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Bryophyte-regulated deadwood and carbon cycling in humid boreal forests

(Régulation des cycles du bois mort et du carbone par les bryophytes dans les forêts boréales humides)

(Regulative Einflüsse von Moosen auf den Totholz- und Kohlenstoffkreislauf in humiden borealen Wäldern)

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Ulrike Hagemann
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Abbreviations

ANOVA	Analysis of Variance	Analyse des variances
BW	Buried deadwood	Bois mort enterré
C	Carbon	Carbone
CBM-CFS3	Carbon Budget Model of the Canadian Forest Sector	Modèle du bilan du carbone du secteur forestier canadien
DBH	Diameter at breast height	Diamètre à hauteur de poitrine
DOM	Dead organic matter	Matière organique particulaire
FRI	Fire return interval	Intervalle entre les feux
LMM	Linear mixed model	Modèle linéaire mixte
MAT	Mean annual temperature	Température moyenne annuelle
MWU-Test	*Mann-Whitney* U-Test	U-Test de *Mann-Whitney*
NRCan	Natural Resources Canada	Ressources naturelles de Canada
OL	Organic layer	Couche organique
pGH-Test	*Games-Howell* Test (*post hoc*)	Test de *Games-Howell* (*post hoc*)
REML	Restricted maximum likelihood	Probabilité maximale restreinte
SW-Test	*Shapiro-Wilk-Test*	Test de *Shapiro-Wilk*
WD	Woody debris	Débris ligneux
Wsr-Test	*Wilcoxon* signed-rank Test	Test de *Wilcoxon*

1 Summary (English/French/German)

Abstract

The presented thesis investigates the role of bryophytes in the deadwood and carbon (C) cycle of boreal black spruce forests in Labrador, Canada. All major forest C pools (live-tree, standing and downed deadwood, organic layer, mineral soil) were quantified for three old-growth, nine clearcut harvested, and three burned forest stands in order to characterize forest C dynamics of a high-latitude humid boreal forest ecosystem. Tree and aboveground deadwood C dynamics of Labrador black spruce forests were similar to those of drier or warmer boreal forests. However, due to bryophyte-driven processes such as woody debris (WD) burial and paludification, the studied forests contained high organic layer, mineral soil, and buried wood C stocks.

The comprehensive field-measured data on C stocks was used to evaluate the CBM-CFS3, a Canadian national-scale C budget model, with respect to its applicability to Labrador black spruce and humid boreal forests elsewhere. After selected biomass estimation and deadwood decay parameters had been adjusted, the CBM-CFS3 represented measured live-tree and aboveground deadwood C dynamics well. The CBM-CFS3 was initially designed for well-drained upland forests and does not reflect processes associated with bryophytes and high forest floor moisture content, thus not capturing the large amounts of buried wood and mineral soil C observed in the studied forests. Suggestions are made for structural changes to the CBM-CFS3 and other forest ecosystem C models to more adequately represent the bryophyte-regulated accumulation of buried wood, organic layer, and mineral soil C.

Accuracy of forest C models could be further improved by differentiating WD decomposition rates by disturbance history, because WD respiration reflects disturbance-induced changes in temperature and moisture regimes. In Labrador, WD respiration was limited by low WD moisture levels and high temperatures in burned stands, and by high WD moisture contents and low temperatures in old-growth stands. Following harvesting, residual vegetation prevents the desiccation of WD, resulting in significantly higher WD respiration compared to old-growth and burned stands. Moreover, the bryophyte layer recovers faster following harvest than following fire, which reduces WD desiccation due to moisture retention, water transfer, and moisture-induced cooling and results in higher WD decomposition rates.

Bryophytes are thus a key driver of the deadwood and C cycle of humid boreal Labrador black spruce forests. The author recommends to classify these and similar boreal forests as a functional ecosystem group called “humid boreal forests”, preliminarily defined as “boreal forest ecosystems featuring a bryophyte-dominated ground vegetation layer associated with low soil temperatures, high moisture levels, low dead organic matter decomposition rates, and subsequently (in the absence of stand-replacing disturbances) an accumulation of buried wood embedded in a thick organic layer”. Bryophytes are also an integral component of many coniferous forests outside the boreal biome. Bryophyte-regulated processes such as WD burial or paludification are thus likely significant to the global C cycle. The potential climate change-induced release of large amounts of CO_2 from buried wood and soil C pools necessitates an increased understanding of how bryophyte productivity and decomposition constraints will change with increasing temperature and varying moisture regimes. Ecosystems such as humid boreal forests with potentially high C losses to the atmosphere may thus be identified and counteractive forest management strategies can be developed and implemented.

Résumé

Cette thèse de doctorat s’intéresse à l’influence qu’exercent les mousses sur les cycles du bois mort et du carbone (C) dans des pessières noires boréales humides du Labrador, Canada. Toutes les réservoirs majeurs de C (arbres vivants, bois mort sur pied et éffondré, l’horizon de matière organique, sol minéral) de trois pessières vierges, neuf coupes à blanc et de trois pessières brûlées ont été quantifiés pour caractériser le cycle du C des forêts humides boréales du nord. Les dynamismes de C des arbres vivants et du bois mort supraterrestre ressemblaient à ceux des forêts boréales plus sèches ou aux températures plus chaudes. À cause des processus régulés par les mousses (l’enterrement du bois mort ou la paludification), les forêts étudiées contenaient des stocks élevés de C au sein de l’horizon de matière organique, le sol minéral et le bois enterré.

Les données ont aussi été utilisées pour évaluer le MBC-SFC3, un modèle national canadien du bilan du C, concernant son applicabilité aux pessières boréales humides de Labrador et d’ailleurs. Suite à l’ajustement de quelques paramètres, p.ex. des taux de décomposition, le MBC-SFC3 reproduisait bien le dynamisme mesuré des arbres vivants et du bois mort supraterrestre. Le MBC-SFC3 a initialement été développé pour les sites bien drainés et ne considère pas les processus associés avec les mousses ou l’humidité élevée du sol. Conséquemment, le MBC-SFC3 ne représentait pas les stocks élevés de C mesurés pour le bois enterré et pour le sol. Les modifications structurelles du MBC-SFC3 et d’autres modèles du C forestier sont nécessaires pour représenter adéquatement l’accumulation du C au sein de ces réservoirs.

La précision des modèles du C forestier pourrait encore être améliorée par une différenciation des taux de décomposition selon le régime de perturbations, parce que la respiration du bois mort reflète les changements de la température et d’humidité associés avec une perturbation spécifique. Dans les pessières brûlés du Labrador, la respiration du bois mort était limitée par a faible humidité du bois et des températures élevées; dans les pessières vierges, par l' humidité élevée du bois et des températures basses. Dans les coupes à blanc, la végétation résiduelle empêchait le dessèchement du bois mort. Il s'y ensuivit que la respiration du bois mort y est nettement plus élevée en comparaison avec des pessières brûlés ou vierges. La décomposition du bois mort après coupe à blanc est aussi favorisée par la récupération plus rapide de la couche de mousses, diminuant conséquemment le dessèchement du bois mort par la conservation d'humidité, les transports vertical et horizontale d'eau et le refroidissement induit par l'humidité.

Ainsi, les mousses sont les facteurs clés dans les cycles du bois mort et du C des pessières noires boréales au Labrador. L'auteur préconise la classification de ces pessières et des forêts semblables comme un groupe fonctionnel d'écosystèmes nommé : « pessières boréales humides » ; provisoirement définies comme « des écosystèmes forestiers avec une végétation terrestre dominée par les mousses et par conséquent associée avec des températures basses du sol, une humidité élevée, des taux de décomposition faibles et (en l'absence de perturbations) l'accumulation du bois enterré dans des couches organiques epaisses ». En outre, les mousses sont des éléments principaux des nombreuses forêts résineuses n'appartenant pas au biome boréal. Les processus régulés par les mousses tels l'enterrement du bois mort ou la paludification sont probablement importants pour le cycle global de C. La libération potentielle de grandes quantités de CO_2 des réservoirs « bois enterré » et « sol » à la suite des changements climatiques exige une meilleure compréhension des transformations de la productivité des mousses et des limitations de la décomposition dues aux températures plus élevées et au taux d'humidités variables. Ainsi, les écosystèmes aux pertes potentielles de C élevées (p.ex. les pessières boréales humides) peuvent être identifiés et des mesures d'aménagement antagonistes peuvent être développées et implémentées.

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Zusammenfassung

Die vorliegende Arbeit untersucht die Einflüsse von Moosen auf den Totholz- und Kohlenstoff-(C)-Kreislauf in borealen Schwarzfichtenwäldern in Labrador, Kanada. Um den C-Kreislauf dieses humiden borealen Waldökosystems zu charakterisieren, wurden alle bedeutenden C-Speicher (lebende Bäume, stehendes und liegendes Totholz, organische Auflage, Mineralboden) von drei Primärwald-, neun Kahlschlags- und drei Brandflächen quantifiziert. Die C-Dynamiken der Bäume und des oberiridischen Totholzes der Untersuchungsflächen ähnelten denen von trockeneren und/oder wärmeren borealen Wäldern, während die organische Auflage, der Mineralboden und das begrabene Totholz bedingt durch von Moosen regulierte Prozesse wie Totholzeinlagerung und Paludifizierung besonders hohe C-Vorräte aufwiesen.

Mit dem umfangreichen C-Datensatz wurde das CBM-CFS3, das nationale kanadische C-Modell, am Beispiel Labradors im Hinblick auf seine Anwendbarkeit in humiden borealen Wäldern evaluiert. Nach Anpassung ausgewählter Parameter, z.B. der Totholzabbauraten, wurden die gemessenen C-Dynamiken der Bäume und des oberiridischen Totholzes vom Modell abgebildet. Das CBM-CFS3 wurde ursprünglich für staunässefreie, terrestrische Waldstandorte entwickelt und berücksichtigt keine mit Moosen oder hoher Bodenfeuchte assoziierten Prozesse, so dass es die hohen C-Vorräte des begrabenen Totholzes und des Bodens nicht widerspiegelte. Eine adäquate Abbildung der Akkumulation von C in diesen Speichern erfordert strukturelle Änderungen des CBM-CFS3 und anderer Wald-C-Modelle.

Die Genauigkeit von Wald-C-Modellen könnte darüber hinaus durch eine Differenzierung der Totholzabbauraten in Abhängigkeit vom Störungsregime verbessert werden, da störungsspezifische Veränderungen von Temperatur und Feuchte von der Totholzatmung widergespiegelt werden. Im Untersuchungsgebiet limitierten geringe Holzfeuchten und hohe Holztemperaturen die Totholzatmung auf Brandflächen. In Primärwäldern wirkten dagegen hohe Holzfeuchten und geringe Holztemperaturen hemmend. Auf Kahlschlägen verhinderte die verbleibende Vegetation die Austrockung des Totholzes, was zu signifikant erhöhten Atmungsraten im Vergleich zu Brand- und Primärwaldflächen führte. Zudem wird der Totholzabbau auf Kahlschlen durch eine schnellere Erholung der Moosdecke als auf Brandflächen gefördert, da Moose durch ihr hohes Wasserspeichervermögen, vertikalen und horizontalen Wassertransport und feuchte-induzierte Kühlung der Austrockung des Totholzes entgegenwirken.

Moose sind somit ein Schlüsselfaktor im Totholz- und C-Kreislauf der humiden borealen Schwarzfichtenwälder Labradors. Die Autorin empfiehlt die Klassifikation dieser und ähnlicher borealer Wälder als eine funktionelle Ökosystemgruppe namens “humid boreal forests”; vorläufig definiert als “boreale Waldökosysteme mit durch Moose dominierter Bodenvegetation und damit assoziierten niedrigen Bodentemperaturen, hohen Bodenfeuchten, geringen Abbauraten und (in Abwesenheit großflächiger Störungen) der Akkumulation von begrabenem Totholz in mächtigen organischen Auflagen”. Auch außerhalb des borealen Bioms sind Moose ein wesentlicher Bestandteil vieler Nadelwälder. Durch Moose regulierte Prozesse wie Totholzeinlagerung und Paludifizierung sind daher wahrscheinlich relevant für den globalen C-Kreislauf. Die durch den Klimawandel bedingte potentielle Freisetzung von großen Mengen CO_2 aus begrabenem Totholz und dem Boden macht ein besseres Verständnis der zu erwartenden Veränderungen von Mooswachstum und Abbauhemmnissen als Folge erhöhter Temperaturen und variabler Feuchteverhältnisse erforderlich. Somit können Ökosysteme mit potentiell hohen C-Verlusten, wie z.B. humide boreale Wälder, identifiziert und diesen entgegenwirkende Bewirtschaftungsmaßnahmen entwickelt und umgesetzt werden.

2 Introduction

2.1 Background

Forests contain large amounts of carbon (C) in biomass, dead organic matter (DOM), and soil, and contribute significantly to annual C exchanges between terrestrial ecosystems and the atmosphere (Denman et al. 2007). All signatory countries of the United Nations Framework Convention on Climate Change (UNFCCC; UNFCCC 1992, Brown 2002), including Canada, must report on emissions and removals of carbon dioxide (CO_2) and non-CO_2 greenhouse gases due to afforestation and reforestation, with the option to elect reporting on C stock changes resulting from forest management. Canada encompasses ~40% of the global boreal forest biome (Burton et al. 2003), which in its entirety contains ~25% and ~60% of the global terrestrial C stored in vegetation and soil, respectively (Fyles et al. 2002). The boreal forest has been identified as particularly sensitive to changes in temperature and moisture regimes resulting from climate change (Malhi et al. 1999, IPCC 2007, Kurz et al. 2008a). Apart from changes in the energy and water exchange between land and atmosphere, climate change is expected to significantly increase the occurrence of disturbances such as forest fire and insect outbreaks in large parts of the boreal forest (Burton et al. 2003). Anthropogenic pressures on boreal forests will likely also be enhanced by the combined impacts of population growth and climate change, resulting in deforestation in the course of agricultural expansion for food production, forest fragmentation, and intensification of forest management to meet an increased demand for wood (Fyles et al. 2002, Burton et al. 2003).

Sophisticated models such as the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) may help to evaluate the impacts of the expected changes (Kurz et al. 2009), but they require a thorough understanding of ecosystem processes and must be evaluated using adequate field data. While large parts of the Canadian boreal forest are well-studied, e.g., in British Columbia, Saskatechewan, Manitoba, and Québec (Gower et al. 1997, Vogel and Gower 1998, Bond-Lamberty et al. 2003, Manies et al. 2005, Boulanger and Sirois 2006), relatively few studies have investigated the humid Eastern boreal forests in Newfoundland and Labrador (Sturtevant et al. 1997, Moroni 2006). Studies of ecosystem processes related particularly to the C cycle of disturbed and undisturbed humid boreal forests are thus required to increase the understanding of management and climate change-induced effects on these forests, and to effectively simulate the observed processes.

2.2 Boreal Forest Carbon Cycle

In mature boreal forests, aboveground biomass C stocks are estimated at 54–64 Mg C ha^{-1} (Malhi et al. 1999, Bhatti et al. 2003), contributing significantly less C to total ecosystem C stocks than in temperate forests (Fyles et al. 2002). In contrast, soil C stocks in boreal forests range between 62 and 274 Mg C ha^{-1} and may amount to 90% of total ecosystem C stocks (Bhatti et al. 2003). Total ecosystem C stocks generally increase from drier to wetter boreal forest sites due to the accumulation of DOM in the organic layer and mineral soil resulting from reduced decomposition rates and long fire return intervals (Bhatti et al. 2003). Boreal forests are currently considered a small terrestrial sink for atmospheric C, sequestering a total of 0.6–0.7 Pg C yr^{-1} in the 1990s (Goodale et al. 2002). Although the projected climatic changes may increase C sequestration by enhancing plant growth due to higher temperatures, longer growing seasons, and CO_2 fertilization (Nemani et al. 2003, Canadell et al. 2007, Körner et al. 2007), augmented decomposition rates and disturbance frequencies may result in increased C emissions (Kirschbaum 1995, Kurz and Apps 1999, Rustad et al. 2000, Canadell et al. 2007), thus possibly converting boreal forests from a net sink to a net souce (Harden et al. 2000, Canadell et al. 2007, Kurz et al. 2008a).

2.2.1 Focus: Humid Northern Boreal Forests

The boreal forest is often treated as a homogenous entity, but it really is a mosaic of upland forests, true wetlands, and more or less poorly drained black spruce forests on the gradient between these (Apps et al. 1993, Bhatti et al. 2006, Bond-Lamberty et al. 2007a). These more or less poorly drained forests are poorly mapped (Peckham et al. 2009) and have so far received little scientific attention despite their large extent (Bhatti et al. 2006). Forested wetlands and peatlands cover at least 250 Mio. *ha* globally (Bond-Lamberty et al. 2007a), and account for up to 102 Mio. *ha* in Canada (Vitt et al. 2001), in addition to a large but unmapped area of poorly drained humid black spruce forests.

These poorly drained humid boreal black spruce forests often feature primary production rates similar to or even higher than their upland neighbours (Harden et al. 1997, Vitt et al. 2001, Turetsky et al. 2010), but are characterized by bryophyte-dominated ground vegetation (Bourgeau-Chavez et al. 2000, Turetsky 2003), low decomposition rates (Foster 1985, Bond-Lamberty et al. 2007a), and a thick layer of mostly bryophyte-derived DOM at the soil surface (Fenton et al. 2005, Hollingsworth et al. 2008). Consequently, organic layer and mineral soil C stocks are considerably higher than in well-drained upland boreal forests (Shaw et al. 2005, Bhatti et al. 2006, Carrasco et al. 2006), due to the balance between high tree and bryophyte productivity and low DOM decomposition rates — processes that determine organic layer C accumulation (Bond-Lamberty et al. 2004b, Hollingsworth et al. 2008). Slight changes in water table, soil temperature, and/or the disturbance regime may break this balance, possibly resulting in the release of large amounts of C to the atmosphere (Bhatti et al. 2006). Understanding the C dynamics of more or less poorly drained humid boreal forests is thus important; particularly, because they are considered highly sensitive to changing climate, disturbance, and management regimes (Bhatti et al. 2006, O'Neill et al. 2006).

Apart from the high water table, the C cycle of humid boreal forests is mainly driven by a bryophyte-dominated ground cover composed of functional groups such as feathermosses (*Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., and *Hylocomium splendens* (Hewd.) BSG.) and *Sphagnum* spp. (Hollingsworth et al. 2008, Peckham et al. 2009). Mosses influence the C cycle by contributing significantly to ecosystem net primary productivity (Bisbee et al. 2001, Harden et al. 1997, Gower et al. 2001, O'Neill et al. 2006, Turetsky et al. 2010), producing recalcitrant litter (Aerts et al. 1999, Hobbie et al. 2000, Turetsky et al. 2010), increasing soil water holding capacity and moisture content (Skre and Oechel 1981), regulating organic matter consumption during wildfire (Shetler et al. 2008), and lowering soil thermal conductivity and temperature (Turetsky 2003), thus limiting decomposition (Carrasco et al. 2006). Mosses are also associated with the processes of topographic and successional paludification (Simard et al. 2009), during which the accumulation of DOM gradually reduces plant-available nutrients (Simard et al. 2007), increases waterlogging (Fenton and Bergeron 2006), and changes the composition of the bryophyte community from feathermoss to *Sphagnum* dominance (Fenton et al. 2007), resulting in a decline of forest productivity, an increase in FRI, and possibly a conversion to peatland (Harden et al. 2000, Fenton et al. 2005, Simard et al. 2007).

Conclusions and general research needs: In order to improve boreal forest C budgets, it is necessary i) to quantify the spatial coverage and functional composition of bryophytes throughout the boreal biome, preferably using remote sensing (Peckham et al. 2009), ii) to identify and map poorly drained boreal forests such as Labrador humid boreal black spruce forests and to clearly differentiate them from upland boreal forests and true wetlands, iii) to increase scientific understanding of the functional role of bryophytes in decomposition processes, iv) to determine the impact of disturbances on bryophytes and their ecology, and v) to introduce bryophytes into forest C models used to simulate boreal forest C stocks and dynamics (Bond-Lamberty et al. 2007a, Turetsky et al. 2010).

2.2.2 Disturbance Impacts on Carbon Stocks and Dynamics

Although being subjected to disturbances at different spatial and temporal scales, the boreal forest biome has been classified as a disturbance type 3 biome, characterized primarily by ecosystems with frequent stand-initiating disturbance events such as wildfire, insect outbreaks, or clearcut harvesting (McCarthy 2001, Parminter 1995). These large-scale disturbances not only change the forest ecosystem with respect to species composition, age class distribution, and vertical and horizontal structure, but also alter C fluxes between ecosystem components and the atmosphere (e.g., photosynthesis, autotrophic and heterotrophic respiration) for considerable time periods and are often associated with significant gaseous emissions, thus exerting a strong and possibly long-term influence on the forest C cycle (KURZ ET AL. 2008b).

Stand-replacing wildfire is the dominant natural disturbance controlling the dynamics of boreal forests (HARDEN ET AL. 2000, MCCARTHY 2001), characterized by fire size, severity, season, and frequency (BOURGEAU-CHAVEZ ET AL. 2000, CERTINI 2005). Fire frequency, commonly expressed as the fire return interval (FRI; PAYETTE 1992), depends on local and regional climate, topography, amount and condition of fuel, and tree species (MCCARTHY 2001, CERTINI 2005, BOND-LAMBERTY ET AL. 2007b). It varies greatly from 40–100 years in western Canada and Alaska (YARIE 1981, NEFF ET AL. 2005), to ∼100–250 years in Québec (BOULANGER and SIROIS 2006, BOUCHARD ET AL. 2008), to 300–500 years in southeastern Labrador (FOSTER 1984). Over the past 20–40 years, fire frequency has increased steadily in parts of the boreal forest (KASISCHKE and TURETSKY 2006, CANADELL ET AL. 2007, GREENE ET AL. 2007), and is expected to increase further in the course of a changing climate (FLANNIGAN ET AL. 2005, BOND-LAMBERTY ET AL. 2007b), resulting in significantly larger amounts of CO_2 released to the atmosphere annually (KASISCHKE 2000).

Forest fire generally kills most or all trees, and converts tree regeneration, shrubs, ground vegetation, and a large proportion of the organic layer to gaseous forms (mainly CO_2, some carbon monoxide (CO) and methane (CH_4)) and to pyrogenic or black C (HARDEN ET AL. 2000, CERTINI 2005, PRESTON and SCHMIDT 2006). In consequence, photosynthesis and autotrophic respiration drastically decline until succession is initiated (O'NEILL ET AL. 2006), heterotrophic soil respiration typically declines for the first years post-fire then increases again (O'NEILL ET AL. 2002, BOND-LAMBERTY ET AL. 2004a), and stands may turn into moderate C sources for 1–2 decades following fire (BOND-LAMBERTY ET AL. 2004b, GOUGH ET AL. 2007). In addition to the immediate release of C stored in vegetation and DOM, fire can influence ecosystem C fluxes for decades by reducing organic layer thickness and physically and chemically altering DOM (CERTINI 2005), thus changing temperature and moisture regimes, microbial community size and composition, decomposition rates, and successional pathways (JOHNSTONE and KASISCHKE 2005, NEFF ET AL. 2005, GREENE ET AL. 2007, O'DONNELL ET AL. 2009b). The proportion of the organic layer consumed during a fire event is determined by the moisture content of the organic layer at the time of the fire, the duration of the combustion period, and other factors such as landscape characteristics and fire history (KASISCHKE and JOHNSTONE 2005). The degree of organic layer combustion decreases with increasing organic layer moisture content; therefore, residual organic layer thickness following fire is generally greater in more humid northern boreal forests (GREENE ET AL. 2007).

