from the ecosystem total, modelled estimates fell within the 95% CI after year-35 of the simulation (Figure 11). This indicates that the magnitude of the model underestimation of the mineral horizon (over 28 Mg C ha\(^{-1}\) in year-67) is responsible for much of the underestimation of total ecosystem C (Figure 6).

**Figure 11.** Total ecosystem carbon, excluding the mineral soil carbon pool. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Chapter 4: Discussion

4.1 Overview

The purpose of this study was 1) to quantify carbon pools in FM and evaluate trends over time following stem-only harvesting, and 2) to compare empirical pools to those predicted in CBM-CFS3 simulations. While the lack of pre-harvest data from FM limits the ability to draw conclusions regarding the recovery of C pools over time, it is possible to assess the dynamics of C pools within this specific rotation period, and evaluate the ability CBM-CFS3 to predict these dynamics. This study was designed to use a robust sampling procedure in order to estimate average C stocks, as well as the variability inherent in forest ecosystems. Nineteen carbon pools were sampled in FM, in an effort to provide an accurate quantification of total ecosystem C, as well as assess the unique trends in individual C pools.

In this discussion, both empirical and modelled estimates will be compared against those reported in the literature for forests with similar species composition and/or environmental conditions. Potential improvements to both the field and modelling methodology will be discussed, as well as the challenges associated with comparing ecosystem carbon pools derived from stand-level empirical data with modelled pools based on ecozone and provincial forest inventory data. Ultimately, the intent of this discussion is to place the results of this research in the context of international debates regarding the feasibility and sustainability of forest bioenergy operations as a means for climate change mitigation.

4.2 Total ecosystem carbon

Total ecosystem carbon in Forêt Montmorency increased significantly over time, reaching 279 Mg C ha\(^{-1}\) at stand maturity. This estimate exceeded values reported in NFI ground plot studies for both balsam fir forests and the Canada’s Boreal Shield East ecozone, which were estimated to be 138.5 Mg C ha\(^{-1}\) and 197 Mg C ha\(^{-1}\) (Shaw et al. 2014; Stinson et al. 2011). Kurz et al. (2013) found that C stocks in managed boreal forests did not vary much between ecozones, and were distributed as follows: 28% in live biomass, 10% in deadwood, 23% in litter, 39% in SOM (25%,
9%, 24% & 43% in the Boreal Shield East ecozone). These estimates vary only slightly from empirical measurements in FM, which when grouped accordingly, account for 34%, 7%, 12% and 47% of total ecosystem C stocks. Compared to global forest C stock averages, boreal estimates have higher proportion of carbon stored in soil and litter, and less in live biomass pools, which is generally expected, due to colder temperatures reducing both decomposition and growth rates in boreal forests (Chen et al. 2013).

Although the Canada-wide estimates from Kurz et al. (2013) and Stinson et al. (2011) use an NFI sampling protocol, which is similar to that used in the field study in FM, the results of this study indicate that FM cannot appropriately be represented by averages for the Boreal Shield East Ecozone. The higher ecosystem C stocks observed in FM at year-67 is particularly noteworthy considering that the Canada-wide estimates are primarily based on NFI plots in managed forests, for which the average age is estimated to be 92 (Böttcher et al. 2008; Stinson et al. 2011; Shaw et al. 2014). Estimates of C pools in FM are more similar to those of forests with similar species composition, climate, and time since disturbance. For example, Hoover et al. (2012) estimated total ecosystem C stocks for softwood stands in New England to be 267 (± 11.2) Mg C ha$^{-1}$, which is within ± 1 SE from the observed value in FM.

The CBM-CFS3 estimate of total ecosystem carbon was within 7% of the empirical average in year-67, but the model predicted an initial drop in C stocks that was not observed in FM. This decline was a result of the decomposition of woody and foliar debris after harvest, and although this trend was observed in the field, the magnitude of the decrease was not sufficient to offset the initial increases in biomass pools. Taylor et al. (2008) also found CBM-CFS3 to predict a decline in total ecosystem C stocks for the first 20 years, which was not supported by the empirical data.

Model simulations estimated that stem-only harvest reduced total ecosystem C by approximately 60 Mg C ha$^{-1}$, which, by end of the simulation, was almost 90% recovered. While it is not possible to determine if total ecosystem C in FM recovered to pre-harvest levels based on empirical data, the reasonable agreement between field and modelled data by the end of the chronosequence helps to validate CBM-CFS3 predictions of recovery of pre-harvest C stocks.

The increase in total ecosystem carbon can be attributed to increasing C stocks in live tree biomass and dead standing wood, the eventual recovery of downed woody debris, and the
relative stability of soil C. The fact that these pools have reached levels comparable with those of mature forests by the end of the chronosequence signifies that stem-only harvesting is not threatening C stocks within this first rotation period. Based on these results, it seems possible that incorporating bioenergy systems into existing SOH operations in this region (using sawmill or pulp mill residues) could be beneficial in terms of climate change mitigation, in the sense that forest C stocks are recovering after disturbance, and atmospheric C emissions could be reduced by contributing to fossil fuel displacement. However, additional research is required to ensure that SOH would not jeopardize forest C stocks over multiple rotations. Furthermore, it is necessary to assess the long-term implications of SOH on other aspects forest sustainability, such as susceptibility to natural disturbances, since the research conducted in FM is focused only on the balance of biogenic C stocks.