Clearcut harvesting is the dominant anthropogenic disturbance in boreal forests, currently affecting up to 1 million *ha* of Canadian forests annually (McRae et al. 2001). The area of managed boreal forest is likely to increase as the global demand for wood products rises, thus increasing the contribution of harvesting to total disturbance effects on the boreal C cycle (Howard et al. 2004). In general, clearcutting removes most or all merchantable trees, results in disturbances of the organic layer and possibly the mineral soil, and thereby considerably changes the forest microclimate (Jandl et al. 2007). However, depending on the harvesting technique and legal regulations, differences in residual vegetation and environmental impacts between individual cuts may be large (McRae et al. 2001).

Live tree C stocks are reduced considerably following harvesting, and slowly recover as first ground vegetation and later tree biomass accumulate (Howard et al. 2004). Substantial amounts of harvest residue C are generated directly following harvest (Pedlar et al. 2002, Moroni 2006), and added to organic layer C stocks (Howard et al. 2004, Jandl et al. 2007, Diochon et al. 2009). However, organic layer C stocks have been reported to increase (Mattson and Swank 1989, Howard et al. 2004, Smith et al. 2000), remain unchanged (Peltoniemi et al. 2004), or decrease following harvest (Olsson et al. 1996, Norris et al. 2009), reflecting difficulties in measurement due to high spatial variability (Diochon et al. 2009) and varying effects of harvesting on decomposition rates (McRae et al. 2001). Soil temperatures and soil moisture typically increase following harvest (Keenan and Kimmins 1993), which may increase decomposition rates in the short-term (Prescott 1997) or only below the organic layer surface (Binkley 1984). Other studies have observed unchanged or decreased decomposition rates following clearcutting (cf. Keenan and Kimmins 1993, McRae et al. 2001). Mineral soil C stocks are generally little affected by harvesting (Johnson and Curtis 2001, Norris et al. 2009), although some studies have observed decreasing mineral soil C stocks post-harvest, for example in humid coniferous forests in Nova Scotia (Diochon et al. 2009).

Conclusions and general research needs: Carbon stocks and dynamics of humid northern boreal forests have received relatively little attention so far, despite the fact that they cover large areas throughout the Canadian and circumpolar boreal region. Studies of boreal forest C dynamics have mostly focused on dry cold-continental boreal forests in North America, Russia, and Scandinavia (Krankina and Harmon 1995, Howard et al. 2004, Martin et al. 2005) or one stage of forest development (Harvey et al. 1981, Thompson et al. 2003, Zielonka 2006), or investigated specific DOM C pools such as woody debris (WD; downed dead wood; Bond-Lamberty et al. 2003, Boulanger and Sirois 2006). Deadwood, organic layer, and mineral soil C dynamics in cool and humid northern boreal forests are expected to differ from those of drier or warmer boreal forests, because accumulation of ecosystem C is higher in regions with low average temperatures (Shaw et al. 2005), high soil moisture contents (Neff et al. 2005), insulating moss layers on top of the organic layer and mineral soil (Hollingsworth et al. 2008), and long fire return intervals (Simard et al. 2009). Research is thus required to examine the impact of disturbance history and time since disturbance on biomass, DOM, and mineral soil C of humid northern boreal forests and to develop forest management strategies aimed at decreasing C sources and increasing C sinks (Canadell et al. 2007).

2.2.3 Carbon Modelling and Accounting

The long-term effects of disturbances and climate change impacts on disturbance regimes can hardly be assessed by means of field studies alone. Experimental databases from regional, chronosequence, and process studies may be used to develop, validate, and calibrate forest ecosystem models (Chertov et al. 2009). Forest ecosystem C stocks and dynamics can be simulated using numerous complex models such as Biome-BGC (Bond-Lamberty et al. 2007a), EFIMOD (Chertov et al. 2009), TRIPLEX (Peng et al. 2002), YASSO (soil C stocks; Liski et al. 2005), FORCARB (Smith and Heath 2001), CARBINE (Matthews and Broadmeadow 2003), and CBM-CFS3 (Kurz et al. 2009). Few of these models comply with the Tier 3 methodology of the Good Practice Guidance (GPG) for Land Use, Land-use Change and Forestry (LULUCF; IPCC 2006), and may be used as tools to account for forest C stocks and C stock changes in compliance with international agreements such as the UNFCCC (UNFCCC 1992).

The CBM-CFS3 is a comprehensive forest ecosystem model which implements Tier 3 GPG standards (Kurz et al. 2009), and is the core component of Canada's National Forest Carbon Monitoring, Accounting and Reporting System (NFCMARS; Kurz and Apps 2006). NFCMARS follows the "one inventory plus change" approach (IPCC 2006), which requires a forest and land inventory, data on land-use change, forest management, and disturbances, as well as models (i.e. the CBM-CFS3) for estimating inter-annual variation within the observation period (Kurz et al. 2009). The CBM-CFS3 is a stand-, landscape-, and national-level model of upland forest dynamics that tracks C stocks, C stock changes, and emissions and removals of CO_2, CH_4, and CO (Kurz and Apps 1999, Kurz et al. 2002) by simulating the impacts of disturbances, including harvesting, insect outbreaks, and fire, on forest C stocks (Kurz and Apps 1999, Kurz et al. 2009). Models such as the CBM-CFS3 can be used to assess the future net greenhouse gas balance of a particular region or country accounting for the expected changes in climate and disturbance regime (Kurz et al. 2008b). However, they should be validated and calibrated using representative field data, which is particularly important for Tier 3 estimates (Köhl et al. 2008).

Conclusions and general research needs: Estimates of organic layer and soil C stocks in particular are linked to high uncertainty due to the high spatial variability associated with organic layer and mineral soil C content (Diochon et al. 2009). With increasing soil water content, bryophyte productivity, and organic layer thickness, the uncertainty of soil C estimates derived from upland forest C models such as CBM-CFS3 is expected to increase

(Bhatti et al. 2002, Bond-Lamberty et al. 2007a). In contrast, wetland C models such as the Peatland Carbon Simulator (PCARS) are optimized for bryophyte-dominated peatlands and incorporate the hydrological complexities of peatlands (Frolking et al. 2002), but yield higher levels of uncertainty for forested peatlands (Bond-Lamberty et al. 2007a). The applicability of the CBM-CFS3 to humid northern boreal forests — located on a gradient between well-drained upland boreal forests and forested peatlands with respect to soil moisture and organic layer thickness — therefore needs to be assessed; particularly regarding the effects of natural and anthropogenic disturbance history on forest DOM and soil C stocks.

2.3 Deadwood in Boreal Forests

Deadwood is an integral component of the forest C cycle (Kurz and Apps 1993, Bond-Lamberty et al. 2003), which is not only a potentially large source of CO_2 (Krankina and Harmon 1995, Manies et al. 2005, Liu et al. 2006), but also a mid- to long-term C store (Kueppers et al. 2004, Boulanger and Sirois 2006). It also provides habitat for a range of plant and animal species (Feller 2003, Harmon et al. 2004, Schwab et al. 2006), and contributes to forest structure (Harmon et al. 2004), nutrient cycling (Laiho and Prescott 2004), and soil development (Feller 2003). In ecosystems such as the boreal forest, where decomposition is limited by low average temperatures (Apps et al. 1993), the C storage function of deadwood is more important than in ecosystems with high turnover rates.

Numerous studies have therefore assessed the contribution of deadwood to the C budget of dry cold-continental boreal forests in Russia (Krankina and Harmon 1995), Scandinavia (Vávřová et al. 2009), and North America (Bond-Lamberty et al. 2003, Manies et al. 2005, Boulanger and Sirois 2006). In contrast to other boreal regions, however, deadwood stocks and dynamics of cold-oceanic forests, e.g., in Labrador, are likely different, because decomposition rates may be limited at high substrate moisture contents despite favourable substrate temperatures (Progar et al. 2000, Laiho and Prescott 2004), while deadwood creation is expected to be similar in small-treed boreal forests with low tree growth rates.

2.3.1 Disturbance Impacts on Deadwood

Abundance and characteristics of deadwood in forest ecosystems, e.g., of woody debris (WD), snags (standing dead trees), and stumps (dead trees <1.3 m in height), are strongly influenced by disturbance history (Krankina et al. 2002, Harmon et al. 2004). In boreal forests, small- and large-scale disturbances play an important role in the creation of deadwood (Pedlar et al. 2002, Boulanger and Sirois 2006, Moroni 2006). While small-scale wind disturbance and senescence constantly create small amounts of deadwood in old-growth boreal forests (McCarthy 2001, Bergeron et al. 2002), stand-replacing fires and clearcut harvesting produce large amounts of deadwood in single events (Harden et al. 2000, Bergeron et al. 2002, Roberts et al. 2006). However, fire and harvesting differ considerably with respect to structural and temporal deadwood characteristics (McRae et al. 2001).

Wildfire generates little WD and large amounts of snags (McRae et al. 2001), which can remain standing for up to ∼30 years (Boulanger and Sirois 2006, Moroni 2006). Snag decomposition rates are usually very low due to low moisture content, charred surfaces, and delayed microbial colonization (Boulanger and Sirois 2006, Remsburg and Turner 2006, Zhou et al. 2007), resulting in small C losses from fire-generated snags (Boulanger and Sirois 2006). Woody debris accumulates throughout the first two to three decades following fire for as long as inputs from falling snags exceed decomposition rates of WD (Bond-Lamberty et al. 2003, Manies et al. 2005, Boulanger and Sirois 2006). Fire-generated WD often features a charred surface, which can be transformed into a decay-resistant shell ("case-hardening phenomenon") as a result of below-fibre saturation WD moisture levels and excessively high air temperatures observed on burned sites (Marra and Edmonds 1996, McRae et al. 2001, Mackensen and Bauhus 2003, Manies et al. 2005), possibly leading to slower decomposition of fire-generated WD compared to harvest-generated WD (Wei et al. 1997).

Clearcut harvesting generates substantial amounts of logging debris, i.e. WD, directly following harvest (Pedlar et al. 2002, Moroni 2006), dominated by smaller and shorter WD pieces than wildfire (Densmore et al. 2004, Stevenson et al. 2006). Although harvesting changes the WD decay class distribution by adding mainly undecomposed WD (Stevenson et al. 2006), harvest-generated WD generally decomposes within 20–40 years depending on tree species due to its high surface to volume ratio and its susceptibility to mechanical damage and microbial colonization (Fridman and Walheim 2000, Moroni 2006). Clearcut harvesting also produces small amounts of stumps (Pedlar et al. 2002, Moroni 2006) and snags as a result of the removal of merchantable trees and the post-disturbance death of uncut trees (Fridman and Walheim 2000, McRae et al. 2001, Pedlar et al. 2002), respectively.

Decomposition rates of WD are required for accurately modelling forest deadwood and C dynamics, and are commonly estimated by assessing mass loss or density change over time (Chambers et al. 2001, Howard et al. 2004, Jomura et al. 2008). However, these variables can generally only be determined by destructive measurements over long time periods (Boddy 1983b,a), and their relation to the individual decomposition processes (i.e. leaching, fragmentation, and respiration) is subject to scientific discussion (Brown 2002), making it important to investigate the decomposition processes separately (Jomura et al. 2008). Woody debris respiration rates are a direct measure of the amount of C released to the atmosphere during decomposition (Herrmann and Bauhus 2008), thus distinguishing between actual WD decomposition rates and WD mass loss due to fragmentation and/or leaching (Marra and Edmonds 1994, Liu et al. 2006). In a boreal black spruce forest in central Canada, WD respiration amounted to 54% of soil respiration – the second-largest C flux in terrestrial ecosystems (Rustad et al. 2000, Bond-Lamberty et al. 2003, Peng et al. 2008) – making WD respiration an important component of the forest C cycle.

Conclusions and general research needs: Previous studies on deadwood in boreal forests have mostly focused on old-growth forests (Thompson et al. 2003), or the impacts of a single disturbance such as fire (Bond-Lamberty et al. 2003, Manies et al. 2005) or harvesting (Sturtevant et al. 1997) on deadwood stocks. Few studies have contrasted the effects of wildfire and harvesting (e.g., Moroni 2006), but none have focused on humid northern boreal forests. Several studies have investigated C fluxes of disturbance-generated WD, e.g., in mature or old-growth forests (Yoneda 1975, Marra and Edmonds 1994, Progar et al. 2000, Chambers et al. 2001, Jomura et al. 2008), or following wildfire (Wang et al. 2002, Bond-Lamberty et al. 2003), selective logging (Liu et al. 2006), or clearcut harvesting (Marra and Edmonds 1996). However, studies comparing respiration rates of WD with different disturbance origins are lacking, which has been identified as an important research objective (Zhou et al. 2007). In addition, few studies have measured WD and soil respiration concurrently (Marra and Edmonds 1994, 1996, Richard and Woodtli 2006), resulting in few estimates of the magnitude of WD respiration compared to soil respiration.

2.4 General research questions

Based on the general research needs identified in the previous sections using current scientific literature, the following general research questions can be formulated:

- How do C and deadwood stocks in humid boreal forests differ from those of drier or warmer boreal forests?
- What are the effects of clearcut harvesting and wildfire on C and deadwood stocks in humid boreal forests, and do they differ from those observed in other boreal forests?
- How does disturbance history influence the respiration rate of woody debris? How does woody debris respiration compare to soil respiration in undisturbed and disturbed humid boreal forests?
- Can C budget models such as the CBM-CFS3 that were developed using data for well-drained upland forests be successfully applied to accurately simulate C stocks and dynamics of humid boreal forests? If not, can the observed differences be captured by calibrating selected model parameters or are structural changes required?

2.5 Objectives

Derived from the identified research needs, the overall objectives of this thesis are therefore:

1. to quantify C and deadwood stocks of undisturbed and disturbed humid boreal forests in Labrador and compare it to those of drier or warmer boreal forests;
2. to assess the impact of harvesting and wildfire on C and deadwood cycles in humid boreal forest ecosystems and identify components and processes differentiating humid boreal forests from drier or warmer boreal forests;
3. to investigate the impact of disturbance history on woody debris respiration rates and to determine the magnitude of woody debris respiration with respect to soil respiration;
4. to evaluate the applicability of the CBM-CFS3 to humid boreal forests and, if required, make recommendations for the modification of model components to more accurately reflect C dynamics of these forest ecosystems.

The data generated during the biomass and C inventory (Section 3.3.1) showed that the selected study sites contained unexpectedly large amounts of woody debris buried in the organic layer (buried wood). The following study objectives were therefore added:

5. to determine amounts and characteristics of buried wood in humid boreal forests;
6. to investigate the burial process with respect to changing decomposition conditions;
7. to determine the age of selected buried wood samples.

The detailed objectives and hypotheses of each individually published study are presented in the introduction section of the respective scientific articles (Section 2.6).

2.6 Structure and Strategy

This manuscripts contains five peer-reviewed scientific articles in their published or accepted form as separate subsections. They are not listed chronologically by time of publication, but in a logical order with respect to subject, data acquisition, and data analysis. The articles contain the majority of data, results, and conclusions generated in the course of this project. While each article includes its respective reference list, references cited in the introduction (Section 2), methodology (Section 3), and discussion section (Section 5) are presented in a separate reference list at the end of this manuscript. The published articles are either cited (e.g., discussion section) or referred to by their roman number (e.g., section titles).

2.6.1 Scientific Articles

I. **Hagemann, U.**, Moroni, M., and Makeschin, F. 2009. Deadwood abundance in Labrador high-boreal black spruce forests. Canadian Journal of Forest Research 39(1): 131–142, doi:10.1139/X08-166 (Impact Factor 1.434)

II. **Hagemann, U.**, Moroni, M., Gleißner, J., and Makeschin, F. 2010. Disturbance history influences woody debris and soil respiration. Forest Ecology and Management (*in press*) (Impact Factor 1.950)

III. **Hagemann, U.**, Moroni, M., Shaw, C., Makeschin, F., and Kurz, W. 2010. Comparing measured and modelled forest carbon stocks in high-boreal forests of harvest and natural-disturbance origin in Labrador, Canada. Ecological Modelling 221: 825–839, doi:10.1016/j.ecolmodel.2009.11.024 (Impact Factor 2.176)

IV. **Hagemann, U.**, Moroni, M., Gleißner, J., and Makeschin, F. 2010. Accumulation and preservation of dead wood upon burial by bryophytes. Ecosystems 13(4): 600–611, doi:10.1007/s10021-010-9343-4 (Impact Factor 3.376)

V. Moroni, M., **Hagemann, U.**, and Beilman, D.W. 2010. Dead wood is buried and preserved in a Labrador boreal forest. Ecosystems 13(3): 452–458, doi:10.1007/s10021-010-9331-8 (Impact Factor 3.376)

2.6.2 Other Publications

Selected data subsets have been included in the the following **Diploma theses**, which were submitted to the Dresden University of Technology, Institute of Soil Science and Site Ecology (Reviewers: Prof. Dr. habil. Franz Makeschin; Martin Moroni, Ph.D.) and co-supervised by Ulrike Hagemann:

I. Diekamp, M. 2009. Moss and lichen decomposition in old-growth and recently harvested high-boreal black spruce (*Picea mariana*) forest stands in Labrador, Canada; *Thesis*

II. Gleißner, J. 2009. Deadwood and soil respiration rates in clearcut, burned, and old-growth high-boreal black spruce forest ecosystems in Labrador, Canada; *Thesis*

Results from the research presented in this manuscript have also been used for preparing the following **oral and poster presentations**:

I. Shaw, C.H., Hilger, A., Kurz, W.A., Smyth, C.E., Moroni, M.T., and **Hagemann, U.** Evaluation of the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) Using the Canadian National Forest Inventory (NFI) Ground Plot Data. SSSA Annual Meeting, 1–5 November 2009, Pittsburgh, PA, USA; *Oral presentation*

II. **Hagemann, U.**, Gleißner, J., Moroni, M.T., and Makeschin, F. Dead wood respiration in harvested, burned, and old-growth high-boreal black spruce stands in Labrador, Canada. 8th International Carbon Dioxide Conference, 13–19 September 2009, Jena, Germany; *Poster*

III. Gleißner, J., **Hagemann, U.**, Moroni, M.T., and Makeschin, F. Changes in dead wood temperature, moisture, and respiration with burial in the organic layer in old-growth high-boreal black spruce in Labrador, Canada. 8th International Carbon Dioxide Conference, 13–19 September 2009, Jena, Germany; *Poster*

IV. **Hagemann, U.**, Gleißner, J., and Moroni, M.T. Dead wood in high-boreal Labrador black spruce forests - buried and forgotten? 7th North American Forest Ecology Workshop, 22–26 June 2009, Logan, UT, USA; *Oral presentation*

V. **Hagemann, U.**, Moroni, M.T., and Makeschin, F. Post-harvest dead wood dynamics and buried wood contribution to dead wood carbon stocks in Labrador black spruce forests. VI International Conference on Disturbance Dynamics in Boreal Forests, 30 May–2 June 2007, Fairbanks, AK, USA; *Poster*

2.6.3 Acknowledgement of Contributions

Ulrike Hagemann was responsible for planning, writing, and publishing the articles I–IV listed above, in collaboration with the different co-authors who have contributed to and commented the manuscripts. Studies III and IV were designed by Ulrike Hagemann, studies I and II by Martin Moroni. The field work, most of the laboratory work, and the statistical analysis upon which articles I to IV are based where carried out by Ulrike Hagemann. Other co-authors contributed to study design (J. Gleißner, M. Moroni, F. Makeschin), field work (J. Gleißner), laboratory work (J. Gleißner), analysis (J. Gleißner, C. Shaw), and discussion (J. Gleißner, M. Moroni, F. Makeschin, C. Shaw, W. Kurz). Article V was conceived and written by M. Moroni, while Ulrike Hagemann was responsible for sampling design and field work, D. Harris for sample preparation, and D.W. Beilman for sample analysis.

3 Methodology

3.1 General Approach

The study encompasses i) data collection in selected field sites along a post-disturbance chronosequence (Section 3.3.1), ii) manipulative field experiments to investigate ecological processes (Section 3.3.2), and iii) subsequent modelling exercises (Section 3.4).

3.2 Study Sites

3.2.1 Study Area

The field study was conducted in central Labrador in the "High-boreal Forest–Lake Melville" Ecoregion (Ecoregion 6; Ecoregions Working Group 1989), which represents the eastern extent of the Boreal Shield Ecozone and is a narrow extension of the boreal forest into the Taiga Shield Ecozone. Mean annual temperatures (MAT) range between -2.4°C and -1.0°C (McKenney et al. 2007), and receive approximately 1000 *mm* of precipitation distributed evenly throughout the year, making it one of the wettest North American boreal forests (Foster 1985, Environment Canada 2010a). Soils are mainly classified as Humo-Ferric and juvenile Ferro-Humic Podzols (Soil Classification Working Group 1998) (Table 3.1, Fig. 3.1), and support the most productive forests of Labrador, which are dominated by black spruce mixed with balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.; Rowe 1972), and have been subject to commercial harvest since 1969 (Roberts et al. 2006).

3.2.2 Site Selection and Description

Investigating the effects of disturbances on forest deadwood and C stocks over a time span of ∼200 years post-disturbance required a space-for-time substitution, or chronosequence, approach (Pickett 1989), which relies on minimizing variability between selected study sites with respect to all attributes other than age (Yanai et al. 2003). The uncertainty of chronosequences may, for example, be decreased by site replication (spatial replication; Yanai et al. 2003, Diochon et al. 2009).

Table 3.1: Selected characteristics of a soil profile typical of the study sites: an Ortstein humo-ferric podzol (Cape Caribou V site). *Charactéristiques d'un profil de sol typique pour les sites d'échantillonage: un podzol humo-ferrique orthique (site Cape Caribou V)*

Horizon abbreviation							
CSSC[a]	**WRB**[b]	**AG Boden**[c]	**Depth [cm]**	**Description**	**%C**	**%N**	**C:N**
LOf	O	LOf	16–5	Undecomposed and semi-decomposed organic matter; fibric; dominantly originating from feathermoss and wood; abundant fine roots; diffuse boundary	51.8	0.77	68
OmOh	O	OfOh	5–0	Semi-decomposed organic matter; mesic and humic; dominantly originating from feathermoss and wood; very abundant fine and coarse roots; sharp smooth boundary	51.2	0.73	71
Ae	E (albic)	Ahe	0–3	Light grey (7.5YR 7/1) and reddish brown (5YR 5/4); moderately silty sand; sub-polyeder structure; low compaction; few round blocks (>63 *mm*); abundant fine and coarse roots; sharp boundary	1.16	0.04	32
Bfc	B (spodic)	Bhms	3–14	Strong brown (7.5Y 5/8) and dark dusty red (10R 2.5/2); moderately silty sand; cemented sub-polyeder structure (ortstein); high to very high compaction; abundant round gravel (2-63 mm) and few round blocks (>63 *mm*); few fine and very few coarse roots; undulating diffuse boundary	4.92	0.13	38
Bfj	Bs	Bs	14–33	Light olive brown (2.5Y 5/6) and yellowish brown (10YR 5/8); very silty sand; sub-polyeder structure; high to very high compaction; some round gravel (2–63 *mm*) and numerous round blocks (>63 *mm*); no fine and very few coarse roots; diffuse boundary with pockets into underlying horizon	0.94	0.04	26
BC	C	Sw-Cv	33+	Light olive grey (5Y 6/2) bleached matrix; prominent dark reddish brown (5YR 3/4) and yellowish red (5YR 5/8) mottles; sandy-loamy silt; coherent structure; high compaction; few round blocks (>63 *mm*); no fine or coarse roots	0.11	0.01	19

[a] Ortstein Humo-Ferric Podzol; (Agriculture Canada Expert Committee on Soil Survey 1998)

[b] Haplic Podzol; (IUSS Working Group WRB 2006); [c] Pseudogley-Podsol; (Ad-Hoc-AG Boden 2005)

A replicated chronosequence of harvested sites was selected for study, composed of i) three sites harvested in 2005 (recently harvested stratum), ii) three sites harvested in 1989 (middle-aged harvested stratum), and iii) three sites harvested in 1970–72 (older harvested stratum; Table 3.2). As no suitable sites were found to complete a corresponding post-fire chronosequence, measurements were restricted to iv) three sites killed by fire in 1985 (burned stratum); and v) three old-growth sites of unknown disturbance history (old-growth stratum). Because past disturbances have the potential to leave a legacy of deadwood in the current rotation (Krankina and Harmon 1994), all disturbed sites were selected to represent stands that were old-growth spruce-dominated forests at the time of the last stand-replacing disturbance, and had regenerated to spruce-dominated stands. Regeneration had failed in all burned sites, but sites were expected to eventually regenerate to spruce (Roberts et al. 2006). Burned sites were not salvage logged. Harvesting removed all stems with a diameter at breast height (DBH) $\geq 9\ cm$, by chainsaw in the middle-aged and older harvested stratum, and by short-wood mechanical harvester in the recently harvested stratum.

As site productivity greatly affects dead organic matter stocks through varying input rates, the fifteen selected sites featured the same pre-disturbance or current forest stand type, bS842M, with the exception of the Echo Lake I site, which contained a spatial mix of medium and poor site productivity classes (Table 3.2). Stand type bS842M s dominated by black spruce ($>$75%) older than 140 years featuring an average height of 12–15 m and a crown closure of 50%-75% on sites of medium productivity. It is the most common productive forest type in Labrador, with stands reaching a maximum gross merchantable volume (GMV) of $\sim$140 m^3ha^{-1} at stand ages of $\sim$110–150 years, before going into gap dynamics at an average GMV of $\sim$113 m^3ha^{-1} (de Grandpré et al. 2000, Government of Newfoundland and Labrador 2006a). Where pre-disturbance stand type was unknown (i.e., burned stratum), stand type was assessed based on the knowledge of local foresters, relief, vegetation, soil type, and adjacent stands. Stand ages of the old-growth and harvested sites were determined from harvesting records and increment bores, respectively, following the methods described in Hagemann et al. (2009).


a) Old-growth b) Harvested c) Burned

Figure 3.1: Ortstein humo-ferric podzols at a) Cape Caribou V, b) Forkin' Brook I, and c) Cape Caribou IV sites. *Podzol humo-ferrique au site a) Cape Caribou V, b) Forkin' Brook I, et c) Cape Caribou IV.*

Strata are generally labeled such that the letter denotes the disturbance origin (H–harvest, B–wildfire, and OG–old growth, likely established following fire), and the number (range) represents the year of disturbance (harvested and burned strata, only). Different notations have been used in publications I to IV due to journal preferences and are explained in the respective methodology sections.

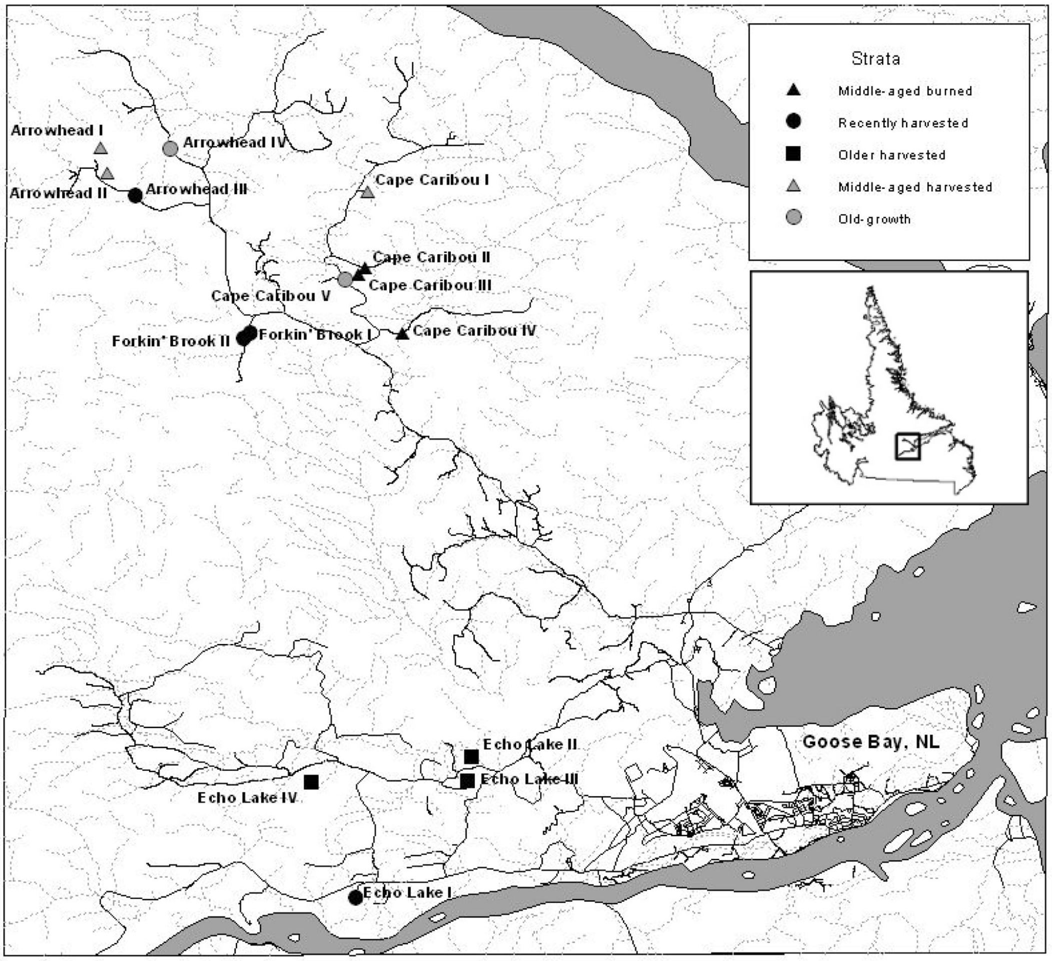


Figure 3.2: Distribution of Labrador study sites by stratum. *Les sites d'échantillonage au Labrador distribués par strate.*

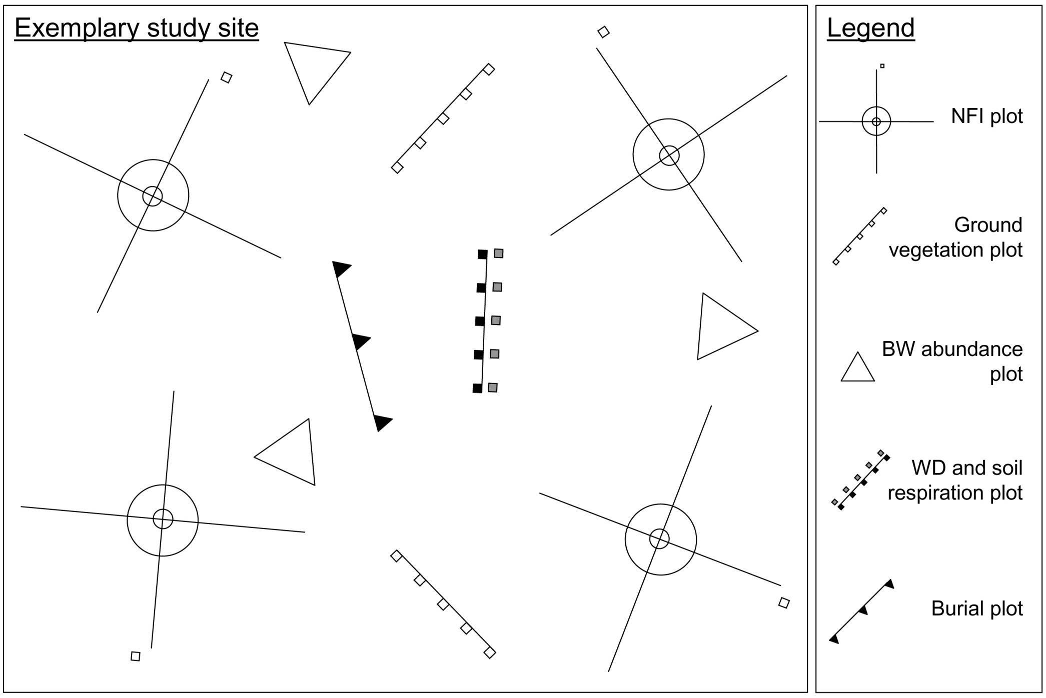


Figure 3.3: Plot distribution in an exemplary study site. *Distribution des plots dans un site d'échantillonage.*

Table 3.2: Characteristics of Labrador black spruce study sites. *Caractéristiques des sites d'échantillon-nage dans les pessières noires au Labrador.*

		Forest age[a] (years)		**Forest type[b]**		**UTM coordinates[c]**		**Climate and topography**		**Stand characteristics**			
Stratum and site	**Year of disturbance**	**Pre-disturbance**	**Current**	**Pre-disturbance**	**Current**	**Easting**	**Northing**	**Mean annual temp.[d] [°C]**	**Elevation [m a.s.l.]**	**Median DBH[e] [cm]**	**Av. tree height[e] [m]**	**Basal area [m^2ha^{-1}]**	**Merch. volume [m^3ha^{-1}]**
Recently harvested stratum													
Forkin' Brook I	2005	>140	na[f]	bS842M[g]	na[h]	647716	5934376	-2.1	281	<9.0	<5.0	0.0±0.0	0.0±0.0
Forkin' Brook II	2005	>140	na[f]	bS842M[g]	na[h]	647403	5934116	-2.0	264	11.3	6.7	0.3±0.2	0.0±0.0
Echo Lake I	2005	>140	na[f]	bS842M/P[g]	na[h]	653971	5904365	-1.1	81	9.3	6.1	0.0±0.0	0.0±0.0
Middle-aged harvested stratum													
Cape Caribou I	1989	>140	16±5	bS842M[g]	na[h]	653873	5942346	-2.4	321	14.4	9.3	0.2±0.1	0.8±0.6
Arrowhead I	1989	>140	15±5	bS842M[g]	na[h]	639244	5943596	-2.1	260	<9.0	<5.0	0.0±0.0	0.0±0.0
Arrowhead II	1989	>140	15±5	bS842M[g]	na[h]	639290	5942753	-2.2	230	9.2	5.0	0.0±0.0	0.1±0.1
Older harvested stratum													
Echo Lake II	1970–1972	>140	32±5	bS842M[g]	bSbF110M[i]	660374	5911564	-1.0	100	11.3	8.0	5.1±0.8	19.7±5.1
Echo Lake III	1970–1972	>140	32±5	bS842M[g]	bSbF110M[i]	660415	5911470	-1.1	108	11.0	7.9	5.6±0.8	22.3±5.3
Echo Lake IV	1970–1972	>140	30±5	bS842M[g]	bSbF110M[i]	656681	5909639	-1.2	134	10.2	6.8	1.9±0.4	6.7±2.2
Middle-aged burned stratum													
Cape Caribou II	1985	>140	na[f]	bS842M[g]	na[h]	653657	5938075	-1.3	99	<9.0	<5.0	0.0±0.0	0.0±0.0
Cape Caribou III	1985	>140	na[f]	bS842M[g]	Scs[h]	653558	5937764	-1.6	194	<9.0	<5.0	0.0±0.0	0.0±0.0
Cape Caribou IV	1985	>140	na[f]	bS842M[g]	Scs[h]	655909	5934525	-1.6	188	<9.0	<5.0	0.0±0.0	0.0±0.0
Old-growth stratum; unknown disturbance origin													
Cape Caribou V	na[j]	na[j]	204±20	na[j]	bS842M[g]	652723	5937344	-1.8	161	14.1	11.2	16.2±0.9	88.1±11.4
Arrowhead III	na[j]	na[j]	146±20	na[j]	bS842M[g]	641393	5941739	-2.0	223	15.1	11.5	31.1±3.3	164.2±24.6
Arrowhead IV	na[j]	na[j]	148±20	na[j]	bS842M[g]	643224	5944172	-2.2	257	12.8	10.3	27.7±1.2	138.4±9.1

[a] Forest age determined in 2006

[b] Newfoundland and Labrador forest inventory data (Government of Newfoundland and Labrador 2006a)

[c] Map datum NAD83; UTM Zone 21N

[d] Site-specific data; refer to (McKenney et al. 2007)

[e] For all trees with DBH >9.0 cm

[f] Regeneration too small for classification

[f] >75% black spruce; older than 140 years; average height 12–15 m; crown closure 50%–75%; medium (M) or poor (P) site productivity

[h] No current forest type classification; Scs = softwood scrub

[i] >50% black spruce with >25% balsam fir; older than 20 years; average height <6 m; crown closure <25%; medium site productivity; determined from neighboring stands, site conditions, and ground vegetation

[j] unknown

3.3 Field Measurements

The following section presents an overview of all conducted field measurements (Table 3.3, Fig. 3.3). Comprehensive descriptions of the applied measurement methods are given in the respective publications. Measurement methods which are unpublished to date are explained in full detail.

Table 3.3: Overview of strata, measurement periods, and conducted measurements. *Vue d'ensemble des strates, des périodes d'échantillonage, et du mesurage et d'échantillonage effectués.*

Strata	Measurement period	Measurements
Recently, midle-aged, and older harvested; Middle-aged burned; Old-growth	June–September 2006	Forest biomass and carbon inventory^a
Recently harvested; Old-growth	July–August 2007	Ground vegetation cover and biomass^a
Recently harvested; Middle-aged burned; Old-growth	July–September 2008	Aboveground woody debris and soil respiration^b
Recently harvested^d; Middle-aged burned; Old-growth	July–September 2008	Buried wood abundance and environment^c

^{a} Section 3.3.1; ^{b} Section 3.3.2; ^{c} Sections 3.3.1 and 3.3.2

^{d} For these measurements, the Echo Lake I site was replaced with a similar site near Forkin' Brook I and II to allow for completion of one measurement cycle within a day.

3.3.1 Disturbance Chronosequence

Biomass and Carbon Inventory (*Art. I, III*): Measurements were conducted from June to September 2006, and followed the National Forest Inventory (NFI) Ground Sampling Guidelines (Gillis et al. 2005, Natural Resources Canada 2010a). Four inventory plots were located randomly within each site, each consisting of two concentric circular subplots (radius 11.28 m and 3.99 m, respectively), two perpendicular 40-m line transects crossing at their mid-point at the plot center, and a 1-m^2 subplot located at the end of one randomly selected transect. Diameter at breast height (DBH) and height of live trees and snags (standing dead trees with height $\geq$1.3 m) with DBH $\geq$9 cm were measured within the 11.28-m radius subplot. Diameter and height of live trees and snags with DBH $<$9 cm and stump (standing dead trees with height $<$1.3 m) height and top diameter inside bark were measured within the 3.99-m radius subplot (Natural Resources Canada 2010a). Live individual-tree and snag aboveground biomass were estimated from regional NFI biomass equations for Ecozone 6 differentiated by site productivity class based on species, tree height, DBH (Lambert et al. 2005), and decay class (Natural Resources Canada 2010a). Stump volume was calculated assuming a cylindrical shape. Live-tree, snag and stump C stocks were estimated by multiplying oven-dry biomass by 0.5 (Matthews 1993, Lamlom and Savidge 2003).

Volume of WD was determined using the line intersect method of van Wagner and Olsen (1964). For >7.5 *cm* WD, individual diameters were measured and decay classes assigned, but only frequencies were recorded for ≤7.5 *cm* WD. Fine woody debris (≤1.0 *cm*) was sampled from the 1-m^2 subplot. All ≤7.5 *cm* WD was assigned an average decay class per diameter class and plot. Biomass of WD was estimated by multiplying WD volume by species and decay class with corresponding WD densities (Natural Resources Canada 2010a). Carbon stocks of snags, stumps, and WD were estimated by multiplying oven-dry biomass by 0.5; for <1 *cm* WD, laboratory-determined C content was used. All C analysis was done using a LECO CNS-2000 combustion analyzer (LECO Corporation 2003).

Thickness of the organic layer and buried wood (BW; WD incorporated more than 50% into the organic layer) was measured at 2-m intervals along each transect. The volume of BW and organic layer was estimated from the average thickness of each multiplied by the area of the plot it occupied. Volume of BW was multiplied with the density of decay class 4 black spruce to estimate BW biomass. Buried wood C content was assumed to be 50%. Organic layer bulk density was estimated from the volume and oven-dry mass of a sample taken from a 20 x 20 *cm* area in the 1-m^2 subplot. Organic layer samples were oven-dried, sieved (850 μm), and analyzed for C content. Mineral soil samples were taken from 0–15 *cm* (all four plots), 15–30 *cm* (two randomly selected plots), and 30–45 *cm* depths (one randomly selected plot). Sample volume was estimated by measuring the volume of glass beads required to fill the hole. Mineral soil samples were air-dried, sieved (2 *mm*), oven-dried, and weighed. Bulk density of <2 *mm* mineral soil was estimated based on sample volume and dry weight. A sub-sample was sieved (850 μm) and analyzed for C content.

Ground Vegetation (*Thesis I*): In old-growth and recently harvested sites, five vegetation plots were placed every 5 *m* along two randomly placed 20-*m* transects. At each plot, coverage of eight cover types was estimated to 5% accuracy within a 50 x 50 *cm* wooden frame: *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Sphagnum spec.* (mainly *S. rusowii* Warst. Hs and *S. capillifolium* (Ehrh.) Hedw.), dead moss, foliose ground lichen (mainly *Peltigera aphtosa* (L.) Willd. and *Nephroma arcticum* (L.) Torss.), dead lichen, vascular plants, and woody debris/bare soil/rock. At every 2nd plot, live aboveground vegetation parts of each ground cover type were clipped, oven-dried, and weighed. Biomass per hectare [$kg\ ha^{-1}$] was calculated based on cover [%] and dry mass [$kg\ m^{-2}$].

Buried Wood Abundance (*Art. IV*): Three BW inventory plots were located randomly within the old-growth sites, each comprising a 9-m equilateral triangle transect. Along each triangle transect, a trench was dug down to the mineral soil. All BW intersecting the transect was measured using the line intersect method (van Wagner and Olsen 1964). Decay classes were assigned to individual BW pieces (Natural Resources Canada 2010a), and BW biomass was estimated by multiplying BW volume with wood density for the corresponding black spruce decay class. Buried wood C stocks were calculated by multiplying

BW biomass with 0.5. Presence of bark, charring, and ingrown roots, and organic layer thickness above and below each BW piece were recorded from the center of the BW piece.

Buried Wood ^{14}C Age Determination (*Art. V*) Within each BW inventory plot, samples of ~150 cm^3 were taken from the approximate centre of 3–4 individual buried stems located near the interface of the organic layer and mineral soil. Care was taken to avoid contamination of samples with modern C, as stems were often mixed with organic or mineral soil material and penetrated by roots and fungal hyphae. Charcoal was identified on the surface of some buried wood from all sites. Excavated samples were air dried and ingrown fungal mycelia and roots were removed by hand under a stereo microscope before three or four individual small wood fragments per sample were randomly combined for ^{14}C measurement.

Potential carbonate and humic acid contamination was removed from the composited samples by Acid-Base-Acid pretreatment (65°C, 0.5 N HCl for 1 hr, 0.5 N NaOH for 1 hr, 0.5 N HCl for 4 hr) at the CHRONO Centre of Climate, Queen's University, Belfast. Samples were combusted to CO_2 at 900°C for 6 h in the presence of CuO and Ag in evacuated quartz tubes. An aliquot of CO_2 was cryogenically purified, then converted to graphite by hydrogen reduction for analysis by AMS. ^{14}C ages were calibrated to calendar ages using the IntCal04 curve and CALIB 5.1 (REIMER ET AL. 2004, STUIVER and REIMER 1993). Ages are reported as years before excavation and measurement (before 2008 AD) and rounded to the nearest decade. Calendar age of one buried wood sample with greater than modern ^{14}C content (bomb carbon) was determined using CaliBomb.

3.3.2 Manipulative Field Experiments

Aboveground WD Respiration (*Art. II, Thesis II*): Fourty-five black spruce decay class 2 (NATURAL RESOURCES CANADA 2010a) sample logs were selected from the WD present within recently harvested, middle-aged burned, and old-growth sites, cut to 30.6 ± 0.5 cm length, and sealed at both ends. Decay class 2 logs were chosen for their i) high abundance in all strata (HAGEMANN ET AL. 2009), ii) low expected variability in wood density, iii) high structural integrity, and iv) higher absolute respiration rates than more advanced decay classes (HICKS ET AL. 2003). A 20-m transect was placed randomly at each site, along which five respiration plots were located every 5 m. At each respiration plot, one sample log was placed on the ground ~2 weeks prior to the first sampling to allow for equilibration.

Respiration, wood and air temperatures, and log mass were measured nine times from July 12 to September 01, 2008, every 5-8 days. Respiration was measured for 180 s by placing sample logs into a clear acrylic closed chamber connected to an EGM-4 infrared gas analyzer (PP Systems; Amesbury, MA, USA). Woody debris respiration was calculated as CO_2 concentration increment in the system volume (corrected for log volume) per unit of emitting (lateral) wood surface and time. Four WD temperatures were recorded in pre-drilled holes (⊘ 4 mm)

using digital type K thermocouple probes (DP8811WP; Mannix, NY, USA): surface temperature, top sapwood temperature at 2 cm depth, heartwood temperature at 7 cm depth, and bottom sapwood temperature at 2 cm depth from below. Between measurements, holes were sealed with wooden dowels to avoid equilibration with ambient air. Simultaneously to WD respiration, organic layer temperature at 3 cm depth below each sample log as well as ambient air temperature and relative humidity at 30 cm above the forest floor were recorded. Log mass was determined using a digital hanging scale. Gravimetric WD moisture content was calculated using date-specific field mass and absolute dry mass determined following completion of the last measurement. Log density was calculated as dry mass $[kg]$ to volume $[m^3]$ ratio.