4.3 Live biomass

Total live biomass C stocks were within the range of those reported for balsam fir forests in Newfoundland (70.6 Mg C ha\(^{-1}\) at age 36) and for mature coniferous forests in Maine (116 Mg C ha\(^{-1}\)) (Moroni et al. 2010a; Smith et al. 1986). The biomass pool also closely aligned in both curve shape and C stocks with those measured in boreal forests in Nova Scotia (Taylor et al. 2008). Relative to other C pools in FM, the increase in biomass was the most significant over time, with almost 90% of variation explained by the fitted regression. It is not clear from the time-span covered in the chronosequence if the pool had begun to stabilize due to stand senescence, or if peak volume had not yet been reached. However, the AG biomass C stocks reported by Hoover et al. (2012), which are intended to serve as benchmarks for old-growth forests, were within ± 1 SE of those observed in FM, indicating that it is reasonable to consider the plots sampled in year-67 as similar to other mature coniferous stands in the region. The fact that biomass values observed by Hoover et al. (2012), were higher than those of FM may be a consequence of the mean annual temperature being ~ 6.5°C higher in New England.

CBM-CFS3 predictions of total biomass followed a similar trend as the empirical pool after the first decade, and this initial offset was caused by a lag in the modelled pool. Biomass in FM may be better described with a truncated sigmoidal curve, which would exclude the pronounced lag in growth following harvest. This lag may be absent in FM due to advanced regeneration after
harvest, which is a common characteristic of boreal balsam fir stands, where deep snow can protect seedlings during winter harvesting (Moroni et al. 2010a). In addition, Forêt Montmorency may have higher site productivity, as temperatures are higher at this southern limit of the boreal forest, relative to those of the stands used to develop yield curves that represent an average for Quebec (Gerardin and McKenney 2001).

The modelled prediction of biomass is based on yield curves that are derived from average values for balsam fir and white birch stands across Quebec. Although the yield curves were selected using empirical height measurements, only three trees were used to determine the average height of a stand at age 50. In addition, stand age had to be inferred from time since disturbance, introducing further uncertainty. The curve selected for balsam fir projects stand senescence at approximately age 110, whereas observations in FM and other boreal balsam fir forests suggest senescence begins much earlier, as indicated by increases in snag and woody debris pools (Moroni et al. 2010a). FM may be reaching peak volume sooner than yield curve estimations due to cold and wet conditions, which may be reducing stand growth and contributing to earlier decay. If stands in FM are potentially reaching maturity after 70 years, the earlier peak in biomass is likely contributing to the higher observed biomass values at the end of the simulation.

4.4 Dead organic matter

The greatest deviation between empirical and modelled estimates of C pools was observed in the downed woody debris (DWD) pool. CBM-CFS3 overestimated DWD following harvest, as well as at stand-maturity, by a factor of 2.5 and 3.1, respectively. Due to the magnitude of this difference, this section will assess individual DOM pools in FM within the context of other relevant studies, as well as how pool dynamics over time may have contributed to the discrepancy in DWD estimates. Carbon transfers to and from the DWD pool will be addressed in an effort to identify potential factors contributing to the models overestimation, and/or field underestimation. The following evaluation of DOM pools will consider both the environmental conditions in FM, as well as the ability of CBM-CFS3 to model stand dynamics associated with these environmental conditions.
4.4.1 Deadwood

Dead wood (standing and downed) in FM reached an average of 19 Mg C ha\(^{-1}\) by year-67, which is very close to the 18 Mg C ha\(^{-1}\) predicted for the Boreal Shield East ecozone (Stinson et al. 2011). The deadwood pool observed in FM was also within the range reported for old-growth softwood forests in New England (22 Mg C ha\(^{-1}\)), and for balsam fir stands in Newfoundland (21.4 Mg C ha\(^{-1}\)) (Hoover et al., 2012; Moroni et al., 2010a). At stand maturity, downed woody debris (DWD) estimates were within ± 1 SE of those reported for managed balsam fir forests across Canada (Shaw et al. 2014). Similar to the results of this study, Shaw et al. (2014) and Moroni et al. (2010), observed that DWD in balsam fir forests was overestimated in CBM-CFS3 by a factor of 2.2 and 2.1, respectively, with both estimates derived from default parameter settings. The results of the field study in FM seem to be well supported in the literature, which suggests that the discrepancy in empirical and modelled DWD estimates may be attributable to model limitations and errors in reproducing the environmental conditions in FM.

4.4.1.1 Environmental conditions in Forêt Montmorency

Precipitation in FM is among the highest recorded for boreal North America, which, depending on the level of saturation, could be contributing to the discrepancy in DWD estimates (Environment Canada 2015). For example, humid conditions in FM may be accelerating the decomposition rates, relative to those used in CBM-CFS3 predictions for the Quebec Boreal Shield East ecozone (Chapin et al. 2011). With high precipitation levels and well-drained soil, woody debris in FM may be transferred to soil pools at a faster rate. Alternatively, with high precipitation and low evapotranspiration (such as when DWD is buried or partially buried), decomposition may be suppressed (Waring and Schlesinger 1985). Under both scenarios, woody debris becomes a smaller C pool in FM, and because CBM-CFS3 is not sensitive to precipitation variability, these stand-level decay dynamics were not accounted for in the simulation (Stinson et al. 2011).

In addition, it is possible that the LFC protocol for sampling DWD is not providing a complete estimation of the carbon stored in this pool. If the high levels of precipitation are creating saturated micro-environments, decomposition rates may be suppressed, particularly for DWD that is buried, or partially buried. Hagemann et al. (2010) suggested that the large C stocks in
buried DWD are preserved in Labrador, Canada, due to cold average temperatures, high precipitation, and extensive cover of bryophytes, which is often associated with these cold and wet conditions. Because bryophytes are also a prominent ecosystem component in boreal Quebec, buried wood may represent an important carbon pool in FM that is not being accounted for under the current LFC or NFI protocol (NFI 2008; Thiffault et al. 2011). This becomes an issue for comparing field and modelled C estimates because buried wood is included in the modelled estimate of DWD in CBM-CFS3. Therefore, part of the discrepancy in the DWD pool may be explained by field underestimation, as opposed to model overestimation.