Measured WD respiration rates per emitting surface area were converted to per-hectare WD respiration rates to allow for comparison to per-hectare soil respiration rates. For each WD diameter class (Section 3.3.1), we calculated the total length of WD with the mid-point diameter of the respective class required to have a cylinder volume equivalent to the WD volume estimates $[m^3 ha^{-1}]$ of the respective WD diameter class. Based on the calculated total WD length and the respective diameters, the total WD surface area for each WD diameter class was calculated and summed up to total WD surface area per hectare $[m^2 ha^{-1}]$. Estimated per-hectare WD respiration rates for each measurement date were calculated by multiplying measured WD respiration rates of decay class 2 sample logs with total WD surface area per hectare, assuming all WD diameter classes to have similar WD respiration rates (Bond-Lamberty et al. 2003) and all WD to be decay class 2.

Soil Respiration (*Art. II, Thesis II*): At each respiration plot, a PVC collar ($\oslash = 10.3$ cm) was inserted 2 cm into the organic layer next to each sample log. Soil respiration was measured for 120 s simultaneously to WD respiration measurements using an SRC-1 chamber connected to an EGM-1 infrared gas analyzer (PP Systems; Amesbury, MA, USA). Organic layer temperature and moisture potential at 10 cm depth were measured concurrently to soil respiration. Organic layer thickness was measured below each collar following the last measurement.

Burial Environment (*Art. IV, Thesis II*): In the three old-growth sites, twelve decay class 2 sample logs were selected from the WD present within each site, cut to 30.7 ± 0.2 cm length, and sealed at both ends. A 25-m transect was placed randomly within each site, along which three burial plots were located at the beginning, center, and end. At each burial plot, four sample logs were placed at four different positions relative to the surface of the forest floor: P1 – on top of the live moss layer, P2 – half-buried in the organic layer but not moss-covered, P3 – completely buried in the organic layer and covered by live moss, and P4 – completely buried in the organic layer and in contact with the mineral soil (Fig. 3.4). A plastic mesh ($\sim$10 cm) was inserted below the live moss layer or the sample piece at plots P3 and P4, respectively, to facilitate handling and reduce disturbance of the organic layer material. In each site, a LogIT LT2 data logger (Supco Inc; Allenwood, NJ, USA) was installed at the center burial plot with two probes recording organic layer temperatures every 15 minutes at 2 and 20 *cm* depth (T1/2; Fig. 3.4). At each plot, a corrodible steel rod of 1.2 *m* length was implanted into the forest floor to assess oxygen availability (FENTON ET AL. 2006).

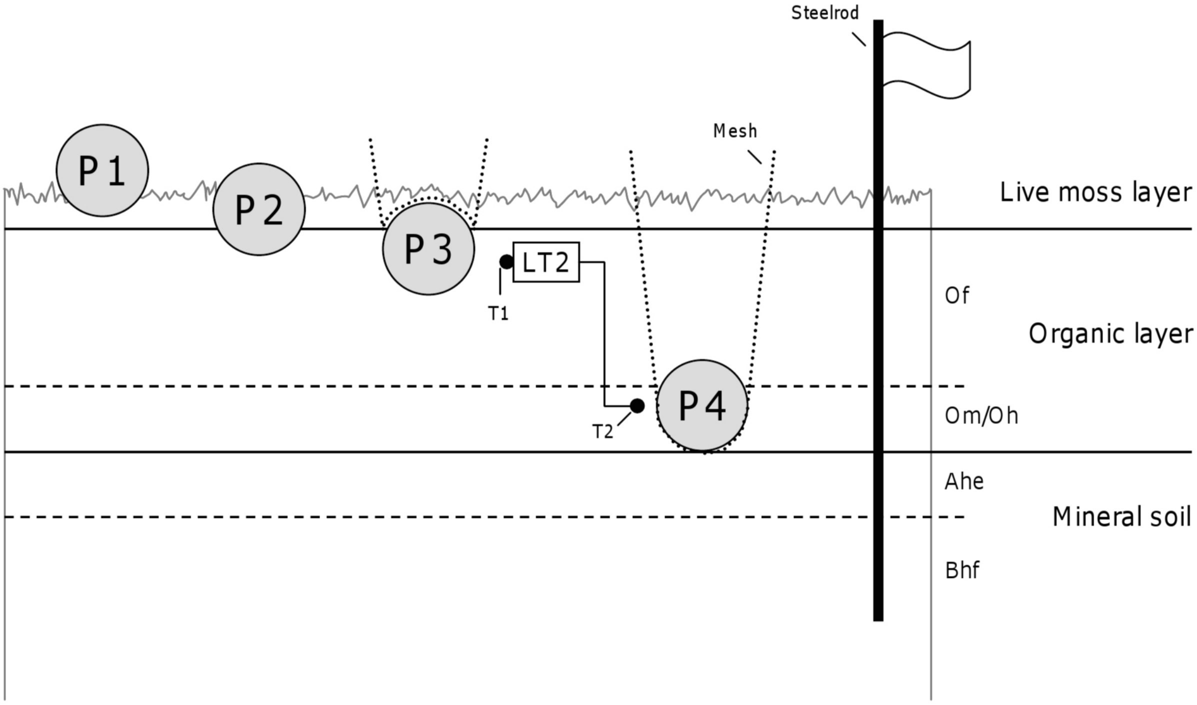


Figure 3.4: Burial positions of standardized sample logs. Organic layer and soil horizon terminology according to SOIL CLASSIFICATION WORKING GROUP (1998). *Positions d'enterrement des bûches standardisées. L'horizon de matière organique et les horizons du sol minéral sont déterminés selon (...)*

Respiration, wood and air temperatures, and log mass were measured seven times from 13 July to 27 August 2008, every 7-10 days. Logs were unearthed, cleaned from attached organic material, and respiration rates were measured following the methods described for WD respiration. Organic layer temperature below each sample log, organic layer moisture potential, top sapwood and heartwood temperature, air temperature, relative humidity, and log mass were also measured following the methods outlined above.

3.4 Carbon Modelling (*Art. III*)

The CBM-CFS3 model was applied to single theoretical stands 1 ha in size, each representative of one of the 15 sites of the field study (Section 3.2). The Labrador administrative boundary and the Boreal Shield East Ecozone were selected during data import. Stands were assumed to follow the growth curves of the respective forest types (Table 3.2) (GOVERNMENT OF NEWFOUNDLAND AND LABRADOR 2006b) adapted to field-measured species composition. For stand ages exceeding the existing growth curves, the volume of the last available age class (190–200 years) was maintained, assuming forest stands to continue under a gap-replacement system (McCarthy 2001). In annual time steps, yield curve-derived merchantable volume is converted into aboveground biomass components based on the volume-to-biomass conversion equation used to estimate Canada's national forest biomass (Boudewyn et al. 2007). Belowground biomass is predicted from aboveground biomass using stand-level regression equations for softwood and hardwood species (Li et al. 2003). Biomass components can be transferred to DOM pools through litterfall, tree mortality, and disturbance impacts. Litterfall and other turnover rates for each biomass pool are defined by regional default parameter sets. Disturbance impacts are modelled through "disturbance matrices" (Kull et al. 2007) that define the impacts of each disturbance type for each biomass and DOM pool in the stand.

During initialization, the CBM-CFS3 uses a spin-up procedure (Kurz and Apps 1999, Kurz et al. 2009) to estimate the quantity of C in soil and DOM pools before simulating scenarios. It requires user-specified assumptions about historic disturbance-return intervals, the historic disturbance type occurring during the spin-up procedure (wildfire), and the type of the last disturbance that preceded the establishment of the current stand (wildfire or clearcut harvest). During the spin-up procedure, stands are grown to the age of the disturbance-return interval and disturbed using the stand's historic disturbance type. At the end of each disturbance-return interval, the CBM-CFS3 compares the slow pool DOM C stocks between the current and previous rotations. If the difference in the stocks is $<1\%$, then the DOM C stocks are assumed to be in a quasi-equilibrium state determined by inputs (a function of net primary productivity, site productivity, disturbance type, and species) and losses from decomposition (a function of MAT) and disturbances (direct losses only from wildfires). Once equilibrium is reached, the CBM-CFS3 simulates one more rotation with the known disturbance and stand history.

Four modifications were made to the regional CBM-CFS3 default settings to better represent conditions at the scale of the studied field sites: i) 1970–2001 MAT values were estimated based on McKenney et al. (2007) rather than using the regional default value of 3.4°C; ii) the post-fire regeneration delay was set to 20 years, because black spruce regeneration in Labrador establishes slower than in central and western Canada (Foster 1985); iii) the regional default FRI (125 years) was changed to 300 years (Foster 1984); and iv) the volume-to-biomass conversion parameters used to predict biomass components were modified to better reflect measured biomass components.

Three sets of model simulations were executed: one set using the model's default parameters for the Boreal Shield East Ecozone in Labrador, a FRI of 300 years, and a 20-year regeneration delay after fire ('Default'); one set using the 'Default' parameters along with modified volume-to-biomass conversion parameters, 300-year FRI, and 20-year regeneration delay ('Modified A' parameter set); and another set to test if modelled estimates could be improved by using an alternative parameter set that included all the changes described for 'Modified A', plus modified fall rates for snag stem and snag branches, and modified base decay rates of WD C pools recommended by previously published C modelling studies, plus modifications to account for the contribution of BW ('Modified B' parameter set). Details and the comprehensive rationale for modification and parameterization of the CBM-CFS3 are given in HAGEMANN ET AL. (2010c) (*II*).

3.5 Statistical Analysis

All statistical analyses were carried out using SPSS, release 15.0.1 (SPSS Inc.). Graphs were designed using SPSS and SigmaPlot 11.0 (Systat Software, Inc.). This document has been created using MiKTeX 2.8, TeXnicCenter 7.01 (Open Source), and Citavi Pro 2.5 (Swiss Academic Software GmbH).

Forest Biomass and Carbon Inventory: Volume and biomass data was square-root transformed to meet normality and homoscedasticity assumptions when grouped by strata, WD type, WD diameter class, and WD decay class. No departures from normality were observed for C stock data within data grouped by stratum and C pool (SW-Test). Deadwood stocks of harvested and old-growth strata were analyzed with hierarchical nested linear mixed models (LMM) and variance components were calculated using Restricted Maximum Likelihood (REML). Differences in deadwood (e.g., grouped by size or decay class) and C stocks between old-growth, harvested, and burned strata were analyzed using one-way nested ANOVA, with stratum (or size class, or decay class, respectively) as a fixed factor ($k = 5$), site nested within stratum as a random factor ($n = 3$), and plot nested within site ($s = 4$). Where differences were significant ($P < 0.05$), pairwise comparisons were tested for significance using the pGH-Test. In analogy to single-parameter exponential decay models (WIEDER and LANG 1982), a single-parameter negative exponential volume reduction function was fitted to harvest-generated WD volume using nonlinear regression, as explained in detail in HAGEMANN ET AL. (2009).

Ground Vegetation: Due to non-normal data distribution, differences in ground vegetation cover [%] and biomass [$kg\ ha^{-1}$] between strata were determined using the MWU-Test.

Aboveground Deadwood and Soil Respiration: Differences in WD respiration, air temperature, WD temperatures, WD moisture content, organic layer (OL) temperatures, and OL moisture potential between strata were analyzed using univariate nested ANOVA with stratum ($k = 3$) and the respective variable as fixed factors, and site nested within stratum as a random factor ($n = 3$). Significance thresholds for multiple comparisons were adjusted using Bonferroni's equation. Differences between WD respiration and soil respiration within strata were calculated using the Wsr-Test. Correlations between WD respiration, soil respiration, air temperature, WD temperatures, WD moisture content, OL temperatures, moisture potential and thickness were calculated using Spearman's ρ. Factor analysis was employed to aggregate all environmental variables. The influence of all variables on WD and soil respiration was determined using a hierarchical nested LMM with stratum and environmental variables as fixed factors, measurement day as a repeated fixed factor, and site nested within stratum as a random factor. Random variance components were calculated using REML.

Buried Wood Abundance: Associations between interval (e.g., BW depth), ordinal (e.g., decay class), and nominal (e.g., presence of charring) variables were determined using Spearman's ρ, the χ^2-Test, and Kendall's τ, respectively.

Burial Environment: Differences in BW respiration, air temperature, BW temperatures and moisture content, OL temperatures and moisture potential between burial positions were analyzed using univariate nested ANOVA with position ($k = 4$) and the respective variable as fixed factors, and site nested within position as a random factor ($n = 3$). Correlations among BW respiration, air temperature, BW temperatures, moisture content, and density, OL temperatures, moisture potential, and thickness were calculated using Spearman's ρ. Factor analysis, LMM analysis, and REML were applied as described above for WD respiration.

Comparison of Measured and Modelled Data: The inventory data (Section 3.3.1) was used to recalculate pools that could be directly compared to the CBM-CFS3 pools prior to comparison of modelled and field-measured estimates. Statistical model evaluation was based on four goodness-of-fit statistics (SMITH and SMITH 2007) and Theil's unequality coefficient (THEIL 1966), which were used to assess model accuracy for nine C pools. Field-measured estimates were compared to those from three CBM-CFS3 simulations. Details on goodness-of-fit statistics and model parameterization are presented in HAGEMANN ET AL. (2010c).

4 Results

4.1 Live Tree Abundance

Live tree merchantable volume measured in the NFI plots ranged between 0 m^3ha^{-1} in the recently harvested and 88.1–164.2 m^3ha^{-1} in old-growth sites, and was generally in range with the volume predicted by the appropriate regional yield curve (Fig. 4.1). Variability of merchantable volume between sites was highest for the old-growth stratum, encompassing sites with considerably lower and higher merchantable volume than predicted by the yield curve. Hardwoods were negligible in all strata.

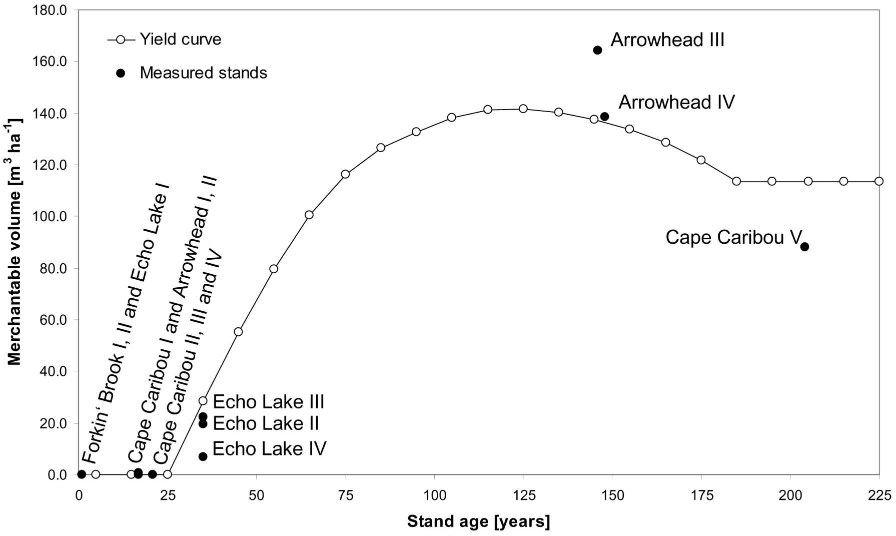
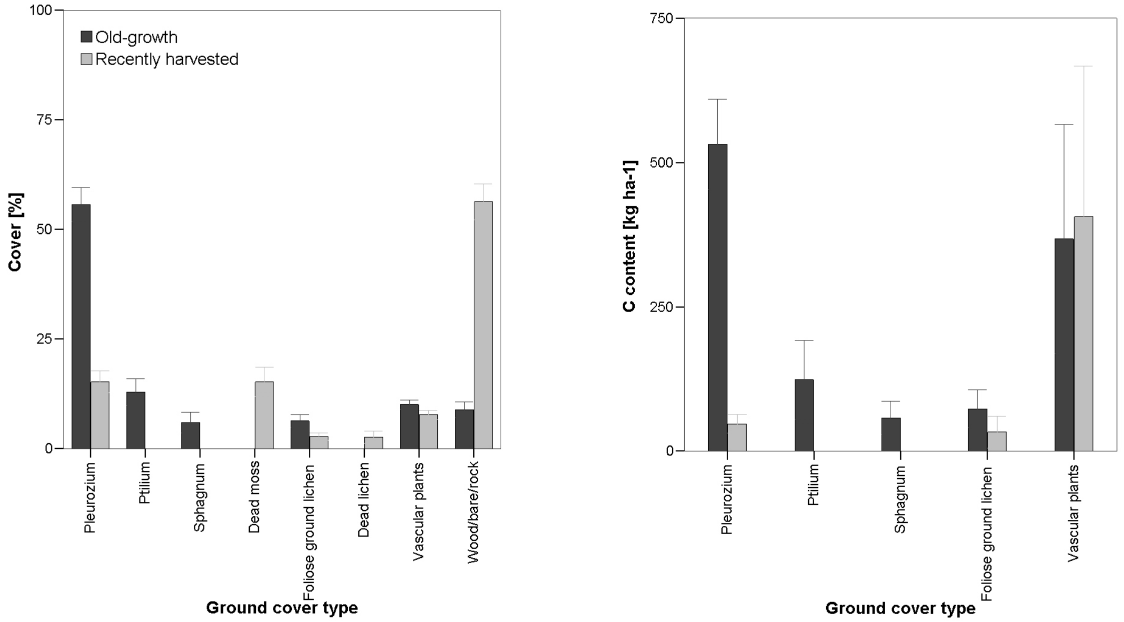


Figure 4.1: Measured merchantable volume of study sites compared to merchantable volume predicted by yield curves. *Volume marchand net des sites d'échantillonage en comparaison avec le volume marchand net selon le table de rendement.*

4.2 Ground Vegetation Abundance

Ground vegetation in the old-growth stratum was dominated by feathermosses (69%), particularly by *Pleurozium schreberi* (Fig. 4.2a), which covered significantly more area in the old-growth than in the recently harvested stratum ($P \leq 0.05$). Occurrence of *Sphagnum* and foliose ground lichen was low (6%), but while *Sphagnum* occurred in patches, foliose ground lichen were distributed relatively evenly throughout the sites. Compared to the old-growth stratum, the recently harvested stratum featured less live and more dead moss ($P \leq 0.05$) and considerably more bare mineral soil, rock, or logging slash ($P \leq 0.05$). Vascular plant cover was low (8-10%) and did not differ significantly between strata.

In the old-growth stratum, live mosses (*Pleurozium, Ptilium*, and *Sphagnum*) contained > 0.7 Mg C ha^{-1}, almost twice as much as vascular plants (~ 0.37 Mg C ha^{-1}; Fig. 4.2b). After harvesting, live feathermoss C stocks decreased significantly ($P \leq 0.05$). *Sphagnum* and foliose ground lichen biomass tended to be lower in the recently harvested than in the old-growth stratum, while vascular plant biomass tended to increase ($P > 0.05$).



a) b)

Figure 4.2: a) Cover percent and b) C stocks (±1.0 SE) of ground cover vegetation types of the old-growth and recently harvested strata. *a) Pourcentage de couverture et b) quantité de C (±1.0 SE) des types de végétation au sol des strates 'pessière vierge' et 'coupe récente'* ($n = 3$; * $\alpha = 0.05$).

4.3 Deadwood Abundance

The NFI Ground Sampling Guidelines (Natural Resources Canada 2010a) allow for detailed assessement of deadwood abundance by stratum, size class, and decay class. The following scientific article presents a detailed analysis of deadwood stocks in the selected Labrador humid boreal forest sites and discusses the impact of disturbance on these deadwood stocks.

4.3.1 Hagemann U, Moroni M, and Makeschin F. 2009. Deadwood abundance in Labrador high-boreal black spruce forests. Can. J. For. Res. 39(1): 131–142

Extended Abstract

Aboveground deadwood abundance in Labrador humid black spruce was similar to values observed in other boreal forests experiencing drier or warmer climates, but less than in larger-treed forests such as Scots pine (*Pinus sylvestris*)-Norway spruce (*Picea abies*) forests in Scandinavia with climatic conditions similar to central Labrador. Consequently, forest diameter structure is likely more important in determining WD abundance than climate.

Clearcut harvest generated large amounts of WD, which had almost completely decomposed 34-36 years following harvesting, with a fitted volume reduction rate of -0.058 yr^{-1}. Total WD in all harvested stands was predominantly composed of $<$10 cm pieces, which contributes significantly to deadwood C stocks. Smaller than 10 cm WD should therefore be included in deadwood inventories of disturbed forests, particularly of small-treed coniferous boreal forests.

Post-fire WD likely peaked ~20 years following disturbance due to the collapse of an estimated 87% of fire-generated snags. Woody debris stocks in the burned stratum were dominated by large amounts of recently collapsed (decay class 2), medium-sized (10.0–19.9 cm) snags. Snag longevity and fall rates in humid black spruce forests were thus similar to other boreal forests, with most snags falling within 25-33 years following disturbance.

Volume of BW exceeded total aboveground deadwood volume by 30–457% in all but the recently harvested and middle-aged burned strata. Old-growth stands contained 179.3 m^3ha^{-1} of buried wood (BW), which largely exceeded most values reported in the literature. The large amounts of BW indicate that a significant proportion of aboveground WD generated by senescence and stand-replacing disturbances must be buried by the vigorously growing moss layer. The long-term accumulation of BW in the organic layer requires significantly depressed rates of WD decomposition following burial and is potentially not significantly interrupted by stand-replacing disturbances such as wildfire. Calculating WD decay rates based on aboveground measurements of WD abundance may, therefore, overestimate decay rates. A combination of climate, micro-topography, ground vegetation, and stand disturbance history may initiate and facilitate the accumulation of BW, likely resulting in high BW abundance in cool and moist coniferous forests with a vigorous moss layer and long fire-return intervals. If BW is excluded from deadwood inventories in these forest ecosystems, total deadwood stocks could be significantly underestimated.

Deadwood abundance in Labrador high-boreal black spruce forests

Ulrike Hagemann, Martin T. Moroni, and Franz Makeschin

Abstract: Deadwood (woody debris (WD), standing dead trees (snags), stumps, and buried deadwood) abundance was estimated in Labrador humid high-boreal black spruce (*Picea mariana* (Mill.) BSP) forests regrown following natural and anthropogenic disturbances. Aboveground deadwood (DW) abundance in Labrador was similar to values observed in other boreal forests experiencing drier or warmer climates. Clear-cut harvest generated large amounts of WD, which had almost completely decomposed 34–36 years following harvesting, with a fitted volume reduction rate of –0.058 year^{-1}. Total WD in all harvested stands was composed of predominantly <10 cm pieces, which should be included in DW inventories of disturbed coniferous boreal forests. Postfire WD likely peaked ~20 years following disturbance, as a result of the collapse of snags, and was dominated by large amounts of medium-sized logs (10.0–19.9 cm). Buried DW stocks considerably exceeded total aboveground DW stocks in old-growth, middle-aged, and older harvested stands. Old-growth stands contained 179.3 m^3·ha^{-1} of buried DW, a vast amount indicative of long-term accumulation requiring significantly depressed rates of WD decomposition following burial. DW stocks could be significantly underestimated if buried DW is excluded from DW inventories in cool and moist coniferous forests with long fire-return intervals.

Résumé : L'abondance du bois mort (débris ligneux (DL), arbres sur pied (chicots), souches et bois mort enterré) a été estimée dans les forêts boréales supérieures humides d'épinette noire (*Picea mariana* (Mill.) BSP) du Labrador qui ont repoussé à la suite de perturbations naturelles et anthropogéniques. L'abondance du bois mort aérien (BM) au Labrador était similaire aux valeurs observées dans d'autres forêts boréales soumises à des conditions climatiques plus sèches et plus chaudes. La coupe à blanc a généré de grandes quantités de DL qui s'étaient presque complètement décomposés 34–36 ans après la coupe avec un taux de diminution du volume calculé de –0,058 an^{-1}. Les DL totaux dans tous les peuplements récoltés étaient surtout composés de pièces de bois de moins de 10 cm qui devraient être incluses dans les inventaires de BM dans les forêts boréales perturbées de conifères. Les DL présents après un incendie ont vraisemblablement atteint un maximum ~20 ans après la perturbation à cause de la chute au sol des chicots, dominés par une grande quantité de billes de dimension moyenne (10,0–19,9 cm). Les stocks de BM enterré excédaient considérablement les stocks de BM aérien dans les peuplements mûrs, d'âge moyen et plus vieux qui avaient été coupés. Les peuplements mûrs contenaient 179,3 m^3·ha^{-1} de BM enterré, vraisemblablement le résultat d'une accumulation à long terme due à un faible taux de décomposition des DL après leur enfouissement. Les stocks de BM pourraient être sous-estimés de façon significative si le BM enterré est exclus de l'inventaire du BM dans les forêts de conifères fraîches et humides où l'intervalle entre les feux est long.

[Traduit par la Rédaction]

Introduction

Deadwood (DW) — consisting of woody debris (WD; downed deadwood), snags (standing dead trees), stumps, and buried DW — is an important component of forest structure. DW is integral to a range of ecosystem functions (Harmon et al. 2004), including carbon and nutrient cycles (e.g., Kurz and Apps 1993; Laiho and Prescott 2004; Manies et al. 2005), and provides habitats for a range of species (e.g., Harmon et al. 2004), including small mammals and birds in Labrador (Simon et al. 2000, 2002; Schwab et al. 2006). Disturbance history strongly influences DW stocks (Harmon et al. 2004; Krankina et al. 2002). Interest in impacts of natural and anthropogenic disturbances on DW dynamics in boreal forests has grown as the area under management increases and expands into the last remaining boreal regions without significant development, such as boreal Labrador (Roberts et al. 2006). In contrast to other boreal regions, the high-boreal black spruce (*Picea mariana* (Mill.) BSP) forest in Labrador features a perhumid high-boreal ecoclimate (Ecoregions Working Group 1989), with an average annual precipitation of ~1000 mm (Environment Canada 2008), resulting in generally high soil moisture levels (Wilton 1964; Roberts et al. 2006). Although tree size and growth rate in these forests are similar to those in other boreal regions, we expect DW abundance in Labrador to differ from that in drier boreal forests such as those in Manitoba and Quebec (Bond-Lamberty et al. 2003; Manies et al. 2005; Boulanger and Sirois 2006), because high wood moisture levels and cool temperatures can suppress decomposition rates (Progar et al. 2000).

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Table 1. Characteristics of Labrador black spruce sites.

		Forest age (years)		Forest type		UTM coordinates[†]			
Site, site group, and forest area	Year of disturbance	Predisturbance*	Current*	Predisturbance*	Current*	Northing	Easting	Mean annual temp. (°C)[‡]	Elev. (m a.s.l.)
Sites harvested 1 year before measurement (H01)									
Forkin' Brook I	2005	>140	na[§]	bS842M[‖]	na[¶]	353131	5934094	–2.1	281
Forkin' Brook II	2005	>140	na[§]	bS842M[‖]	na[¶]	352812	5933840	–2.0	264
Echo Lake I	2005	>140	na[§]	bS842M/P[‖]	na[¶]	358754	5903956	–1.1	81
Sites harvested 17 years before measurement (H17)									
Cape Caribou I	1989	>140	16±5	bS842M[‖]	na[¶]	359455	5941933	–2.4	321
Arrowhead I	1989	>140	15±5	bS842M[‖]	na[¶]	344854	5943491	–2.1	260
Arrowhead II	1989	>140	15±5	bS842M[‖]	na[¶]	344882	5942647	–2.2	230
Sites harvested 34–36 years before measurement (H34–36)									
Echo Lake II	1970–1972	>140	32±5	bS842M[‖]	bSbF110M[**,††]	365307	5911019	–1.0	100
Echo Lake III	1970–1972	>140	32±5	bS842M[‖]	bSbF110M[**,††]	365346	5910925	–1.1	108
Echo Lake IV	1970–1972	>140	30±5	bS842M[‖]	bSbF110M[**,††]	361574	5909172	–1.2	134
Sites killed by wildfire 21 years before measurement (B21)									
Cape Caribou II	1985	>140[††]	na[§]	bS842M[‖]	na[¶]	359143	5937667	–1.3	99
Cape Caribou III	1985	>140[††]	na[§]	bS842M[‖]	Scs[¶]	359044	5937358	–1.6	194
Cape Caribou IV	1985	>140[††]	na[§]	bS842M[‖]	Scs[¶]	361326	5934070	–1.6	188
Old-growth forest sites of unknown disturbance origin (OG)									
Cape Caribou V	na	na	204±20	na	bS842M[‖]	358200	5936956	–1.8	161
Arrowhead III	na	na	146±20	na	bS842M[‖]	346964	5941589	–2.0	223
Arrowhead IV	na	na	148±20	na	bS842M[‖]	348846	5943983	–2.2	257

*Newfoundland and Labrador forest inventory data (Newfoundland and Labrador Provincial Forest Service, Data Dictionary for District Library).

[†] Map datum NAD83; UTM Zone 20.

[‡] Site-specific data; refer to McKenney et al. (2007).

[§] Regeneration too small for classification.

[‖] >75% black spruce; older than 140 years; average height 12–15 m; crown closure 50%–75%; medium site productivity.

[¶] No current forest type classification. Scs, softwood scrub.

**>50% black spruce with >25% balsam fir; older than 20 years; average height <6 m; crown closure <25%, medium site productivity.

[††] Determined from neighboring stands, site conditions, and ground vegetation.

Table 2. Gross merchantable volume (GMV) for forest type bS842M based on regional yield curve (stand volume development with stand age), measured GMV, and measured total live tree wood volume (includes stem, top, bark, and branches) for harvested and old-growth sites.

			GMV ($m^3 \cdot ha^{-1}$)†			Total volume ($m^3 \cdot ha^{-1}$)‡		
Age-class	GMV*	Site group	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
0–10	0.0	H01	0.0	0.0	0.0	0.5	2.6	0.8
11–20	0.0	H17	0.8	0.0	0.1	3.0	0.8	1.0
31–40	28.4	H34	19.7	22.3	6.7	40.9	41.5	17.8
141–150	137.6	OG		164.2	138.4		258.5	216.5
>181	113.6	OG	88.1			133.6		

*GMV from yield curve (Newfoundland and Labrador Department of Natural Resources 2008).
†Measured GMV calculated according to Warren and Meades (1986) for District 19, Labrador.
‡Measured total volume calculated according to Natural Resources Canada (2008).

Clear-cut harvest is the major anthropogenic forest disturbance in Labrador, with a total cut area of roughly 21 000 ha in the central regions since the start of commercial harvesting in 1969, most of which have regenerated to black spruce and balsam fir (*Abies balsamea* (L.) Mill.) (Roberts et al. 2006). The major natural disturbance is wildfire (Wilton 1964), but the fire-return interval for central and southeastern Labrador is uncertain, with estimates ranging from 250 to 500 years — longer than the fire-return interval for other boreal forests (Foster 1983; McRae et al. 2001). Although large-scale clear-cut harvesting and wildfire are both stand-replacing disturbances, they differ with respect to a wide range of ecological implications, such as postdisturbance stand structure, nutrient cycling, and DW dynamics (McRae et al. 2001; Pedlar et al. 2002).

Immediately following disturbance, harvesting generates large amounts of WD (Pedlar et al. 2002; Moroni 2006), generally dominated by small-diameter WD, which will decompose quickly because of its high surface to volume ratio and its susceptibility to mechanical damage and desiccation (Fridman and Walheim 2000; Moroni 2006). Unlike harvesting, wildfire generates little WD and large amounts of snags, which remain standing for as long as 20–30 years because of low snag decomposition rates (Moroni 2006; Zhou et al. 2007; Zielonka 2006). WD accumulates throughout the first two decades following fire for as long as inputs from falling snags exceed decomposition rates (Manies et al. 2005; Boulanger and Sirois 2006). Previous studies on DW in boreal forests have mostly focused on the impacts of a single disturbance such as fire (Bond-Lamberty et al. 2003) or harvesting (Sturtevant et al. 1997). Few studies have contrasted the effects of wildfire and harvesting.

Study objectives were threefold: (*i*) to quantify DW stocks in the humid high-boreal spruce stands of Labrador and compare them with those reported for boreal forests elsewhere, (*ii*) to analyze the impact of clear-cut harvesting on DW stocks in Labrador, accounting for the influence of DW decay and size class, and (*iii*) to contrast DW stocks in harvested sites with those in old-growth stands aged >140 years and sites burned 21 years before measurement.

Materials and methods

Site selection and description

The study area is situated near Goose Bay, Labrador, in Ecodistrict 452 in the High-boreal Forest – Lake Melville Ecoregion (Ecoregion 6; Ecoregions Working Group 1989), which represents the eastern extent of the Boreal Shield Ecozone and is a narrow extension of the boreal forest into the Taiga Shield Ecozone. Mean annual temperatures range between –2.4 and –1.0 °C (McKenney et al. 2007). Annual precipitation of ~1000 mm is well distributed throughout the year and is among the highest rates for the North American boreal forest (Foster 1985; Environment Canada 2008). The upland forests, the most productive forests of Labrador, are dominated by black spruce mixed with balsam fir and white birch (*Betula papyrifera* Marsh.) (Rowe 1972) and have been subject to commercial harvesting since 1969 (Roberts et al. 2006).

Fifteen forest sites located near Happy Valley – Goose Bay, central Labrador, supporting black spruce dominated forests and regenerating following harvesting and fire, were selected for study (Table 1). As site productivity greatly affects dead organic matter stocks through varying input rates, the selected sites supported forests of the same stand type, bS842M; i.e., dominated by black spruce (>75%), older than 140 years, featuring an average height of 12–15 m and a crown closure of 50%–75%, and growing on sites of medium productivity (Government of Newfoundland and Labrador 2006). The forest type bS842M is the most common productive forest type in Labrador, with stands reaching a maximum gross merchantable volume of ~140 $m^3 \cdot ha^{-1}$ at stand ages of ~110–150 years, before going into gap dynamics at an average gross merchantable volume of ~113 $m^3 \cdot ha^{-1}$ (Table 2). Only Echo Lake I contained a spatial mix of medium and poor site productivity classes (Table 1). Where predisturbance stand-type data were unavailable (i.e., burned sites), the stand type was assessed based on the knowledge of local forestry professionals, on site-specific relief and vegetation, on soil type, and on characteristics of adjacent stands. Stand age of old-growth and harvested stands was determined from increment bores (Table 1). All disturbed stands had regenerated or were regenerating to forests dominated by black spruce.

Sites are labeled such that the letter denotes the disturbance origin (H, harvest; B, fire or burn; OG, old growth, likely originating following fires), followed by a numerical that represents the years since disturbance. Harvested sites were selected to form a chronosequence consisting of three site groups replicated three times for a total of nine sites: (1) three sites harvested 1 year before measurement (H01); (2) three sites harvested 17 years before measurement

Table 3. Description of decay classes used to classify deadwood within study sites, and deadwood density by species and decay class.

	Decay class				
	1	2	3	4	5
Decay class attributes*					
Wood texture	Intact, hard	Intact, hard to partly decaying	Hard, large pieces, partly decaying	Small, blocky pieces	Many small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging near ground or broken	All of log on ground, sinking	All of log on ground, partly sunken
Twigs <3 cm (if originally present)	Twigs present	No twigs	No twigs	No twigs	No twigs
Bark	Bark intact	Intact or partly missing	Trace bark	No bark	No bark
Shape	Round	Round	Round	Round to oval	Oval
Invading roots	None	None	In sapwood	In heartwood	In heartwood
Wood density by species (kg·m^{-3})*					
Picea mariana	410	341	272	203	134
Abies balsamea	340	271	202	133	64
Betula papyrifera	506	424	342	259	177

*Based on Canada's National Forest Inventory (Natural Resources Canada 2008).

(H17); and (3) three sites harvested 34–36 years before measurement (H34–36). H01 sites are referred to as "recently disturbed", H17 sites as "middle-aged", and H34–36 sites as "older". No suitable sites were found to complete a corresponding postfire chronosequence, thus postfire measurements were restricted to sites temporally equivalent to the H17 sites: three sites killed by fire 21 years before measurement (B21). Harvesting removed all stems with a diameter at breast height (DBH) ≥9 cm to a top diameter of 8 cm, by chainsaw in the H17 and H34–36 sites, and by shortwood mechanical harvester in the H01 sites. All fires were stand replacing, and the sites were not salvage logged.

Because of the clustered nature of harvesting operations and wildfire, all sites are located within one of four forest areas: Arrowhead Lake, Forkin' Brook, Cape Caribou, and Echo Lake (Table 1). The data hence included three hierarchical levels of clustering: forest area, site group, and site. Four sample plots were located randomly within each site. Each plot contained two concentric circular subplots (radius 11.28 and 3.99 m, respectively) with two 40 m line transects, perpendicular to each other, crossing at their midpoint at the plot center. At the end of one randomly selected transect, a square subplot (1 m^2) was established. All field measurements were conducted from June to September 2006.

Field measurements

Field measurements were based on the National Forest Inventory Ground Sampling Guidelines (Natural Resources Canada 2008). The diameter and height of snags (standing dead trees ≥1.3 m in height) with DBH ≥9 cm and DBH <9 cm were measured within the 11.28 and 3.99 m radius circular subplots, respectively. Where snag tops had fallen, intact snag heights were estimated, and the proportion of snag volume remaining was determined from stem volume distribution equations (Honer 1965). Stump (dead stems <1.3 m in height) volume was estimated from stump height and top diameter inside bark for all stumps located within the 3.99 m radius subplot, assuming a cylindrical stump shape (Natural Resources Canada 2008).

At the point of intersection with the line transect, WD diameters were measured across the full length of each transect to calculate WD volumes using the line intersect method (van Wagner and Olsen 1964; eq. 8 in Marshall et al. 2000) along the 40 m transects. Individual diameters were recorded for >7.5 cm diameter WD, but only the frequency of 1–3, 3–5, and 5–7.5 cm WD diameter classes was recorded. Large slash piles (accumulation) of WD were visually compressed to measure the actual rectangular cross-sectional area of wood (Natural Resources Canada 2008). All 0–1.0 cm diameter WD lying above the litter layer was sampled from the 1 m^2 plot, dried in a forced air oven at 55 °C for 4 days, and weighed.

Decay classes (Table 3; Natural Resources Canada 2008) were assigned to individual snags, stumps, and >7.5 cm WD. Snag branch and bole biomass (dry mass) estimates were based on regional biomass equations for Ecozone 6 differentiated by site productivity class (Lambert et al. 2005). Decay class 1 snags were assumed to have retained all bark and branches, whereas decay class 2 snags retained all bark and 50% of original branch volume. Based on visual observations from the study sites, older snags were as-

Table 4. Summary statistics of hierarchical nested linear mixed models describing the influence of site group, forest area, and site on the volume of aboveground deadwood (DW), buried DW, total woody debris (WD), <10 cm WD, and snags.

	Factor type	*F*	Wald *Z*	*p*	Variance (%)
Aboveground DW volume					
Intercept		549.726		<0.001*	
Site group	F	30.702		<0.001*	82.6
Forest area(site group)	R		na†	na†	0.0
Site(forest area(site group))	R		1.267	0.205	5.4
Error			4.243	<0.001*	12.0
Buried DW volume					
Intercept		42.750		0.030*	
Site group	F	1.201		0.471	2.1
Forest area(site group)	R		0.301	0.763	15.1
Site(forest area(site group))	R		0.862	0.389	17.9
Error			4.243	<0.001*	64.9
Total WD volume					
Intercept		444.466		<0.001*	
Site group	F	29.737		<0.001*	4.0
Decay class	F	64.119		<0.001*	14.1
Size class	F	38.210		<0.001*	5.4
Site group × decay class	F	15.150		<0.001*	18.8
Site group × size class	F	4.846		<0.001*	3.1
Decay class × size class	F	7.592		<0.001*	6.6
Forest area(site group)	R		na†	na†	0.0
Site(forest area(site group))	R		0.258	0.797	0.1
Error			18.385	<0.001*	47.9
<10 cm WD volume					
Intercept		123.863		0.008*	
Site group	F	6.184		0.103	0.0
Decay class	F	97.788		<0.001*	13.5
Size class	F	1.795		0.128	0.0
Site group × decay class	F	37.930		<0.001*	30.5
Site group × size class	F	1.182		0.291	0.2
Decay class × size class	F	2.627		<0.001*	1.5
Forest area(site group)	R		0.482	0.669	0.5
Site(forest area(site group))	R		0.848	0.397	0.5
Error			23.875	<0.001*	53.4
Snag volume					
Intercept		3.822		0.110	
Site group	F	454.121		<0.001*	8.4
Decay class	F	3.808		0.037*	3.5
Site group × decay class	F	454.121		<0.001*	12.9
Forest area(site group)	R		0.831	0.406	0.8
Site(forest area(site group))	R		na†	na†	0.0
Error			15.069	<0.001*	74.4

Note: All data were square-root transformed. Site group is a fixed factor (F); forest area nested within site group and site nested within forest area nested within site group are random factors (R). Snag and WD analyses include decay class and its interaction with site group as a fixed factor; WD analyses also include size class and its interaction. Statistics shown include individual test statistics, significance, and variance partitioning among fixed and random factors.

*Significant at $\alpha = 0.05$

†This parameter is redundant. Test statistic could not be calculated.

sumed to have no bark or branches. Woody debris biomass was estimated by multiplying WD volume by species and decay class with corresponding WD densities (Table 3; Natural Resources Canada 2008). Unidentifiable DW and 0–7.5 cm diameter WD were assumed to be black spruce. All 1–7.5 and <1 cm diameter WD were assigned an average decay class per plot. Average decay classes were estimated from visual observation of all 1–7.5 and <1 cm WD encountered along the line transects within each plot.

At 2 m intervals along each transect, a shovel was driven into the surface of the forest floor to observe buried DW and to measure organic layer depth. We defined buried DW as WD that is more than half buried in the organic layer, and measured the organic layer depth range occupied by buried

Table 5. Volume and biomass of deadwood observed in the study sites.

	Postharvest stands				
Variable	H01	H17	H34–36	Postfire stand, B21	Old-growth stand, OG
Volume ($m^3 \cdot ha^{-1}$)					
Woody debris	144.0 (126.1–162.5)Aa	61.5 (34.6–91.9)Ab	6.4 (3.8–9.3)ADc	91.5 (83.3–100.0)Ad	46.9 (34.8–59.8)Ab
Snags					
DBH≥9 cm	1.0 (0.4–1.7)a	2.3 (1.4–3.2)a	0.6 (0.2–1.0)a	12.9 (3.3–25.1)b	37.6 (22.8–54.1)c
DBH<9 cm	0.2 (0.0–0.5)a	0.0 (0.0–0.0)b	0.0 (0.0–0.0)b	0.5 (0.0–1.2)a	0.0 (0.0–0.0)ab
Total snags	1.2 (0.7–1.8)Ba	2.3 (1.4–3.2)Ba	0.6 (0.3–1.0)BCa	13.5 (3.5–25.9)Bb	37.6 (22.8–54.1)Ac
Stumps	7.6 (4.9–10.6)Ca	8.9 (8.0–9.9)Ca	3.3 (0.2–7.8)ACb	2.2 (1.0–3.6)Cb	1.2 (0.0–3.1)Bb
Aboveground total	152.9 (137.0–169.2)a	72.7 (54.9–102.3)b	10.3 (4.5–17.1)c	107.2 (102.3–112.2)a	85.7 (57.8–116.0)ab
Buried wood	57.5 (12.6–115.3)Cab	94.3 (35.6–164.9)ACab	57.4 (32.4–85.5)Dab	46.4 (10.7–92.0)BCa	179.3 (49.0–342.7)Ab
Total	210.4 (143.2–283.5)a	167.0 (84.4–261.9)a	67.7 (37.7–101.5)b	153.6 (110.8–199.3)a	264.9 (118.5–436.2)a
Biomass ($Mg \cdot ha^{-1}$)					
Woody debris	50.9 (45.4–56.6)Aa	16.7 (9.6–24.6)Ab	1.6 (0.9–2.3)ADc	28.0 (25.0–31.2)Ad	12.7 (9.5–16.2)Ab
Snags					
DBH≥9 cm	0.3 (0.1–0.6)a	0.6 (0.3–0.9)a	0.2 (0.0–0.4)a	4.2 (1.0–8.3)b	11.0 (6.6–16.1)c
DBH<9 cm	0.1 (0.0–0.2)ac	0.0 (0.0–0.0)b	0.0 (0.0–0.0)b	0.2 (0.0–0.4)c	0.0 (0.0–0.0)ab
Total snags	0.4 (0.2–0.6)Ba	0.6 (0.3–0.9)Ba	0.2 (0.1–0.4)BCa	4.4 (1.0–8.6)Bb	11.1 (6.6–16.1)Ac
Stumps	2.8 (1.6–4.0)Ca	2.6 (2.1–3.2)Ca	0.7 (0.1–1.6)ABb	0.5 (0.3–0.8)Cb	0.2 (0.0–0.7)Bb
Aboveground total	54.1 (49.5–58.8)a	9.9 (13.0–27.5)b	2.5 (1.1–4.0)c	32.9 (30.8–35.0)d	24.0 (16.0–32.7)bd
Buried wood	11.7 (2.6–23.4)Cab	19.2 (7.2–33.5)ACab	11.6 (6.6–17.4)Dab	9.4 (2.2–18.7)BCa	36.4 (9.9–69.6)Ab
Total	65.7 (50.5–82.0)a	39.0 (21.5–58.9)a	14.0 (7.8–21.1)b	42.3 (32.9–52.2)a	60.4 (31.0–94.0)a

Note: Values are means with 95% confidence intervals in parentheses; lowercase letters denote significant differences within rows; uppercase letters denote significant differences between biomass or volume of woody debris, total snags, stumps, roots, and buried wood within column; nested ANOVA; $n = 3$, $k = 5$; $s = 4$; post-hoc Games–Howell; $P < 0.05$.