Although an accurate estimate of buried DWD in FM is not currently available, other studies have attempted to quantify this pool. Moroni et al. (2010a) found approximately 2.3 Mg C ha\(^{-1}\) of buried wood in old-aged balsam fir stands in Newfoundland, but given the challenges of point sampling techniques, this pool was likely underestimated. In central Labrador, buried wood represented over 70% of the DWD pool in old-aged black spruce sites (Hagemann et al. 2010). However, conditions in Labrador are colder than FM (MAT of -1.0° to - 2.4° C) and biomass C stocks only reach half of those observed in FM, making it difficult to draw comparisons between these sites (Hagemann et al. 2010). It is clear that more accurate estimates of the buried wood are required for Canadian boreal forests in order to fairly assess modelled predictions of the DWD pool. In addition, a fundamental issue is that the CBM-CFS3 does not currently model the role of bryophytes in ecosystem carbon dynamics, both directly (carbon stored in this pool) and indirectly (impact on decomposition dynamics). Other studies have suggested that this issue may be particularly problematic for modelling balsam fir forests, where bryophytes often make a substantial contribution to ecosystem NPP (Moroni et al. 2010; Shaw et al. 2014). However, the modelled estimate of pre-harvest DWD was over 30 Mg C ha\(^{-1}\) greater than the observed pool at stand-maturity. Given the magnitude of this overestimation, there are likely other factors contributing to the observed difference. Modifications to both user-assumptions and default model parameters may be necessary to more accurately model in the DWD in FM.

4.4.1.2 Modelling deadwood in Forêt Montmorency

Downed woody debris was one of the most dynamic DOM pools, with high inputs of harvest slash decomposing over about five decades, during what is referred to as the residual decay
stage, before increasing again with natural stand decay (Sturtevant et al. 1997). The eventual upswing in woody debris that occurs as the stand regenerates and begins to senesce results in a U-shaped curve, which was observed in FM, as well as other boreal forests in North America (Rothstein et al. 2004; Martin et al. 2005; Moroni et al. 2010a). The 27-year chronosequence in Thunder Bay was not long enough to capture the recovery of the DWD pool, but it did show the rapid decomposition of DWD after harvest (Seedre et al. 2014). The recovery of DWD after harvest was not observed in the first 100 years of the CBM-CFS3 simulation, which suggests that stand regeneration and senescence are not being modelled accurately for this region of the boreal forest.

CBM-CFS3 may be limited in its ability to simulate the relatively complex dynamics of the DWD pool in FM due to issues with the model assumptions and default parameter settings that were used in this simulation. The stem-only harvest that occurred in the beginning of the simulation contributed 20 Mg C ha$^{-1}$ to the DWD pool, but these residues decayed with the first two decades. Prior to harvest, DWD estimates were 5x greater than those of FM at stand maturity (Appendix 1, Figure 8). This indicates that the source of over-estimation is predominately related to issues in the model initialization procedure, as opposed to C transfer parameters associated with the harvesting disturbance.

In the SBW simulation, the stand was subjected to SBW outbreaks every 40 years. Pre-harvest DWD could have been overestimated in this simulation due to a combination of the following factors: 1) the frequency of epidemics, 2) the transfer of carbon from snag pools to DWD pools, and 3) decay parameters used to transfer DWD to soil pools.

**Live biomass to standing deadwood transfers**

SBW outbreaks were scheduled to occur in simulated stands every 40 years, as this has been found to be the average outbreak interval for Quebec (Boulanger and Arseneault 2004). However, the disturbance history of FM before the chronosequence began in 1933 is relatively unknown. Based on paleoecological research, SBW outbreaks are presumed to have occurred over at least the past 450 years (Boulanger and Arseneault 2004). However, in order to stabilize DOM pools, model initialization had to extend over a 1000-year period, for which tree-ring chronologies are unavailable. In addition to uncertainty in outbreak frequency, assumptions
regarding the severity and location of the outbreaks had to be made for the model initialization procedure. Given the high levels of spatial variability, it is unlikely that outbreaks would have consistently impacted the sampled plots in FM at the assumed frequency and severity. In light of these uncertainties, it is possible that pre-harvest levels of DWD were overestimated due to high levels of mortality, and the subsequent collapse of snags after SBW outbreaks.

**Standing deadwood to downed woody debris transfers**

The trends in empirical and modelled DOM pools suggest that there may be a relationship between the underestimation of standing snags and the overestimation of DWD in CBM-CFS3, and C transfer rates between these pools may be causing the observed discrepancies. Standing deadwood increased significantly over time in FM, which is likely due to the self-thinning that occurs in balsam stands in middle-aged stands following harvest (Thompson et al. 2003; Moroni 2006). CBM-CFS3 predictions did not suggest recovery of the snag pools to the extent observed in FM, despite the fact that their initial values after harvest were closely aligned. One possible explanation for this is that the collapse of standing deadwood in FM might not be well represented in the Quebec Boreal Shield East averages used for C transfers. Soils in FM are well-drained, which may allow snags to remain standing for longer periods of time as they decay (Russel et al. 2012). If CBM-CFS3 is transferring snags to DWD at a faster rate than is appropriate for this region, this may be contributing to the over-estimation of the DWD pools. However, the snag pool was estimated fairly accurately at stand maturity (within 7 Mg C ha\(^{-1}\)), and even substantial reductions in snag transfer rates would not be sufficient to offset the discrepancy in total DWD at stand maturity (16 Mg C ha\(^{-1}\)). Another possibility is that the snags falling in CBM-CFS3 are transferring a disproportionate amount of carbon to the DWD pool.

Hilger et al. (2012) found that snag fall transfer rates (based on stem counts) used in CBM-CFS3 were underestimating carbon mass transfers, due to the fact that small diameter stems had disproportionately lower C mass. Because stem counts are not a very reliable proxy for stem mass, C transfer rates were calculated to more accurately simulate DOM pools for the ecozones. The mean difference in snag fall rates and C transfer rates was greatest for the Boreal Shield East ecozone (Hilger et al. 2012). This suggests that CBM-CFS3S simulation of stand dynamics in
FM (using Boreal shield East parameters) is particularly likely to have overestimated the fall rates of snags, and consequentially, the levels of DWD.