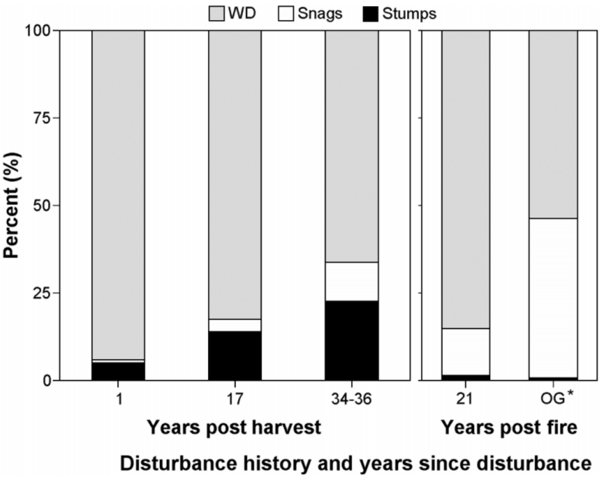
DW. The area of the forest floor overlaying DW was determined from the proportion of 2 m observations that encountered buried wood. The average depth of DW and the area of forest floor overlaying DW were used to determine DW volume per plot. The majority of buried wood observed in this study had maintained wood structure and was thus assumed to have the average density of decay class 4 black spruce wood (Table 3), enabling the calculation of DW mass per plot.

Statistical analyses

Statistical analysis was carried out using SPSS, release 16.0.2 (SPSS Inc., Chicago, Illinois). Departures from normality within data groups were examined using a Shapiro–Wilk test (Bortz 1999). All data had to be square-root transformed to meet normality and homoscedasticity assumptions. DW stocks along the harvesting chronosequence, including old-growth reference sites, were analyzed with hierarchical nested linear mixed models using the SPSS MIXED procedure. Models were set up with site group as a fixed factor, and forest area, site, and plot as random factors (Piepho et al. 2003). Models analyzing WD stocks additionally included decay class and size class as well as their interactions with site group as fixed factors. Variance components were calculated using restricted maximum likelihood.

As forest area nested within site was never a significant random factor, contrasting of old-growth, harvested, and burned sites with respect to size class and decay class was done using mixed ANOVA, with site group (or size class or decay class, respectively) as a fixed factor ($k = 5$), site nested within site group as a random factor ($n = 3$), and plot nested within site ($s = 4$; Box et al. 1978). Where differences were significant ($P < 0.05$), pairwise comparisons were tested for significance using the Games–Howell test.

Fig. 1. Relative contribution of woody debris, snags, and stumps to total aboveground deadwood biomass by disturbance history and years since disturbance. *, old growth of unknown origin.



Harvesting was assumed to have generated all aboveground WD in decay classes 1 and 2 for H01 sites, in decay classes 2 to 4 for H17 sites, and in decay classes 3 to 5 for H34–36 sites. In analogy to single-parameter exponential decay models (Wieder and Lang 1982), a single-parameter negative exponential volume reduction function was fitted to harvest-generated WD volume using nonlinear regression (SPSS), where V_t is WD volume at time t after clear-cut harvest, and k_V is an empirically derived volume reduction constant (Mackensen and Bauhus 1999):

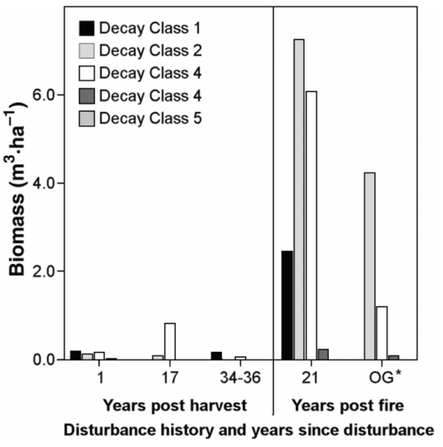
$$[1] \qquad V_t = V_0(e^{k_V t})$$

Table 6. Woody debris volume and biomass by size class and decay class in the study sites.

	Postharvest stands				
Variable	H01	H17	H34–36	Postfire stand, B21	Old-growth stand, OG
Volume ($m^3 \cdot ha^{-1}$)					
Diameter range (cm)					
≥20	8.1 (1.0–17.9)Cab	12.4 (10.6–14.2)a	0.0 (0.0–0.0)Bb	6.0 (3.4–8.9)ACab	8.3 (4.3–12.7)Bab
10 to <20.0	22.3 (17.1–27.8)Bab	13.8 (9.6–18.3)b	1.5 (1.2–1.8)Bc	46.2 (36.4–56.5)Ba	23.3 (17.3–29.6)ABa
0 to <10.0	38.2 (35.3–41.1)Aa	21.3 (9.8–34.8)b	4.9 (2.5–7.6)Ac	31.8 (28.3–35.5)Aa	13.1 (8.7–17.9)Ab
Accumulations–piles	28.1 (19.0–38.1)Aa	75.3 (49.4–103.9)Aa	0.0 (0.0–0.0)Bb	7.7 (2.3–14.2)Cc	0.6 (0.2–1.0)Bbc
<10 cm diam. WD (cm)					
>7.5 to <10.0	3.9 (3.5–4.4)Ca	3.6 (1.0–6.8)a	0.4 (0.1–1.1)ABb	9.9 (7.1–12.9)Bc	3.9 (2.2–5.8)Aa
>5.0 to 7.5	6.9 (5.7–8.2)ABa	5.6 (1.5–10.7)ac	1.1 (0.4–1.9)ABb	8.1 (7.1–9.2)Ba	2.3 (0.8–4.1)ABbc
>3.0 to 5.0	4.7 (3.3–6.1)Ca	2.5 (0.9–4.3)b	0.7 (0.4–1.0)Bc	5.3 (3.7–6.9)Aa	1.5 (0.7–2.3)Bbc
>1.0 to 3.0	9.0 (8.0–10.1)Ba	4.4 (2.3- 0.9)bd	1.0 (0.3–1.8)ABc	4.9 (3.5–6.5)Ad	2.4 (1.7–3.1)ABb
≤1.0	13.7 (12.7–14.6)Aa	5.3 (4.0–6.7)b	1.7 (0.9–2.6)Ac	3.6 (3.2–4.0)Ab	3.1 (2.5–3.8)Ab
Decay class					
1	54.1 (50.3–57.9)ABa	0.0 (0.0–0.0)ABDbc	0.1 (0.0–0.2)Ab	0.0 (0.0–0.0)ADbc	1.6 (0.5–2.8)Ac
2	74.8 (61.1–89.1)Aa	13.3 (1.4–29.7)Bb	0.3 (0.1–0.7)Bc	59.0 (46.5–72.1)Ba	13.3 (6.4–21.2)BCc
3	9.8 (9.4–10.1)Ba	40.7 (12.3–75.7)Cb	3.5 (1.9–5.4)Ca	19.2 (11.6–27.7)Ca	25.6 (18.9–32.8)Ca
4	5.4 (1.4–10.3)Cab	7.6 (3.6–12.3)ACa	2.5 (1.1–4.3)Bb	13.4 (9.8–17.3)ACb	6.5 (2.1–11.8)ABab
5	0.0 (0.0–0.0)D	0.0 (0.0–0.0)D	0.0 (0.0–0.0)D	0.0 (0.0–0.0)D	0.0 (0.0–0.0)D
Biomass ($Mg \cdot ha^{-1}$)					
Diameter range (cm)					
≥20	2.7 (0.2–6.4)Cab	3.5 (3.2–3.7)a	0.0 (0.0–0.0)Bb	1.5 (1.1–1.9)ACab	2.1 (0.9–3.5)Bab
10 to <20.0	6.8 (4.9–8.8)Bab	3.6 (2.2–5.1)b	0.3 (0.2–0.4)Bc	13.9 (113–16.6)Ba	6.6 (4.9–8.5)ABab
0 to <10.0	13.5 (12.3–14.7)Aa	6.4 (2.6–11.0)b	1.3 (0.6–2.0)Ac	10.5 (9.5–11.5)Aa	3.7 (2.4–5.0)Ab
Accumulations–piles	28.1 (19.0–38.1)Aa	3.8 (0.1–9.6)bc	0.0 (0.0–0.0)Bb	2.2 (0.7–4.0)Cc	0.6 (0.2–1.0)Bbc
<10 cm diam. WD (cm)					
>7.5 to <10.0	1.2 (1.1–1.3)Da	1.0 (0.3–1.9)a	0.1 (0.0–0.3)b	3.2 (2.2–4.2)Bc	1.0 (0.6–1.5)a
>5.0 to 7.5	2.5 (2.0–3.0)BCa	1.7 (0.4–3.4)ab	0.3 (0.1–0.5)c	2.7 (2.3–3.2)Ba	0.7 (0.2–1.2)bc
>3.0 to 5.0	1.7 (1.2–2.3)CDa	0.8 (0.3–1.4)b	0.2 (0.1–0.3)c	1.7 (1.3–2.2)Aa	0.4 (0.2–0.7)bc
>1.0 to 3.0	3.3 (2.8–3.8)ABa	1.4 (0.6–2.2)bd	0.3 (0.1–0.5)c	1.7 (1.1–2.2)Ad	0.7 (0.5–0.9)b
≤1.0	4.8 (4.3–5.2)Aa	1.5 (1.0–2.1)b	0.4 (0.3–0.6)c	1.2 (1.1–1.3)Abc	0.9 (0.7–1.1)bc
Decay class					
1	22.2 (20.6–23.7)Aa	0.0 (0.0–0.0)ACb	0.0 (0.0–0.1)Ab	0.0 (0.0–0.0)Ab	0.6 (0.2–1.1)Ac
2	25.3 (20.7–30.2)Aa	4.5 (0.5–10.0)BCb	0.1 (0.0–0.2)BCc	20.1 (15.9–24.6)Ba	4.3 (2.2–6.8)Bc
3	2.4 (2.2–2.6)Ba	10.8 (3.3–20.1)Bb	0.9 (0.5–1.5)Bc	5.2 (3.1–7.5)Cac	6.7 (4.9–8.6)Bc
4	1.0 (0.2–2.0)Cab	1.5 (0.7–2.4)ABa	0.5 (0.2–0.9)Cab	2.7 (2.0–3.5)Db	1.1 (0.4–1.9)Aab
5	0.0 (0.0–0.0)D	0.0 (0.0–0.0)C	0.0 (0.0–0.0)D	0.0 (0.0–0.0)E	0.0 (0.0–0.0)C

Note: Values are means with 95% confidence intervals in parentheses; lowercase letters denote significant differences within rows; uppercase letters denote significant differences in biomass or volume between diameter classes, <10 cm diameter classes, or decay classes within column; nested ANOVA; $n = 3$, $k = 5$; $s = 4$; post-hoc Games–Howell; $P < 0.05$.

Fig. 2. Distribution of snag biomass by disturbance history, years since disturbance, and decay class. *, old growth of unknown origin.



Results

Statistical independence of sites was not violated, with forest area never being a significant explanatory variable in hierarchical nested linear mixed models analyses of aboveground DW, WD, snag, and buried DW volume (Table 4). Nevertheless, the variable forest area has been retained in the analyses to account for data variability due to forest area.

Aboveground and belowground deadwood

Recently harvested sites (H01) and older harvested sites (H34–36) contained the largest and smallest aboveground DW volume, respectively (Table 5), with H34–36 total aboveground DW volumes amounting to <7% of H01 total aboveground DW volume (Fig. 1). Volume reduction of harvest-generated WD at H01, H17, and H34–36 sites followed a single-parameter negative exponential function, decreasing at a rate k_V of –0.058 ± 0.011 (SE) year^{-1} ($r^2 = 0.89$; $p = 0.001$).

Table 7. Selected studies of woody debris (WD), snags, and buried deadwood in subboreal and boreal forests of North America.

Study*	Location	Species	Stand age (years)	Stand origin	Mean annual precipitation (mm)
Bond-Lamberty et al. 2003	MB	Boreal black spruce	130	Wildfire	536
Brais et al. 2005	QC	Jack pine	43–81	Wildfire	890
Clark et al. 1998	BC	Subalpine boreal black spruce	150–200	Wildfire	440–900
Harvey et al. 1981	MN	Douglas-fir	250	Unknown	787
Lang et al. 1981	NH	Subalpine balsam fir	<90	Senescence	1600
Macadam 1987	BC	Subboreal black spruce	<2	Clear-cutting	440–900
Manies et al. 2005	SK	Black spruce	<154	Wildfire	518
Moroni 2006	NL	Boreal black spruce – balsam fir	68–109	Wildfire	1100–1500
Moroni 2006	NL	Boreal black spruce – balsam fir	2–3	Clear-cutting	1100–1500
Payer and Harrison 2000	MA	Balsam fir – hardwood	13–21	Clear-cutting	940
Pedlar et al. 2002	ON	Boreal mixedwood	5	Clear-cutting	735
Sturtevant et al. 1997	NL	Boreal black spruce – balsam fir	<110	Unknown	1200–1300

*Studies are listed in alphabetical order.

More than 82% of the variability in total aboveground DW volume was explained by site group, whereas belowground (i.e., buried) DW variability was not accounted for by site group, forest area, or site (Table 4). Buried DW volume ranged from 46.4 to 179.3 m^3·ha^{-1} (Table 5), exceeding total aboveground DW volume in all but the recently harvested (H01) and middle-aged burned sites (B21) by 30%–457%. The lowest and greatest volumes of buried DW were found in middle-aged burned sites (B21) and old-growth sites (OG), respectively, whereas harvested sites had intermediate amounts of buried wood.

Woody debris

Abundance of WD was as follows: recently harvested sites (H01) > middle-aged burned sites (B21) > middle-aged harvested = old-growth sites (H17 and OG) > older harvested sites (H34–36) (Table 5). Site group accounted for a significant but small portion of the variability in total WD volume (<5%; Table 4). Recently harvested sites contained a significantly larger proportion of WD biomass (93%) in decay classes 1 and 2 than all other stands (Table 6). Seventeen years after harvest, the majority of WD was in decay class 3 (64%), whereas 21 years after fire (B21), WD was less decayed (71% in decay class 2). Old-growth sites featured the most balanced WD decay class distribution. No aboveground decay class 5 WD was encountered in this study.

Woody debris at all sites was dominated by <20 cm debris, but almost half the WD in the middle-aged burned (B21) sites was >10 cm (Table 6). In recently harvested sites (H01), WD piles and <10 cm WD combined accounted for more than 88% and 78% of WD biomass and volume, respectively, and <10 cm WD was mainly <3 cm (Table 6). The contribution of WD to total amounts of aboveground DW significantly decreased from recently harvested (H01) to older harvested (H34–36) to old-growth sites (94% to 54%; Fig. 1).

Snags and stumps

Old-growth forest sites contained the largest amount of snags (Table 5). All harvested sites had significantly fewer snags than middle-aged burned sites (B21). Outside of site variability, variability in snag volume was most strongly explained by site group, decay class, and their interaction (Table 4). The contribution of snags to total aboveground DW volume significantly increased from <1% in recently harvested (H01) to ~44% in old-growth (OG) sites (Fig. 1). Snag volume was significantly smaller than WD volume in all but old-growth sites (Table 5). Mean snag numbers per hectare were 63, 17, and 19 for recently (H01), middle-aged (H17), and older (H34–36) harvested stands, and 232 and 388 for middle-aged burned (B21) and old-growth (OG) stands, respectively. In recently harvested (H01) sites, 74% of all snags were in decay classes 1 and 2, indicating their recent creation either during or shortly following harvesting (Fig. 2). Seventeen years following harvest (H17), no decay class 1 snags remained, but decay class 2 and 3 snags predominated (11% and 89%, respectively). In contrast, this ratio was reversed in middle-aged burned sites (81% and 18%; Fig. 2).

All harvested sites had significantly greater stump than snag volume, in contrast to middle-aged burned and old-growth sites, but stump volume never exceeded 8.9 m^3·ha^{-1} (Table 5). Recently (H01) and middle-aged (H17) harvested sites featured significantly greater stump biomass than the other sites. The biomass of stumps in decay classes 1 and 2 decreased from 87% in recently harvested (H01) to 69% in middle-aged (H17) harvested and 0% in older harvested (H34–36) sites.

Discussion

Woody debris (WD) abundance in humid high-boreal old-growth forests of Labrador was similar to values reported for other old-growth and mature small-treed boreal forests elsewhere (Table 7). However, larger-treed old-growth forests such as Scots pine (*Pinus sylvestris* L.) – Norway spruce (*Picea abies* (L.) Karst.) forests in Scandinavia with climatic conditions similar to those of central Labrador had considerably larger amounts of WD, in particular >10 cm WD (110–201 m^3·ha^{-1}; Linder et al. 1997; Siitonen et al. 2000), and higher snag volumes, dominated by >10 cm DBH snags (40.1–56.3 m^3·ha^{-1}; Karjalainen and Kuuluvainen 2002; Rouvinen et al. 2002), than small-treed Labrador black spruce. We conclude that climate is less important in

Mean annual temp. (°C)	WD volume or biomass	Snag volume, biomass, or density	Buried DW volume or biomass
–3.4	10.5 Mg·ha^{-1}	0.3 Mg·ha^{-1}	
0.7	4.3 Mg·ha^{-1}		0.2–15.0 Mg·ha^{-1}
<5.0	<70 m^{3}·ha^{-1}	~600 ha^{-1}	
5.3			373–430 m^{3}·ha^{-1}
0.0			0.4–8.1 Mg·ha^{-1}
<5.0	33.2–75.0 Mg·ha^{-1}		
–3.2			6.9–13.0 Mg·ha^{-1}
>3.3	30.3–114.3 m^{3}·ha^{-1}	7.3–22.6 Mg·ha^{-1}	<7.8 Mg·ha^{-1}
>3.3	96.2–119.5 m^{3}·ha^{-1}	52.2–62.3 Mg·ha^{-1}	5.0–5.6 Mg·ha^{-1}
3.7	22.1–94.1 m^{3}·ha^{-1}	0.7 m^{3}·ha^{-1}	
0.0	~110 m^{3}·ha^{-1}	<3 m^{3}·ha^{-1}	
4.0	~70 m^{3}·ha^{-1}	~1000 ha^{-1}	

determining WD abundance than forest diameter structure, as previously speculated by Harmon et al. (2004).

The amount of woody debris produced after clear-cutting in Labrador black spruce forests, which is approximated by the initial modelled WD volume V_0 (138.6 ± 11.9 m^{3}·ha^{-1}), was similar to that in other forests composed of similar-sized trees ($p < 0.001$, Table 7). Particularly in small-treed forests such as Labrador black spruce, clear-cut harvesting produces large proportions of <7 and <10 cm WD, as has been observed for black spruce in British Columbia and central Newfoundland (Macadam 1987; Moroni 2006); however, WD of this size is usually not tallied (e.g., Sturtevant et al. 1997; Payer and Harrison 2000; Pedlar et al. 2002). Smaller than 10 cm WD not only provides essential growing and breeding substrate for numerous saproxylic plants, fungi, and animals (Kruys and Jonsson 1999; Nordén et al. 2004), but must also be accounted for if estimates of total DW stocks are needed, e.g., for carbon accounting (Kurz and Apps 1993).

In addition, clear-cut harvesting in Labrador produced small amounts of snags (1.2 m^{3}·ha^{-1}) as a result of the post-disturbance death of uncut trees (McRae et al. 2001); these amounts are similar to those reported for Canadian boreal mixedwoods 5 years after clear-cut harvest (Pedlar et al. 2002; Table 7) and for managed coniferous and mixedwood forests in northern Sweden (1.2–2.0 m^{3}·ha^{-1}; Fridman and Walheim 2000). Stumps constituted a minor DW pool in harvested Labrador high-boreal forests. Stump biomass in this study was similar to that found in clear-cut Newfoundland black spruce (3.3 Mg·ha^{-1}; Moroni 2006), but stump volume was less than that reported for more productive Ontario black spruce forests (~15 m^{3}·ha^{-1}; Pedlar et al. 2002).

Unlike harvesting, wildfire generates large amounts of snags (McRae et al. 2001), some of which can remain standing for up to ~30 years (Boulanger and Sirois 2006). A peak of WD ~20 years following fire has repeatedly been observed for small-treed boreal forests (e.g., Bond-Lamberty et al. 2003; Boulanger and Sirois 2006) and is attributable to the postfire collapse of snags (Moroni 2006). If snag abundance in recently burned Labrador sites is assumed to be equivalent to that of old-growth sites (~1400 stems·ha^{-1}; data not shown), 21 years following fire an estimated 87% of all snags had fallen, and WD was dominated by large amounts of recently collapsed (decay class 2), medium-sized (>10 cm) snags. Snag longevity and fall rates in humid high-boreal spruce forests are thus similar to those in other boreal and high-boreal forests, with most snags falling within 25–33 years following disturbance (Manies et al. 2005; Boulanger and Sirois 2006; Moroni 2006), and thus measured WD abundance 21 years following fire likely approximates the maximum amounts of postfire WD fire at B21 resulting from the collapse of snags.

The large amounts of buried DW observed in Labrador high-boreal black spruce, particularly in the old-growth sites, largely exceeded most values reported in the literature (Table 7). Larger amounts of buried DW have only been observed in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* (Beissn.) Franco) stands (Harvey et al. 1981), which contain much larger trees producing considerably more DW for burial than Labrador black spruce. For such large buried DW stocks to occur in Labrador black spruce forests, a significant amount of aboveground WD generated in old-growth stands must be buried. The lack of decay class 5 aboveground WD (Table 3) indicates that as WD collapses to the ground it is buried before reaching the most advanced stages of decay. The volume reduction of DW with time results from the combined processes of decomposition, leaching, and fragmentation (Mackensen and Bauhus 1999; Zhou et al. 2007), as well as burial. Thus, assuming that harvesting generated similar amounts of slash at all sites, and decomposition rates in cool, humid high-boreal Labrador black spruce are similar to or lower than estimated decomposition rates for boreal black spruce in warmer and drier boreal climates in Manitoba and Quebec (0.016 to 0.045 year^{-1}; Bond-Lamberty et al. 2003; Manies et al. 2005; Boulanger and Sirois 2006), the relatively high volume reduction rates of aboveground DW following harvesting (0.058 year^{-1}) are also indicative of significant burial of harvest slash in these humid high-boreal forests.