**Downed woody debris to soil transfers**

In addition to high transfer rates, the accumulation of DWD may be partially explained by issues with modelling the fragmentation and decay of debris in this region. At present, 17% percent of DWD in the ‘medium’ pool is transferred to soil pools, with the remaining 83% treated as physically intact, even after centuries from the original tree death (Kurz et al. 2009). There are considerable challenges in simulating the fragmentation of debris into soil pools, as this represents one of the more poorly understood soil processes (Yanai et al. 2003). Default decay rates may be underestimated for this region of the boreal forest, which may explain why the DWD pool is overestimated while the total soil pool is underestimated. Both Moroni et al. (2010) and Hagemann et al. (2010) found that increasing decay rates resulted in better agreement between measured and modelled DWD pools. DWD may be decaying faster in these cool and humid forests, relative to rates used to represent the Quebec Boreal Shield East ecozone (Hagemann et al. 2010). Hagemann et al. (2010) increased default base decay rates only for DWD > 10 cm, as opposed to for both DWD pools (as recommended by Moroni et al. (2010)). Because model predictions of SWD and FWD were in reasonable agreement with the observed pool in FM, modification of the base decay rate for this pool may not be appropriate for this region either. Discrepancies in SWD and FWD were greatest approximately four decades after harvest, when CBM-CFS3 shows recovery while harvest residues in FM are still be decomposing. It is possible that this discrepancy is related to smaller debris being buried by bryophytes, as opposed to decaying at a faster rate than predicted by CBM-CFS3 (Shaw et al. 2014).

Agreement between empirical and modelled predictions would likely be improved if processes driving the transfer of DWD to soil were better represented in CBM-CFS3. The observed discrepancy in the DWD pool in this study, as well as others in the boreal region, is partially related to the fact that the model has no sensitivity to precipitation and other hydrological factors, which may actually be more important than temperature in terms of decomposition dynamics (Harmon et al. 2000; Stinson et al. 2011). In addition to improvements in decay parameters, the
physical fragmentation of deadwood should be explicitly considered in the model. However, there is a high degree of uncertainty regarding soil processes such as fragmentation, humification, and stabilization; and modelling these processes has generated considerable debate among soil scientists (Shaw et al. 2014). Species-specific woody debris input parameters may also improve the accuracy of model simulations, and for regions such as FM, where bryophytes are a prominent ecosystem component, integrating the burial of woody debris would also be an important addition to CBM-CFS3. In light of the complexity associated with C transfers from DWD to soil, Hagemann et al. (2010) suggests using terminology such as “reduction rates”, as opposed to decay rates, particularly for cold and humid boreal forests.

4.4.2 LFH and mineral horizons

4.4.2.1 Forêt Montmorency soils in context

Soil pools in FM were relatively stable over time, with no significant changes in C stocks either following harvest, or at stand maturity. At stand maturity, the LFH C stocks were comparable to pre-harvest values reported in Smith et al. (1986) for red spruce – balsam fir forests in Maine (32 Mg C ha\(^{-1}\)) and for spruce –fir forests in Northern Lake States (33 Mg C ha\(^{-1}\)) (Smith et al. 2006). The pool was also within the range observed by Marty et al. (2015) across 21 forests in Quebec, but appear to fall in the lower range of estimates for boreal forests from several other studies (Lang et al. 1981; Moroni et al. 2010a; Hoover et al. 2012; Seedre et al. 2014; Poirier et al. 2014).

At stand maturity, the mineral soil pool was estimated to be 131 Mg C ha\(^{-1}\), which was within ± 1 SE of the average observed for boreal and temperate forests across Quebec (Marty et al. 2015). Mineral soil C stocks in FM fell between values reported for mature boreal forests in Newfoundland (97 Mg C ha\(^{-1}\)) and New England (167 Mg C ha\(^{-1}\)), and the range may be partially explained by differences in sampling depth (Smith et al. 1986; Moroni et al. 2010a). The mineral soil pool exhibited a slight downward trend, however, it was not significant over time, and the high variation in this pool, combined with a lack of data at the onset of the chronosequence, reduces the likelihood that there has been a real change over the observed time period in this pool.
4.4.2.2 Adequacy of the sampling procedure

In many of studies (with the exception of Hoover et al. 2012) in which the LFH was found to be higher than observed in FM, the mineral soil estimates were less than observed. It is possible that the sampling procedure in the LFC protocol may have been biased towards underestimating the LFH horizon and over-estimating the mineral horizon. For example, sieving the organic horizon samples represents a source of systematic error, as it is very difficult to control for the amount of pressure applied to samples, and fine roots and other coarse organic matter will consequently pass through the sieve to varying degrees, which impacts the total carbon content (Yanai et al. 2003). Buried wood in FM may be more physically intact, due to cold and wet conditions within the LFH horizon decelerating decomposition (Hagemann et al. 2010). In boreal regions where environmental conditions are not conducive to this form of preservation, disaggregation of woody debris may occur to a greater extent, and when samples are sieved, the woody material may more readily disintegrate with pressure.

In order to collect compete soil samples without resistance, the LFC sampling protocol avoids sampling in areas with dense coarse roots, or high stone content, which may have resulted in overestimation of the mineral soil pool. Volumetric rock content in the mineral horizon was not determined, which means that the carbon content in the mineral fine earth fraction was almost invariably overestimated. Although mineral soil carbon content was determined based on the depth sampled, this is not an accurate representation of stone content per hectare, and an informed estimate using soil pits would be required to reduce this source of bias in the mineral soil C pool estimate (Burton and Pregitzer 2008).

4.4.2.3 Comparison of field and modelled soil estimates

CBM-CFS3 predictions of C stocks in the FH horizon were only slightly higher than observed, however, with this is not surprising given that the model over-estimated DWD C stocks for 1000 years during the initialization period, and 17% of this pool is transferred to soil (Kurz et al. 2009). Overall, model predictions were in reasonable agreement with empirical estimates, remaining within the confidence interval and exhibiting the same stability over time. However, when the L horizon was included, the trend in the modelled prediction deviated from empirical estimates. The modelled LFH pool followed a trajectory that has been supported by ecological
theory, decreasing first after disturbance, and then increasing slightly over time with litterfall input (Sturtevant et al. 1997; Peltoniemi et al. 2004; Seedre et al. 2014). Although the empirical L horizon pool did exhibit a significant u-shaped trend, it was not as pronounced as the modelled pool, and was almost completely obscured by variability in the FH horizon.

Mineral soil C stocks observed in FM at stand maturity (131 Mg C ha\(^{-1}\)) were at the upper range of those observed in other boreal forest studies, and were about 21% higher than CBM-CFS3 predictions. This difference is particularly noteworthy as modelled estimates account for carbon in the mineral soil horizon to a depth of 1 meter, while only the first 55 cm were sampled in FM. Stinson et al. (2011) reported an average value of 84 Mg C ha\(^{-1}\) for the Boreal Shield East ecozone, and Shaw et al. (2014) found only 57 Mg C ha\(^{-1}\) in the mineral soil for balsam fir forests. These values suggest that soils in FM are not well represented by averages for these broader regions. The cold and wet conditions in FM are conducive to the development of deep podzolic soils, which can accumulate high levels of C in the mineral horizon, in part due to stabilization by Al and Fe oxides (Sanborn et al. 2011; Poirier et al. 2014). As previously discussed, the cold and wet environment may also be slowing decomposition of buried DWD in FM. Both the size and stability of the mineral horizon may be explained by the eventual disaggregation and incorporation of this DWD pool into the mineral horizon, where it may remain relatively recalcitrant over time.

4.4.2.4 Stability and variability in boreal soils

The effects of harvesting disturbance on carbon recovery in soil pools has been a topic of considerable attention in recent decades, in part because field studies in boreal North America have produced conflicting results regarding the vulnerability of forest floor C stocks. Nave et al. (2010) observed a 20% decrease in soil carbon stocks following harvests in temperate forests, lending support to the research of Covington et al. (1981), which suggested a decline of 50% within 15 years of harvest. The “Covington curve” had an immediate impact, and has been applied on a global scale to calculate the disturbance impacts on forest soils. The theory behind this research has become so widely accepted that it is considered to be ecological paradigm (Yanai et al. 2003). However, given the inconsistencies in sampling procedures, forest floor definitions, and site conditions, there has been considerable misuse of the Covington curve, and
researchers have been challenged to reproduce the results of this chronosequence study (Yanai et al. 2003; Ter-Mikaelian et al. 2008).

The lack of a temporal trend in LFH C stocks following disturbance has been observed in numerous other studies in the boreal forest (Lang et al. 1981; Smith et al. 2000; Taylor et al. 2008; Moroni et al. 2010). The stability of the LFH pool is perhaps slightly related to high inter-site variability obscuring any potential trends over time. This variability is a fundamental issue associated with chronosequence studies, which are based on the assumption that variation in site conditions is attributable to age alone. This technique, known as time-for-space substitution, may be particularly problematic for soil pools, where there is substantial short-range variability in organic matter contents, in addition to the variability among chronosequence plots (Kristensen et al. 2015).

At stand maturity, the LFH pool varied by 17 Mg C ha\(^{-1}\), which amounted to over half of the average for this pool. The total soil pool varied by 102 Mg C ha\(^{-1}\), which is remarkable, seeing as this inter-site variability amounts to over half of that which was observed across 21 temperate and boreal forests in Eastern Quebec (Marty et al. 2015). At such a magnitude, inter-site variability is capable of masking any potential effects of disturbances on the biotic or abiotic factors driving soil C dynamics. For example, it may not be possible to discern if carbon is being lost to the atmosphere due to increases in decomposition rates (associated with changes in the moisture regime or litterfall input), as suggested in Covington et al. (1981), or if C is being transferred to the mineral horizon as a result of mechanical disturbance (Yanai et al. 2003; Poirier et al. 2014). From a carbon sequestration perspective, if organic matter in the forest floor is being mixed into the mineral soil with harvesting, carbon may actually be more stable over time (Yanai et al. 2003). However, substantial mixing of soil horizons would likely have other implications on nutrient cycling and biodiversity, which may not be ecologically sustainable over time.

There may also be some aspects of the FM ecosystem that are promoting stability in the LFH horizon after harvest. For example, the advanced regeneration of balsam fir saplings in this region may be providing more continuous input of litterfall after harvest, compared to ecosystems that experience delayed regeneration after harvest (Lang et al. 1981). In addition, the
theory that carbon loss is in part due to accelerated decomposition (due to exposure of the forest floor following harvest) may not be applicable to regions such as FM, where cool and humid conditions may keep decomposition rates more constant (Covington et al. 1981; Lang et al. 1981). Given the relative stability and high variability observed in soil pools of numerous boreal forests studies, it seems as though soil may be more influenced by site factors, as opposed to disturbance history (Moroni et al. 2010a). Overall, the stability observed in the LFH horizon is significant in terms of assessing the potential sensitivity of boreal ecosystems to harvest related disturbances. If the LFH horizon, which has been perceived to be a relatively fragile carbon pool, is potentially less sensitive to harvesting disturbances, this may be a favourable outcome in terms of the environmental sustainability of stem-only harvesting.