Burial of aboveground DW in deep organic layers is due to the vigorous growth of the moss layer (Sturtevant et al. 1997; Moroni 2006), typical of many humid or wet boreal forests (Wilton 1964; Bisbee et al. 2001). Although moss growth is initially slowed because of exposure following harvesting, moss cover and growth potentially recover ~5 years following harvest (Palviainen et al. 2005), enabling the burial of harvest slash. In Labrador the forest floor is snow covered from October–November until May–June, which, combined with an average May–September precipitation of 397 mm (Environment Canada 2008), results in extended periods with low soil temperatures and elevated soil moisture levels, commonly associated with anaerobic conditions. The cool, wet conditions likely persist for significant periods of the growing season under the insulating effects of the moss layer (Foster 1985; Kasischke and Johnstone 2005), likely resulting in buried DW decay rates that are dramatically lower than decay rates of unburied wood, as previously suggested by Foster (1985) and Manies et al. (2005). Calculating WD decay rates based on aboveground measurements of WD abundance may, therefore, overestimate decay rates, as WD is being buried but not decayed.

The enormous amounts of buried DW observed in Labrador old-growth stands indicate that WD in the organic layer of maturing and old-growth gap-driven Labrador forests must have accumulated over a very long time period, potentially without significant interruptions as a result of stand-replacing disturbances such as wildfire. Wildfires often consume only a portion of the organic layer — and wood buried within it — especially when organic layers are wet (Kasischke and Johnstone 2005; Manies et al. 2005). Thus, buried DW may accumulate over several stand generations. Moreover, where the moss layer recovers quickly following fire, a likely occurrence in humid conditions such as those encountered in Labrador, wildfires generate large amounts of DW for burial. The accumulation of buried DW appears to depend on a combination of climate (e.g., temperature and precipitation), microtopography (e.g., drainage), ground vegetation (e.g., moss growth), and stand disturbance history (e.g., fire intensity and return interval), and buried DW abundance can thus be expected to be highest in cool and moist coniferous forests with a vigorous moss layer and long fire-return intervals. Excluding buried DW from DW inventories in these forests can result in massive underestimates of DW stocks and carbon stored in DW.

Based on the reduction of DW volume along the postharvest chronosequence, we assume harvest slash in Labrador will completely disappear ~40–50 years following harvesting. As DW abundance in Labrador is similar to that reported elsewhere, we assume postfire DW will completely disappear within ~70 years of burning, as has been observed in Newfoundland black spruce (Moroni 2006), when DW stocks in stands originating from wildfire and harvesting will converge at low levels. Fire-generated DW persists longer than harvest slash because of low snag decomposition rates (Boulanger and Sirois 2006) and larger initial DW abundance (Moroni 2006). Following the decomposition of disturbance-generated DW, regeneration produces little DW until senescence (Harmon et al. 2004; Hély et al. 2000; Moroni 2006), particularly in low-density black spruce forests with little self-thinning (Wilton 1964; Roberts et al. 2006). The rotation age for the studied forests is 120 years (Newfoundland and Labrador Department of Natural Resources 2008) — beyond the life-span of DW — so amounts of DW will not significantly decline following the second managed rotation. Following the harvesting of old growth, there will be a decline in DW in the second rotation, because managed stands are typically harvested before senescence generates DW that is inherited by the next rotation. Also, the conversion of forest landscapes from unmanaged to managed stands will reduce landscape-level DW stocks because of reductions in the area of senescent forest and the suppression of natural disturbances generating large amounts of DW. Disturbances produce very transient sources or stores of carbon, nutrients, habitat, and fuel for fires in forests with small-diameter trees (McRae et al. 2001), even in the cold, humid high boreal. Without fresh additions of DW, middle-aged to mature regenerated stands following stand-replacing disturbance will contain little DW. Where DW is an important consideration for forest management, harvested stands should retain living trees as future sources of DW and associated sources or stores of carbon, nutrients, and habitat, or a portion of the managed forest could be allowed to become senescent.

Black spruce in high-boreal Labrador is longer lived and slower growing than that in most other boreal and subboreal regions (Newfoundland and Labrador Department of Natural Resources 2008), delaying the onset and progression of senescence. Hence, postharvest DW stocks in Labrador likely remain below old-growth levels for significantly longer periods than elsewhere, and significantly longer periods following harvest will be required to replenish DW stocks to old-growth levels. Deadwood management is thus more difficult in the high-boreal than in more productive boreal forests. In addition, the rapid burial of DW in Labrador must be accounted for in habitat (e.g., Simon et al. 2002) and forest carbon models (Kurz et al. 2008).

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4.4 Woody Debris and Soil Respiration

Analysis of WD stocks confirmed that WD abundance is significantly influenced by disturbance type and time since disturbance (Hagemann et al. 2009). Although stand-replacing fires and clearcut harvesting create large amounts of WD in single events (Harden et al. 2000, Bergeron et al. 2002), temporal dynamics of WD abundance differ considerably between these disturbance types (Pedlar et al. 2002, Moroni 2006), with maximum amounts of WD occurring 20–30 years following fire and immediately after harvesting (Bond-Lamberty et al. 2003, Moroni 2006). As WD characteristics (size, colour, etc.) and WD decomposition environment (e.g., temperature and moisture) are altered to a different degree by fire and harvesting (Section 2.2.2 and 2.3.1), decomposition rates of WD are expected to differ between sites of different disturbance origin.

4.4.1 Hagemann U, Moroni M, Gleißner J, and Makeschin F. 2010. Disturbance history influences woody debris and soil respiration. For. Ecol. Manage. (*in press*)

Extended Abstract

Woody debris moisture content was the dominant environmental control of WD respiration, followed by WD temperature. Moisture levels were lower in the disturbed strata, particularly in the burned stratum (24.1–35.5%), where respiration was limited by low WD moisture content. Within-log differences in WD moisture resulted from drying of the log surface and water transfer from the live moss layer to the lower log parts, illustrating the potential impact of an intact moss layer or its absence on decomposition dynamics.

The disturbed strata featured higher WD temperatures than the old-growth stratum. Within-log temperatures generally decreased from the top WD surface to the bottom sapwood. In the disturbed stands, however, top surface and top sapwood WD temperatures exceeded ambient air temperatures resulting in desiccation particularly in the burned stratum, where wind is not slowed by vegetation and the WD surface receives unimpeded insolation.

In the old-growth stratum, high WD moisture contents combined with mainly low WD temperatures resulted in low summer WD respiration rates. In contrast, WD respiration in the burned stratum was limited by low WD moisture levels in combination with high temperatures. The harvested stratum featured a combination of high WD temperatures and moderate WD moisture content and consequently higher WD respiration rates than the other strata. While WD temperature limited WD respiration at lower temperatures (i.e. old-growth stratum), WD moisture limited WD respiration at higher temperatures (i.e. burned stratum). Disturbance-induced changes in forest temperature and moisture regimes are thus reflected by WD respiration rates, and accuracy of forest C models would be improved by differentiating decomposition rates of WD by disturbance history.

Compared to soil respiration, WD respiration (based on estimate WD surface area per hectare) reached similar (83%; following fire) or equal (100%; following harvest) rates in disturbed sites ($P < 0.05$), but considerably lower rates in old-growth sites (9%; $P \leq 0.001$). Soil respiration rates were highest in the old-growth stratum where a high contribution of root respiration to total soil respiration was expected. In the harvested stratum, soil respiration was 30-50% lower compared to the old-growth stratum, reflecting partial losses of root respiration after tree removal. Compared to soil respiration, WD respiration is thus an important component of the forest C cycle particularly in recently harvested sites with large amounts of decaying woody residues.

Disturbance history influences downed woody debris and soil respiration

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Abstract

In boreal forests, disturbances such as stand-replacing fires and clearcut harvesting create large amounts of downed woody debris (DWD), which release considerable amounts of CO2 to the atmosphere during decomposition. Harvesting and fire differ with respect to DWD characteristics (e.g., size), decomposition environment (temperature and moisture), and abundance; hence, differences in piece- and stand-level DWD respiration rates between stands of different disturbance at origin can be expected. From July to September 2008 (every 5–9 days), we measured temperatures, moisture content, weight, and respiration of 45 standardized black spruce logs placed in three old-growth (>140 years), three clearcut harvested (3 years prior), and three burned (23 years prior) black spruce forest stands in Labrador, Canada. Concurrently, soil temperatures, soil moisture potential, and soil respiration were measured next to each log. Moisture content was the dominant environmental control of DWD respiration, followed by temperature. Within-log differences in moisture and temperature resulted from drying of the log surface and water transfer from the live moss layer to the lower log parts. Downed woody debris temperatures and respiration rates were higher in harvested and burned stands compared to old-growth stands, and piece-level DWD respiration rates were highest in harvested stands. Downed woody debris moisture levels were lower in disturbed stands, particularly in burned stands, where respiration was limited by low moisture content. Compared to soil respiration, stand-level DWD respiration (based on estimated DWD surface area per hectare) reached similar (83%; following fire) or equal (100%; following harvest) rates. Disturbance-induced changes in forest temperature and moisture regimes are reflected by DWD respiration rates; hence, for purposes of forest C modeling, decomposition rates of DWD should be differentiated by the decomposition environment created by different disturbance types.

Keywords: downed woody debris respiration; soil respiration; clearcut harvesting; wildfire; decomposition

1. Introduction

Downed woody debris (DWD) is an integral component of boreal forest ecosystems, contributing to carbon (C) and nutrient cycles (Kurz and Apps 1993, Laiho and Prescott 2004), structural integrity (Debeljak 2006), and habitat availability (Harmon et al. 2004). Small and large-scale disturbances play an important role in the creation of DWD in boreal forests (Pedlar et al. 2002, Boulanger and Sirois 2006, Moroni 2006). Small-scale wind disturbance and senescence constantly create small amounts of DWD in old-growth boreal forests (McCarthy 2001, Bergeron et al. 2002). In contrast, a considerable portion of boreal forest is periodically affected by stand-replacing fires and clearcut harvesting (Harden et al. 2000, Bergeron et al. 2002, Roberts et al. 2006) which create large amounts of deadwood (snags and/or DWD) in single events. Recent studies have shown harvest-generated and fire-generated DWD to differ with respect to several attributes, such as abundance, diameter and length, colour, and decay class distribution (McRae et al. 2001, Lloyd and Todd 2003, Stevenson et al. 2006). Clearcut harvesting generates substantial amounts of DWD directly following harvest (Pedlar et al. 2002, Moroni 2006), whereas fire-generated DWD peaks 20–30 years after fire following the collapse of fire-generated snags (standing dead trees; Bond-Lamberty et al. 2003, Moroni 2006, Hagemann et al. 2009). Clearcut harvesting generally produces smaller and shorter DWD pieces than wildfire (Lloyd and Todd 2003, Densmore et al. 2004), resulting from the input of small short logging debris (Stevenson et al. 2006). Unlike logging debris, fire-generate DWD features a charred surface, which can be transformed into a decay-resistant shell as a result of below-fibre saturation moisture levels and excessively high air temperatures (“case-hardening phenomenon”; Marra and Edmonds 1996, Mackensen and Bauhus 2003, Manies et al. 2005).

While DWD amounts (C stocks) and characteristics following harvesting and wildfire are well-studied, few studies have investigated post-disturbance DWD respiration rates (C flux). Documented studies of wood respiration rates are limited to those following wildfire (Wang et al. 2002, Bond-Lamberty et al. 2003), selective logging (Liu et al. 2006), and clearcut harvesting (Marra and Edmonds 1996). Similar to studies examining DWD abundance, most respiration studies have focused on mature forests, e.g., old-growth coniferous forests (Marra and Edmonds 1994, Progar et al. 2000), old growth Amazon forests (Chambers et al. 2001), secondary broad-leaved forests (Yoneda et al. 1975, Jomura et al. 2008), and alpine floodplain forests (Richard and Woodtli 2006). Wei et al. (1997) studied mass loss and nutrient dynamics in harvested and burned pine forests, but we are unaware of any study comparing respiration rates of DWD with different disturbance origins, which has been identified as an important research objective (Zhou et al. 2007).

Deadwood respiration rates are a direct measure of the amount of C released to the atmosphere during decomposition (Herrman and Bauhus 2008). Unlike other methods, e.g. mass loss or density change studies, DWD respiration measurements distinguish between decomposition rates and mass loss due to fragmentation and/or leaching (Marra and Edmonds 1994, Bond-Lamberty et al. 2003, Liu et al. 2006), and thus provide valuable data on the contribution of DWD decomposition to the global C cycle (Chambers et al. 2001, Howard et al. 2004, Jomura et al. 2008). In a boreal black spruce forest in central Canada, stand-level DWD respiration amounted to 54% of soil respiration – the second-largest C flux in terrestrial ecosystems (Rustad et al. 2000, Bond-Lamberty et al. 2003, Peng et al. 2008). Thus, DWD respiration is an important component of the forest C cycle, but few studies have measured DWD and soil respiration concurrently (Marra and Edmonds 1994, 1996, Richard and Woodtli 2006).

Temperature and moisture have been identified as the main drivers of the decomposition process for woody and non-woody litter (Rustad et al. 2000, Bond-Lamberty et al. 2003, Liu et al. 2006). In general, DWD respiration increases with increasing temperature (Peng et al. 2008), but it exhibits an inverse U response curve to moisture content, becoming inhibited at both low and high moisture levels (Boddy 1983, Progar et al. 2000, Jomura et al. 2007). Both temperature and moisture can be influenced by disturbances (McRae et al. 2001, Devine and Harrington 2007). Forest floor temperatures generally increase post-disturbance due to canopy removal, but the increase is typically more pronounced for wildfire than for clearcut harvesting due darkened charred surface colour (McRae et al. 2001). Soil moisture levels generally decrease post-fire following the reduction of organic layer mass and increased evaporation (McRae et al. 2001). Following harvesting, soil moisture levels can increase due to less plant transpiration (Adams et al. 1991, Elliott et al. 1998), or decrease due to increased evaporation (Londo et al. 1999), depending on factors such as forest type, aspect, or slope (McRae et al. 2001).

Based on expected differences in DWD characteristics (e.g., size) and decomposition environment (temperature and moisture), differences in piece-level respiration rates can be expected between sites of different disturbance origin. At the stand-level, differences in respiration rates will be further influenced by differences in abundance and state of DWD. Objectives of this study are i) to determine the impact of disturbance history on piece-level DWD respiration and its driving environmental variables, hypothesizing respiration rates in disturbed Labrador stands to be higher than in old-growth stands due to increased temperatures and decreased moisture levels, ii) to compare piece-level DWD respiration rates to soil respiration rates, expecting a) DWD respiration to be lower than soil respiration, and b) smaller differences between DWD and soil respiration in disturbed stands than in old-growth stands due to discontinued root respiration, and iii) to compare estimated stand-level DWD and soil respiration rates.

2. Materials and methods

2.1. Site selection and description

The study area is situated near Goose Bay, Labrador in the “High-boreal Forest–Lake Melville” Ecoregion (Ecoregions Working Group 1989), an extension of the Boreal into the Taiga Shield. Mean annual temperatures are -2.4°C to -1.0°C (McKenney et al. 2007). The region receives ~1000 mm of precipitation evenly distributed throughout the year, making it one of the wettest North American boreal forests (Foster 1985). The upland soils are mainly classified as Humo-Ferric Podzols (Soil Classification Working Group 1998) or as Typic Haplorthods (Soil Survey Staff 2006), and support the most productive forests of Labrador (Roberts et al. 2006).

Nine previously studied forest sites (Table 1 in Hagemann et al. 2009) were investigated in greater detail from July to September 2008. Sites support (or supported prior to disturbance) forests dominated by black spruce (>75%) older than 140 years featuring an average height of 12–15 m and a crown closure of 50%–75% on sites of medium productivity (Government of Newfoundland and Labrador 2006). Sites had three different disturbance origins (stand types): three 146–204 year-old old-growth stands likely of wildfire origin (OG), three stands clearcut 3 years prior to sampling (H), and three stands subject to wildfire 23 years prior to sampling (B). Disturbed stands were selected to have DWD amounts typical of Labrador old-growth black spruce stands (35–60 m^3 ha^{-1}; data from Hagemann et al. 2009), or near-maximum amounts of disturbance-generated DWD, i.e. shortly following clearcut (126–163 m^3 ha^{-1}) and ~20 years following wildfire (83–100 m^3 ha^{-1}). Detailed information on the studied stands is presented by Hagemann et al. (2009).

2.2. Field measurements

2.2.1. Woody debris respiration

Forty-five black spruce decay class 2 (Natural Resources Canada 2010) sample logs with a middle diameter of 13.9±0.2 cm were selected from the DWD present within each stand, cut to 30.6±0.5 cm length, and sealed at the ends with Water Stop polymer paint (MEM Bauchemie, Leer, Germany). Decay class 2 logs were chosen for several reasons: i) high abundance in all stand types (Hagemann et al. 2009), and ii) low expected variability in wood density, iii) high structural integrity which reduces the risk of fragmentation during handling, and iv) higher absolute respiration rates than more advanced decay classes (Natural Resources Canada 2010) as a result of sufficient resource quality and fungal colonization (Hicks et al. 2003). Each stand contained a randomly placed 20-m transect, along which five plots were located every 5 m. One sample log was placed on the ground at each plot and its position marked to avoid inadvertent relocation after measurements. Plots were prepared 2 weeks prior to the first sampling to allow for equilibration with ambient conditions.

Piece-level respiration, wood and air temperatures, and log weight were measured nine times from July 12 to September 01, 2008, every 5–8 days. Measurements could not be conducted simultaneously at all sites; hence, the order of measurement for the three stand types (morning 900-1200h, noon 1200-1500h, afternoon 1500-1800h) and the sites within stand types was rearranged for each measurement day to avoid temporal sampling bias. Respiration of sample logs was measured for 180 s using a clear acrylic, closed chamber (19385 cm^3; Newell Rubbermaid Inc., Freeport, IL, USA) connected to an EGM-4 infrared gas analyzer (PP Systems, Amesbury, MA, USA). Piece-level DWD respiration (R_{DWD}) was calculated as CO_2 concentration increment in the system volume per unit of emitting (lateral) wood surface and time. System volume was determined by deducting average log volume per stand from the volume of the chamber and gas analyzer. Wood temperatures were recorded in pre-drilled 4-mm holes using waterproof digital type K thermocouple probes (DP8811WP, Mannix, NY, USA): $T_{DWDsurface}$ at the wood surface, T_{DWDtop} at 2 cm depth in the top sapwood, $T_{DWDheart}$ at 7 cm depth in the heartwood, and $T_{DWDbottom}$ at 2 cm depth in the bottom sapwood. Between measurements, all holes were sealed with wooden dowels to avoid equilibration with ambient air. Organic layer temperature (T_{OL3}) 3 cm below each sample log was measured simultaneously to DWD respiration using a temperature probe connected to the EGM-4. Ambient air temperature (T_{Air}) and relative humidity (*RH%*) were recorded at 30 cm above the forest floor using a digital hygro-thermometer (SPER Scientific). Log masses were determined using a digital hanging scale. Gravimetric woody debris moisture content (u_{DWD}) for each sampling date was calculated as water mass (date-specific field mass minus absolute dry log mass) divided by dry log mass (105°C) determined on completion of the last measurement. Log density (D_{DWD}) was calculated as dry log mass to log volume ratio.

Measured piece-level DWD respiration rates per emitting surface area were converted to per-hectare stand-level respiration rates to allow comparison with per-hectare soil respiration rates. Data on total DWD volume (m^3 ha^{-1}) per diameter class (≤1.0 cm; >1.0–3.0 cm; >3.0–5.0 cm; >5.0–7.5 cm; >7.5–<10.0 cm; 10.0–<20.0 cm; ≥20.0 cm; piles) measured on the same study sites was taken from Hagemann et al. (2009). For each diameter class, we calculated the total length of DWD with the mid-point diameter of the diameter class required to produce a cylinder with a volume equivalent to the total diameter class volume. Based on the calculated total length and the respective diameters, we estimated the total per-hectare DWD surface area for each diameter class (cylinder shape) and summed all diameter class surface areas to estimate total DWD surface area per hectare (m^2 ha^{-1}). Estimated stand-level respiration rates were calculated by multiplying measured piece-level respiration rates per unit surface area of decay class 2 sample logs with total DWD surface area per hectare for each measurement date, assuming all diameter classes to have similar respiration rates (Bond-Lamberty et al. 2003) and all DWD to be decay class 2 due to the lack of measured respiration data for other decay classes.

2.2.2. Soil respiration

At each plot, a PVC collar (Ø = 10.3 cm) was inserted 2 cm in the organic layer next to each sample log 2 weeks prior to sampling. Soil respiration (R_S) was measured for 120 s simultaneously to DWD respiration measurements using an SRC-1 chamber connected to an EGM-1 infrared gas analyzer (PP Systems, Amesbury, MA, USA). Organic layer temperature (T_{OL10}) and moisture potential (Ψ_{OL}) at 10 cm depth were measured concurrently to soil respiration using a temperature probe connected to the EGM-1 and a 2900F1 Quick Draw Tensiometer (Soil Moisture Equipment Corp., Santa Barbara, CA, USA), respectively. Organic layer thickness (*OLT*) was measured below each PVC collar following the last measurement.

2.3. Statistical analyses

Differences in R_{DWD}, T_{Air}, $T_{DWDsurface}$, T_{DWDtop}, $T_{DWDheart}$, $T_{DWDbottom}$, T_{OL3}, T_{OL10}, u_{DWD}, and Ψ_{OL} between strata were analyzed using univariate nested ANOVA with stand type ($k = 3$) and the respective variable as fixed factors, and site nested within stand type as random factor ($n = 3$). Significance thresholds for multiple comparisons were adjusted using *Bonferroni*'s equation. Differences between R_{DWD} and R_S within stand types were calculated using the *Wilcoxon* signed-rank test. Correlations between R_{DWD}, R_S, T_{Air}, $T_{DWDsurface}$, T_{DWDtop}, $T_{DWDheart}$, $T_{DWDbottom}$, T_{OL3},

T_{OL10}, u_{DWD}, Ψ_{OL}, and *OLT* were calculated using Spearman's ρ. A factor analysis was employed to aggregate the environmental variables. The influence of all variables on DWD and soil respiration was determined using a hierarchical nested linear mixed model with stand type and environmental variables as fixed factors, measurement day as a repeated fixed factor, and site nested within stand type as random factor. Time of measurement was considered as an individual fixed factor in the LMM analysis accounting for bias due to measurement time. Random variance components were calculated using Restricted Maximum Likelihood. Statistical analyses were conducted and figures created using SPSS 15.0.1 and SigmaPlot 7.1 (SPSS Inc.). All abbreviations used are listed in Table 1.

3. Results

3.1. Temperature

The range of average air temperatures at time of measurement increased from the old-growth (OG; 14.5–28.2˚C) to the harvested (H; 16.6–33.2˚C) to the burned (B; 14.6–34.7˚C) stands (Fig. 1). Downed woody debris and organic layer temperatures also followed the order OG < H < B (Fig. 1). For example, top and bottom sapwood temperature were highest for the burned stands on seven of nine measurement dates. In all stands, differences between the different substrate temperatures (air, DWD, and organic layer) were considerably less pronounced on days with lower absolute temperatures, e.g. 01/08 (Fig. 1).