4.5 Challenges in estimating forest carbon stocks

Some of the discrepancies in empirical and modelled C pool estimates may be associated with the experimental design of this study, and the assumptions made in quantifying C pools over time. Several of these issues are inherent in chronosequence studies, and others are more specific to the Forêt Montmorency field study. Because CBM-CFS3 simulations were partially informed by user assumptions regarding the history of ecosystem dynamics in FM, it is important that the associated sources of error are addressed. This section will first discuss challenges in the experimental design of the field study, and then the ways in which model accuracy was affected by these uncertainties in the field study, as well as general limitations related to model parameterization.

4.5.1 Field experimental design

Chronosequence studies assume that sites are formed from the same parent material, and are consistent in terms of biotic and abiotic environmental variables, differing only in time since the last disturbance (Walker et al. 2010). For this to be true, the following assumptions must be satisfied.

1) Successional changes in species composition and forest structure did not occur over time.
2) Plots have been equally affected by historical natural disturbances.
3) All plots are the same at the onset of the chronosequence with regard to soils properties, topography, hydrology, and species composition.
4) Climate and CO₂ concentration were stable throughout the chronosequence.

It is clear that satisfying these assumptions of stability and uniformity is highly improbable, particularly when assessing vegetative dynamics (Johnson and Miyanishi 2008). In addition to these general challenges, the design of the chronosequence in FM also may be contributing to errors in empirical C estimates. These issues can be traced to a lack of data availability information, either in terms of an insufficient time span sampled, gaps in the chronosequence, or uncertainties in the disturbance history of FM.

Although the chronosequence study extended over a relatively long period of time (77 years), it may not have been sufficient for determining if the stand has reached maturity. This time period was actually shortened, as the plot replication in year-67 made it a more statistically valid endpoint for the chronosequence. Therefore, the analysis of final C stocks was based on the assumption that stands in FM can be considered to be mature by year-67. This assumption was supported with values found in the literature for similar forests, as well as the reasonable agreement with model simulations of live biomass pools. Although regression analysis indicated a reduction in the rate of increase of C stocks in the aboveground biomass pool, the study would need to be extended to more accurately conclude if this decline can be interpreted as stand senescence (Figure 4). Finally, even if stands in FM have reached maturity after 67 years, they do not necessarily represent pre-disturbance C levels, as the oldest plots in the chronosequence were sampled after the first harvesting rotation. It is therefore difficult to determine if C pools are recovering over time, as the levels for ‘old-growth’ or unmanaged stand in this region are unknown.

The replication at year-67 and year-0 was fortunate in the sense that it allowed for more robust end-points for the chronosequence. This replication allowed insight into the inter-site variability in environmental conditions, which, although valuable, can make it difficult to validate the single points in time that comprise the rest of the chronosequence. There is also a substantial gap in the chronosequence data, between year-43 and 67, which further limits the degree to which conclusions related to dynamics in this 24-year period can be made.
Quantifying forest carbon pools with the LFC sampling procedure may also provide an incomplete assessment of ecosystem carbon dynamics. For example, several pools, such as roots, buried wood, coarse material in the FH horizon, rock content, and understory vegetation (including bryophytes) were not accounted for in the total ecosystem carbon estimate. Buried wood could be particularly problematic, as this pool was included in the CBM-CFS3 estimate of total carbon. In addition, it was not possible to isolate atmospheric and DOC fluxes out of FM. It is therefore not possible to determine if the atmospheric C flux used in CBM-CFS3 to model decomposition processes was appropriate for FM (Kurz et al. 2009).

4.5.2 Modelling Forêt Montmorency: assumptions and limitations

The ability of CBM-CFS3 to model stand-level ecosystem dynamics in FM may be limited for numerous reasons, related to challenges in representing the environmental conditions in FM, or to the limitations associated with current parameterization of CBM-CFS3.

4.5.2.1 User assumptions

Several assumptions are made in compiling import files with regards to the growth curves and disturbance history used for CBM-CFS3 simulations. The yield curves selected for this study represent average volumes for the province of Quebec, and therefore may not reflect the disturbance history and regeneration dynamics for a specific region (i.e. FM) (Taylor et al. 2008). Assumptions regarding disturbance history in FM also impact the validity of model simulations. In addition to the challenges in simulating the history of SBW epidemics in FM, there is some uncertainty in the history of forest management in FM. Although forestry records and aerial photographs provide strong evidence for consistent stem-only harvesting throughout the chronosequence, it is possible that there was some variation in the intensity of the harvest, or the species targeted. Harvesting intensity, and the subsequent transfers between C pools, were determined using empirical data from the plots sampled before and after the 2010 harvest. For example, the woody debris in the lowest state of decomposition (classes 1 and 2) was compared before and after harvest to calculate the transfer in CBM-CFS3 from merchantable stemwood to CWD (> 10 cm). Although empirical data was the best available indicator of these transfers in
FM, there are obvious issues with the reliability of this method, particularly given the observed variability among plots.

The harvesting method changed in FM in the 1960s, shifting from horse skidding to machine harvests, which may have impacted the amount of harvest residues left on site, or the extent of mechanical disturbance for the forest floor. It is possible that even if the intensity of the harvest did not change over time, that the transition in harvesting method might have impacted C stocks and fluxes in DWD and soil carbon pools.

### 4.5.2.2 Model Limitations

Agreement between empirical and modelled estimates may also be influenced by the model initialization procedure, and CBM-CFS3s constraints in simulating partial disturbances. A procedure had to be developed for this study, because the MAKELIST initialization procedure required historic disturbances to be stand-replacing. The pseudo-initialization overcame this issue by originating the modelled stand from an afforestation event. However, there are several potential sources of error associated with this approach. The afforestation even required all carbon pools to be empty in time-step 0, with the exception of the podzolic mineral soil pool (belowground slow), which contained only 74 Mg C ha$^{-1}$ (Kull et al. 2014). This starting value for cultivated soils may have been too low for soils in FM, which have been developing since the last deglaciation, as opposed to recovering over only 1,000 years. The initialization period may not have been sufficient for developing soil C pools in this region, and extending the duration (e.g. up to 10, 000 years) may help improve agreement between empirical and modelled C estimates.

Partial disturbances from insect epidemics have driven stand regeneration in this region over the past 4,500 years, and have created a much more structurally diverse forest ecosystem than CBM-CFS3 can currently model (Morin 1993; Couillard et al. 2013). The structural diversity observed in FM is a result of complex gap dynamics and advanced regeneration, which have contributed to trends in carbon cycling, and current carbon stocks (Morin 1993). Attempting to model these complex stand dynamics in CBM-CFS3 is a fundamental challenge, given the model assumption that even-aged stands originated from stand replacing disturbances (Kurz et al. 2009). In the pseudo-initialization procedure, stand age was reset along the yield curve after SBW outbreaks to
the corresponding volume. This set back in age partially mimics regeneration after disturbance, but the decreases in volume were minimal (7.5 or 17%), compared to the continuous seedling regeneration observed in forests where insect epidemics are the primary source of disturbance (Boulanger and Arseneault 2004).

The degree to which independent field data can accurately be used to validate model predictions is also limited by the fact that comparisons are being made between stands that represent different spatial scales. Although CBM-CFS3 is both a stand and landscape level model, many of the parameters used are based on broader ecozone and provincial averages that are designed for landscape level analysis (Taylor et al. 2008; Kurz et al. 2009). In this simulation, C stocks are predicted for the specified administrative and ecological boundary (Quebec - Boreal Shield East), using data to represent average environmental conditions for this spatial unit. The data associated with each ecozone are designed to represent the region with regard to parent material, soil properties, DOM turnover rates (including decay rates, snag fall rates, foliage fall rates, atmospheric flux rates, etc.) and biomass turnover rates (including coarse root turnover and HW decay relative to SW decay, and transfers of “other” biomass to snag branches) (Kull et al. 2014). Some of the underlying assumptions that determine these C transfers may not be appropriate for FM, particularly given the ecological effects of high precipitation levels in this forest (Rowe 1972).

The creation of partial disturbances also introduced more uncertainty in the modelling procedure, simply due to the number of assumptions that were required. CBM-CFS3 is designed for analysis of forests that are subjected to stand-replacing disturbances at regular intervals. For example, the Quebec -Boreal Shield East spatial unit is scheduled to have stand-replacing disturbances every 125 years, which is typically due to wildfire (Kull et al. 2014). In the absence of regular stand-replacing disturbances in FM, it was necessary to define outbreak frequency, severity, and duration. Cumulatively, these disturbance matrices created more opportunity for error, particularly when expected to represented relatively small spatial scale over a long time period (Royama 1984).
Chapter 5: Conclusion

The primary purpose of this research was to evaluate trends in carbon stocks following harvesting in a balsam fir - white birch boreal forest, and to compare these trends with those predicted by CBM-CFS3 for the Quebec – Boreal Shield East ecozone. In a broader context, the results of this research can help us to determine if and when carbon pools are recovering following stem-only harvesting, and if there is potential in this region of the boreal for bioenergy production from the residues of existing harvesting operations. For some carbon pools, such as live biomass, recovery is expected following harvesting. Regenerating stands uptake more carbon from the atmosphere than stands that have reached maturity, and in this sense, forest management can increase carbon sequestration (Lippke et al. 2011; Stinson et al. 2011). Bioenergy systems have often been described as carbon neutral, under the assumption that carbon emissions from biomass combustion are offset through sequestration in the following rotation (Lamers et al. 2013a).

However, there are several issues with this assumption of neutrality, and the role of bioenergy in climate change migration is still a contentious area of research (Dymond et al. 2010; Lemprière et al. 2013). Issues regarding the temporal balance of C release and sequestration, as well as long-term effects of harvesting on forest carbon cycling have been scrutinized in recent years, in an effort to determine the degree to which bioenergy systems can contribute to climate change mitigation. While thorough life cycle accounting is required to evaluate issues with the timing of the mitigation, field studies can help indicate how C cycling is affected by SOH operations, and if some C pools may be more vulnerable than others.

5.1 Field Study

The chronosequence in FM allows for insight into C cycling following stem-only harvesting in the boreal forest, and the C stock estimates from this experiment can be used as a reference scenario in assessing the carbon consequences of bioenergy production. Carbon pool estimates from the end of the chronosequence in FM were well supported by values found in the literature.
for mature boreal forests, with the exception of the soils pool. Soil C in FM was higher than observed in similar forest ecosystems, which may be explained by the relatively high precipitation, cold temperatures, and prominent bryophyte cover in this region of the boreal. Soil pools in FM were also stable over time, with no appreciable decrease in C following harvest. These results lend further support to the argument that soil carbon pools do not necessarily decrease with harvesting, and that the research presented in Covington et al. (1981) needs to be reconsidered in light of alternative explanations and failure to produce the results observed in the original chronosequence (Lang et al. 1981; Yanai et al. 2003; Ter-Mikaelian et al. 2008).

The stability of the soil pools in FM, as well as the fact that the deadwood and biomass pools reached levels comparable to those observed in mature boreal forests, indicates that the stem-only harvesting in FM is not causing significant carbon losses over time. Overall, the results of this study suggest that ecosystem carbon pools are fairly resilient in response to stem-only harvesting. This is a favourable outcome in terms of the viability of bioenergy production from mill residues, assuming that the harvesting intensity and biomass removal would not increase. However, it is important to keep these results in an appropriate spatial and temporal context. Issues such as: the variability between plots, the use of FM as a representative boreal forest of Quebec, the use of only one harvesting rotation, and the lack of pre-harvest C data, all need to be factored into the interpretation and application of these field study results.

5.2 Model Evaluation

Models such as CBM-CFS3 provide an opportunity to overcome some of the aforementioned issues, by broadening the spatial scale through the use of average regional data and allowing for both forward and backward extrapolation of model projections. However, the appropriateness of these applications is contingent upon reasonable agreement between the model projections and available field data. Field and model comparison studies are therefore critical for model validation, and the development of reliable, site-specific carbon stock estimates.

In this study, CBM-CFS3 was initialized with data that best represented the stand history and ecosystem dynamics in FM, and the model output was compared with data from an independent field trial. Results suggest that while CBM-CFS3 reasonably predicted biomass trends, and was within 7% of total ecosystem carbon stock at year-67, there are some issues with the ability of
the model to simulate DOM dynamics under current parameters and user assumptions. Some of these issues may be associated with gaps in model parameterization, such as the lack of precipitation sensitivity and the inability to simulate bryophyte dynamics. Such issues may not be as apparent in larger, regional studies (i.e. for modelling the Quebec- Boreal Shield East ecozone), but they could be problematic for stand-level analysis. In particular, forests with unique environmental conditions, such as FM, may not be well represented by the regional averages used for stand initialization in CBM-CFS3.

In some instances, discrepancies in observed and modelled estimates can have serious implications for forest management, particularly with regard to assessing the feasibility of bioenergy systems. For example, CBM-CFS3 is not only predicting different recovery trends in woody debris pools, the C stocks were vastly overestimated, with CWD predicted to be more than 11x greater after harvest (or over 43 Mg C ha\(^{-1}\) greater). Using these model estimates alone, as assessment of the availability of harvest residues for bioenergy in this region would be overly optimistic. Although CBM-CFS3 is an invaluable tool in terms of testing and improving our understanding of ecosystem C dynamics and estimating landscape level, there are still risks associated with depending on modelled predictions for guiding forest management decisions.

### 5.3 Recommendations for Future Research

This research represents an important contribution to site-specific C stock estimates for the boreal forest, and can help inform the development of sustainable forest management policies. However, there are still considerable uncertainties in estimating C stocks over time, several of which could be addressed through improvements to field and modelling methodology in future research projects. Some of the risks associated with chronosequence experiments could be reduced if longer time-spans, and ideally multiple harvesting rotations, were covered. Although the field study in FM indicates that carbon is recovering by the end of the chronosequence, it is likely that after multiple short rotations (i.e. 50- 70 years), these practices could become unsustainable (Boucher et al. 2009). Including pre-harvest C stock values is critical for this reason, as it is possible that continued disturbance may result in a progressive lowering of organic C in the forest floor (Yanai et al. 2003). These remaining uncertainties, as well as the substantial inter-site variability associated with boreal forests, must be accounted for in the
development of forest management policies that will preserve carbon pools and foster long-term ecological sustainability.
References


Appendix I

**Figure 1.** Balsam fir Station Quality Index (SQI) curves and yield curves, based on data and equations from Pothier and Savard (1998). Empirical height and dominant height values are plotted with SQI curves.

**Figures 2-7.** Hardwood and Softwood carbon pools in Forêt Montmorency, including empirical and modelled estimates, when applicable. Empirical data (red filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.

**Figure 8.** Woody debris (> 0 cm) and stumps, with modelled output showing 20 years of pre-harvest data before the simulation began in year-0.
**Figure 1(A-B).** (A) Balsam fir Station Quality Index curves (marked lines), showing dominant height (m). Empirical data includes observed heights (m) of representative trees in Forêt Montmorency (diamonds), and calculated dominant heights (circles), as determined by DBH measurements from the 4 largest trees per plot. Empirical dominant heights were fitted with a second order polynomial regression (smooth line), indicating an SQI of 16.5 m. (B) Balsam fir yield curves (m$^3$/ha) based on IQS curves (above), showing volume as a function of age at 1 m in height for trees with a DBH $\geq$ 9.1 cm (Pothier and Savard 1998).
Figure 2(A-B). Hardwood live tree biomass. (A) Stemwood & bark of hardwood trees (≥ 9 cm DBH). (B) Stemwood & bark of hardwood trees (< 9 cm DBH), and branches of all hardwood trees. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 2(C-D). **Hardwood live tree biomass.** (C) Foliage from large and small live hardwood trees. (D) Coarse roots, which were calculated using Li et al. (2003) equations based on empirical estimates of total aboveground hardwood biomass. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 2(E). Hardwood fine roots, which were calculated using Li et al. (2003) equations based on empirical estimates of total aboveground hardwood biomass.

Figure 3(A). Stemwood & bark of softwood trees (≥ 9 cm DBH). Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 3(B-C). Softwood live tree biomass. (B) Stemwood & bark of softwood trees (< 9 cm DBH), and branches of all trees. (C) Foliage from large and small live softwood trees. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 3(D-E). (D) Coarse and (E) Fine roots, which were calculated using Li et al. (2003) equations based on empirical estimates of total aboveground hardwood biomass. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 4(A-B). Hardwood standing deadwood. (A) Snag stemwood & bark from large trees (≥ 9 cm DBH). (B) Snag stemwood and bark from small trees (< 9 cm DBH), and snag branches. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 5(A-B). Softwood standing deadwood. (A) Snag stemwood & bark from large trees (≥ 9 cm DBH. (B) Snag stemwood and bark from small trees (< 9 cm DBH), and snag branches. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.
Figure 6(A-B). Woody debris (≥ 3 cm in diameter), divided into (A) Hardwood and (B) Softwood classes. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines).
Figure 7 (A-B). Stumps (height < 1.3 m, top diameter ≥ 4 cm, measured inside bark). (A) Hardwood stumps (B) Softwood stumps. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines).
Figure 8. Woody debris (> 0 cm) and stumps, with modelled output showing 20 years of pre-harvest data before the simulation began in year-0. Empirical data (filled circles), fitted with a second order polynomial regression (solid line) and 95% confidence intervals (dashed lines). CBM-CFS3 predictions are shown with open circles.