Downed woody debris temperatures decreased in the order $T_{DWDsurface} > T_{DWDtop} > T_{DWDheart} > T_{DWDbottom}$ in the old-growth and harvested stands, while T_{DWDtop} mostly exceeded $T_{DWDsurface}$ in the burned stands (Fig. 1). Wood surface and top sapwood temperatures exceeded air temperatures in the disturbed stands, but not in the old-growth stands.

All DWD temperatures were highly correlated with air temperature ($\rho > 0.74$; $P \leq 0.001$; Table 2a), featuring decreasing correlation strength with increasing depth, i.e., from $T_{DWDsurface}$ to $T_{DWDbottom}$. Correspondingly, correlation strength between DWD and organic layer temperatures increased from $T_{DWDsurface}$ to $T_{DWDbottom}$ ($\rho > 0.51$; $P \leq 0.001$; Table 2a). All DWD temperatures were strongly correlated ($\rho > 0.79$; $P \leq 0.001$), hence only T_{DWDtop} and $T_{DWDbottom}$ were analyzed subsequently unless stated otherwise.

3.2. Moisture

The range of average DWD moisture content at time of measurement was significantly lower in the burned stands (24.1–35.5%) compared to the harvested (46.3–58.7%) and old-growth (48.8–60.3%) stands (Fig. 2a). The range of average organic layer moisture potential was also significantly lower in the burned stands (7.5–23.7 kPa) than in harvested (5.0–11.8 kPa) and old-growth (3.8–10.1 kPa) stands (Fig. 2b). Differences in u_{DWD} and Ψ_{OL} between the old-growth and harvested stands were small and generally non-significant.

Downed woody debris moisture content and organic layer moisture potential were significantly correlated ($\rho = 0.38$; $P \leq 0.001$; Table 2b), but between-measurement date variability was more pronounced for Ψ_{OL}. Organic layer moisture potential was more responsive to temperature increases and precipitation events than u_{DWD} (Fig. 1, 2), e.g. very low Ψ_{OL} on a warm day following a drier period (26/07) and high Ψ_{OL} on a cool day following heavy precipitation (01/08). This effect was particularly pronounced in the burned stands, which generally featured the highest variability of Ψ_{OL} (Fig. 2). The variability of Ψ_{OL} between sample pieces decreased in the order OG ≥ H > B, whereas the opposite was observed for u_{DWD} (Fig. 1, 2).

3.3. Respiration

The range of average piece-level DWD respiration tended to decrease in the order harvested (0.16–0.34 g CO_2 m^{-2} h^{-1}) > burned (0.11–0.27 g CO_2 m^{-2} h^{-1}) ≥ old-growth (0.09–0.19 g CO_2 m^{-2} h^{-1}), whereas the range of average soil respiration significantly decreased from old-growth (0.55–0.91 g CO_2 m^{-2} h^{-1}) > harvested (0.26–0.55 g CO_2 m^{-2} h^{-1}) > burned (0.11–0.19 g CO_2 m^{-2} h^{-1}; Fig. 3) stands. Downed woody debris respiration was highest in harvested stands on almost half of the measurement dates (Fig. 3a), and tended to be lowest in old-growth stands. In contrast, soil respiration rates in old-growth stands considerably exceeded soil respiration rates in disturbed stands on all measurement dates (Fig. 3b). Between-stand type patterns of measured variables differed: R_{DWD} (H > B ≥ OG), R_S (OG > H > B), u_{DWD} (OG > H > B), Ψ_{OL} (OG ≥ H > B), and DWD temperatures (B > H > OG).

Soil respiration steadily increased from early July until early August in old-growth and – to a lesser degree – in harvested stands, which was not the case for organic layer temperatures or organic layer moisture potential (Fig. 1–3). The variability of soil respiration decreased strongly in the order OG > H > B, whereas the variability of DWD respiration did not differ between stand types. Measured soil respiration rates were significantly higher than piece-level DWD respiration rates in old-growth and harvested stands ($P \leq 0.001$), whereas in burned stands R_{DWD} was similar or slightly higher than R_S ($P = 0.076$).

Stand-level (kg CO_2 ha^{-1} h^{-1}) and piece-level (g CO_2 m^{-2} h^{-1}) respiration rates, previously measured total and ≤3.0 cm volume (Hagemann et al. 2009), and surface area of DWD decreased by stand type in the same order (H > B ≥ OG; Table 3). When compared with soil respiration at the stand-level, DWD respiration was equivalent in harvested stands (mean 100%; range 73–127%), slightly lower in burned stands (83%; 44–115%) ($P < 0.05$), and considerably lower in old-growth stands (9%; 6–13%) ($P \leq 0.001$).

Downed woody debris respiration was significantly correlated to T_{DWDtop} ($\rho = 0.26$; $P \leq 0.001$) and u_{DWD} ($\rho = 0.29$; $P \leq 0.001$), while T_{DWDtop} and u_{DWD} were negatively correlated ($\rho = -0.303$; $P \leq 0.001$). Aggregation of all independent environmental factors yielded three components which explained 78.2% and 77.0% of total variable variance for R_{DWD} and R_{S}, respectively (Tables 4a, 5a). For R_{DWD}, the first and second component accounted for 62.2% and 16.0% of total variance, respectively. Factors dominating each component were (1) T_{Air}, $T_{\mathrm{DWDsurface}}$, T_{DWDtop}, T_{DWDheart}, $T_{\mathrm{DWDbottom}}$, and T_{DWWheart}, T_{OL3}, T_{OL10}, Ψ_{OL}, and *RH%*, and (2) u_{DWD} and D_{DWD} (Table 4a). For R_{S}, the first and second component accounted for 57.1% and 19.9% of total variance, respectively. Factors dominating each component were (1) T_{Air}, T_{OL3}, T_{OL10}, Ψ_{OL}, and *RH%*, and (2) *OLT* (Table 5a).

The hierarchical nested LMM showed u_{DWD} and $T_{\mathrm{DWDbottom}}$ to be the most influential environmental variables in determining R_{DWD}, followed by T_{DWDtop}, D_{DWD}, and stand type (Table 4b). For R_{S}, the most influential environmental variables were stand type and T_{Air}, followed by *RH%*, T_{OL10}, and T_{OL3}. The interactions between T_{OL10} and Ψ_{OL} or *OLT* also significantly influenced R_{S}, whereas Ψ_{OL} and *OLT* as individual factors had no measurable influence (Table 5b). Random variance was mainly attributed to error.

4. Discussion

4.1. Ecological drivers of DWD respiration

Moisture content was the strongest correlate with piece-level DWD respiration in this study (Table 4b), although temperature is often most strongly correlated with decomposition processes (Wang et al. 2002, Mackensen and Bauhus 2003). Downed woody debris respiration rates were low at moisture contents <40%, mainly encountered in burned stands, which is similar to the black spruce fibre saturation point (43%; Griffin 1977) and values reported by Bond-Lamberty et al. (2003) (43%). Decomposition can be limited at moisture contents below the fibre saturation point, because many wood-rotting fungi cannot access water below this point (Griffin 1977, Wang et al. 2002, Laiho and Prescott 2004, Boulanger and Sirois 2006). As pore volume gradually increases during the decay process (Boddy 1983, Christensen 1984, Chambers et al. 2001, Bond-Lamberty et al. 2003), and influences DWD water retention capacity, living conditions for the decomposer community change (Boddy 1983, Sollins et al. 1987, Chambers et al. 2001). The interaction between moisture content and density is thus critical in understanding DWD respiration (Chambers et al. 2001, Barker 2008, Jomura et al. 2008), as indicated by the grouping of both internal variables during factor analysis (Table 4a), setting them apart from external variables such as temperatures or relative humidity.

The drying and wetting of DWD proceeds slower than these processes in the bryophyte-dominated organic layer, as DWD moisture content was less responsive to precipitation events and changes in temperature than organic layer moisture potential. Short-term fluctuations of atmospheric relative humidity and amounts of water added in precipitation events only influence the wood surface, because of its smaller surface area available for water exchange compared to mosses (Beringer et al. 2001). Although the thermal diffusivity of wood (1.5–1.6 x 10^{-7} m^2 s^{-1}; Simpson and TenWolde 1987; TenWolde et al. 1988) and dead moss (peat: 0.92–1.37 x 10^{-7} m^2 s^{-1}; Zuidhoff 2003) are fairly similar, water transport is slower in DWD than in mosses, which are characterised by high hydraulic conductivity and a high degree of surface infiltration (Simpson and TenWolde 1987; Beringer et al. 2001).

Temperature limited DWD respiration at lower temperatures, while moisture likely limited DWD respiration at higher temperatures. In contrast to moisture, DWD respiration increased steadily with increasing temperature, similar to observations by Peng et al. (2008). Variability in DWD respiration also increased with increasing temperature, suggesting that, as temperature increases, other factors such as moisture (Boddy 1983, Progar et al. 2000), decay class (Bond-Lamberty et al. 2003), or fungal colonization (Barker 2008) limit respiration. For example, due to the higher demand of decomposers for respirable oxygen at higher temperatures, the limiting impact of high wood moisture contents may become apparent earlier at high temperatures than at low temperatures (Boddy 1983).

Bryophytes are important factors in regulating within-log differences in moisture content and temperature, thus influencing DWD respiration. Although wood temperature and surface moisture content are mainly regulated from above, i.e. by radiation and air temperature, moisture retention in the lower log parts is favoured by contact with moisture-retaining bryophytes – the dominant ground vegetation cover of the studies old-growth black spruce sites (>82%; unpublished data) – resulting in heartwood and bottom sapwood temperatures that were up to 10°C lower than top sapwood and surface temperatures, and showed stronger correlations with 3-cm organic layer temperature (Table 2). In contrast to standing dead trees (snags) or suspended deadwood, moisture is generally retained below DWD (Devine and Harrington 2007, Jomura et al. 2007), resulting in decreased evaporation rates, increased moisture content through vertical and lateral water transfer, and thus lower bottom sapwood temperatures, as observed for logs buried in the organic layer (Hagemann et al. 2010). Differences in DWD moisture and temperature are thus particularly pronounced when comparing stands with partly or fully intact bryophyte layers (e.g., harvested stands) to stands where the live bryophyte and most of the organic layer have been combusted (e.g., burned stands).

4.2. Impact of disturbance history on DWD respiration

Disturbance history strongly influenced DWD temperature and moisture, which were the key to explaining the effect of stand type (i.e., disturbance) on DWD respiration. However, the factor 'stand' was barely significant ($P = 0.043$; Table 4b), because it is characterized by a combination of environmental factors such as temperature and moisture. The introduction of moisture and temperature as individual explanatory variables to a basic linear mixed model (data not shown) caused a shift in significance from stand type to these variables ($P \leq 0.0001$; Table 4b). Between-stand type differences in DWD respiration rates can thus be largely explained by differences in temperature and moisture regimes, despite small but significant contributions of variability arising from plots, measuring day, and time.

In old-growth Labrador black spruce stands, low summer DWD respiration rates resulted from high moisture contents combined with mainly low temperatures. Measured old-growth air (13.9–29.0˚C), and DWD (5.8–26.9˚C) temperatures were typical of growing season temperatures in boreal forests, e.g. air temperatures of ~10–34˚C (Bond-Lamberty et al. 2003; Dannoura and Jomura 2006), and wood temperatures of ~7–18˚C (Wang et al. 2002). Downed woody debris moisture content in high-boreal Labrador black spruce (29–127%) was comparable to values reported for drier black spruce forests in Manitoba (~40–120%; Bond-Lamberty et al. 2003). However, *in situ* DWD respiration rates in Labrador (0.01–0.30 g CO_2 m^{-2} h^{-1}, equiv. to 0.0007–0.0204 g CO_2 kg^{-1} h^{-1}) are in the lower range of values reported for decay class 2 black spruce wood in laboratory analyses at various temperatures (0–0.0586 g CO_2 kg^{-1} h^{-1}; Wang et al. 2002, Bond-Lamberty et al. 2003).

As expected, air, DWD, and soil temperatures in burned Labrador black spruce were significantly higher and more temporally variable than in old-growth stands (Devine and Harrington 2007). High post-fire organic layer and wood temperatures (McRae et al. 2001, Dannoura and Jomura 2006) lead to decreased post-fire wood moisture contents due to increased evaporation rates and the partial combustion of the moisture-regulating organic layer (Mattson et al. 1987, McRae et al. 2001). Downed woody debris moisture levels in burned stands (12–48%) were thus less variable than in unburned stands (34–127%) and mostly below fibre saturation point. Low moisture levels in combination with high temperatures therefore likely limited summer DWD respiration in burned stands. However, at similar moisture levels (18±5%), DWD respiration rates in Labrador 23 years post-fire (0.05–0.38 g CO_2 m^{-2} h^{-1}, equiv. to 0.003–0.026 g CO_2 kg^{-1} h^{-1}), were higher than in Alaskan black spruce 2 years post-fire (0.0004±0.00026 g CO_2 kg^{-1} h^{-1}; Jomura and Dannoura 2006), reflecting progressing decomposition, albeit slow, despite limitations to decomposition during summer months.

In contrast to burned and old-growth stands, where DWD respiration was limited by low moisture content and temperature, respectively (Fig. 1, 2), high respiration rates in harvested stands resulted from high temperatures and moderate moisture contents. While organic layer and DWD temperatures generally increase following harvesting (McRae et al. 2001), moisture levels may increase or decrease after canopy removal depending on site factors such as climate, slope, or litter quality (cf. McRae et al. 2001, Yanai et al. 2003). If post-harvesting moisture levels are sufficiently high for DWD to support decay fungi, respiration and decomposition rates can be expected to increase under warmer post-harvest compared to pre-harvest conditions (Progar et al. 2000). The decomposition of harvest residues is often desired to ensure nutrient availability for the regenerating stand, e.g., in forests limited by nitrogen or phosphorus availability (Laiho and Prescott 2004). In drier regions, decomposition of DWD and the release of associated nutrients can be enhanced by measures such as retention harvesting or slash retention, which decrease wind movement and summer warming of the organic layer. In consequence, the evaporation and desiccation of the organic layer surface and DWD and the associated decrease in decomposition rates are reduced (Prescott et al. 2004, Devine and Harrington 2007, Moroni et al. 2009).

4.3. Soil respiration

Measured soil respiration rates in old-growth and disturbed Labrador black spruce (0.02–1.07 g CO_2 m^{-2} h^{-1}) were within the range reported for other boreal black spruce forests, e.g. in Newfoundland (3-13 µmol CO_2 m^{-2} s^{-1}, equiv. to 0.2–2.1 g CO_2 m^{-2} h^{-1}; Moroni et al. 2009), Saskatchewan (0.01–1.81 g CO_2 m^{-2} h^{-1}; Singh et al. 2008), and Alaska (0.34–0.92 g CO_2 m^{-2} h^{-1}; O'Neill et al. 2003). Except for burned stands, soil respiration showed a seasonal pattern with maximum rates recorded in early August, but measured peak soil temperatures (26/07) did not coincide with high soil respiration rates (Fig. 1, 3b). This seemingly temperature-independent seasonal pattern has previously been reported by O'Neill et al. (2003), and can be explained by seasonal patterns of photosynthate flux to the roots, which is a more important driver of autotrophic soil respiration than soil temperature (Högberg et al. 2001, Gaumont-Guay et al. 2008). Hence, this pattern was most pronounced and soil respiration rates were highest in the old-growth stands where a high contribution of root respiration to total soil respiration could be expected due to closed tree canopy (up to 74%; Vogel et al. 2005, Gaumont-Guay et al. 2008). Soil respiration rates in harvested stands were 30-50% lower compared to old-growth stands, reflecting partial losses of root respiration after tree removal (Hanson et al. 2000), which masked any potential increases in microbial respiration due to higher soil temperatures and freshly input litter and dead roots (Moroni et al. 2009).

The studied burned stands featured low soil respiration rates and were mostly non-vegetated (Hagemann et al. 2009), thus neither showing signs of elevated microbial respiration nor of recovery of root respiration 23 years after disturbance. While clearcut harvesting removes most trees leaving their roots for decomposition, fire kills most or all trees and combusts part of the organic layer, the main rooting zone for boreal black spruce (Strong and La Roi 1983), and the roots and microbes located within it (Harden et al. 2000, McRae et al. 2001). Root respiration drastically decreases immediately following fire (O'Neill et al. 2003, Bergner et al. 2004), but increases in microbial respiration due to higher soil temperatures and decomposition of dead roots have been shown to last only a few months to years following disturbance (O'Neill et al. 2003, 2006, Singh et al. 2008).

4.4. DWD and soil respiration

Our estimates of stand-level DWD respiration reflect the actual abundance and diameter distribution of DWD at the studied sites thus accounting for disturbance-related differences of volume and size, and the higher surface-to-volume ratio of small-diameter DWD. They are based on the a) realistic assumption that DWD respiration (i.e. density loss, not fragmentation) is not influenced by diameter class (Mattson et al. 1987, Marra and Edmonds 1996, Bond-Lamberty et al. 2003); and b) the unrealistic assumption that all DWD was in decay class 2, which is due to the lack of respiration data for decay classes other than 2. Several studies have shown wood respiration rates to increase slightly (Marra and Edmonds 1996) or significantly (Wang et al. 2002, Bond-Lamberty et al. 2003) with progressing decay status. If decay class were accounted for, stand-level DWD respiration rates would increase relative to our values, which are therefore conservative estimates of daytime summer respiration rates in undisturbed and disturbed Labrador black spruce forests.

Compared to soil respiration, DWD respiration contributes significantly to the forest-atmosphere C exchange, particularly in sites with large amounts of decaying DWD and low soil respiration rates. In old-growth stands, stand-level DWD respiration amounted to only 9% of the high, autotrophic-dominated soil respiration (Table 3), resulting from low piece-level DWD respiration rates and volume, and a high proportion of >10 cm DWD with low surface-to-volume ratio. In alpine riverine-forest systems, DWD respiration was 40–74% of soil respiration (Richard and Woodtli 2006). Following clearcut harvest, soil respiration rates decreased and stand-level DWD respiration increased to 100% of soil respiration (Table 3; Fig. 3), reflecting high piece-level respiration rates and abundance of harvest-generated DWD, particularly of <3.0 cm DWD with extremely high surface-to-volume ratio. Similarly, average monthly DWD respiration partly exceeded average monthly soil respiration in clearcut Western hemlock-Douglas fir forests (Marra and Edmonds 1994, 1996). In contrast, piece-level DWD and soil respiration rates in burned stands were very low, but stand-level DWD respiration amounted to 83% of soil respiration due to moderate abundance of DWD.

5. Conclusions

Disturbance-induced changes in the temperature and moisture regime are reflected by DWD and soil respiration rates. In cool humid Labrador black spruce, clearcut harvest and wildfire resulted in higher DWD temperatures and respiration rates compared to old-growth stands, but the increase in respiration was more pronounced following harvesting. Downed woody debris moisture levels decreased following disturbance, particularly in burned sites, where respiration was limited by low moisture contents. In forest C modeling, decomposition rates of DWD should therefore be differentiated by the disturbance-specific decomposition environment to adequately reflect post-disturbance C dynamics. Compared to soil respiration, DWD respiration is particularly important in disturbed forest ecosystems, where it can release similar (following fire) or equal (following harvest) amounts of CO_2 to the atmosphere.

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Figure captions

Fig. 1. Air, downed woody debris, and organic layer temperatures (˚C) by measurement date and stand. Error bars indicate ±1 SE.

Fig. 2. Daily precipitation (10/07–04/09/2008) and a) downed woody debris moisture content (%) and b) organic layer moisture potential (kPa) by measurement date and stand. Significant differences are indicated as follows, * H, OG > B; ° OG > B; ^ OG > H ($\alpha = 0.05$). Error bars indicate ±1 SE.

Fig. 3. a) Downed woody debris and b) surface respiration rates (g CO_2 m^{-2} h^{-1}) by measurement date and stand. Significant differences are indicated as follows, a) * H > B; ° H > OG; b) ^ OG > H > B; ˜ OG > B ($\alpha = 0.05$). Error bars indicate ±1 SE.

Figure 1

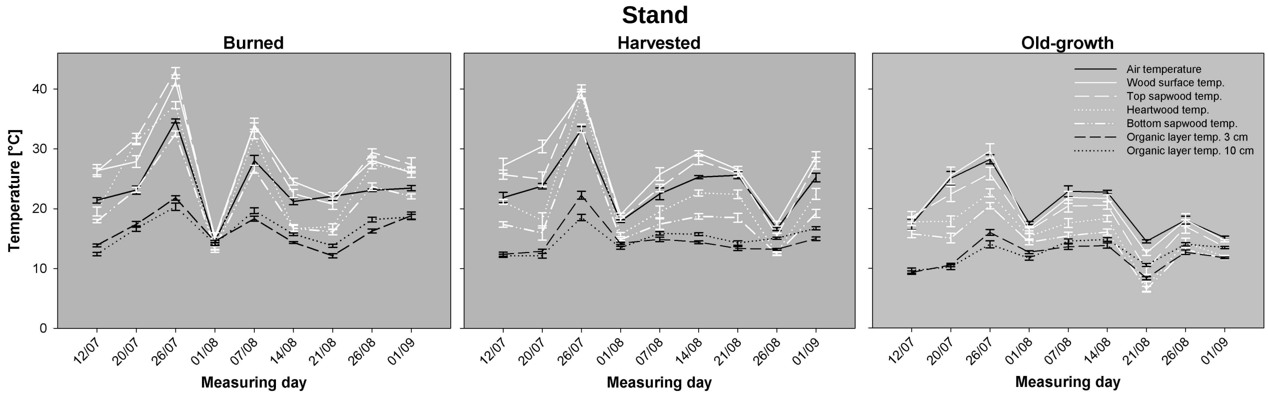


Figure 2

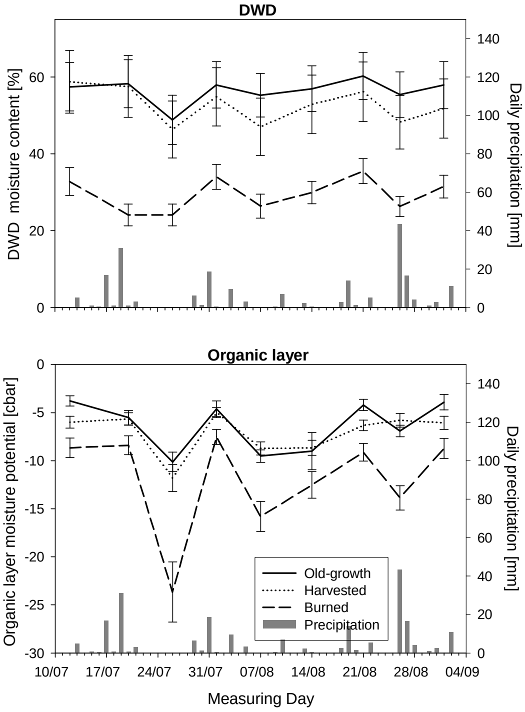
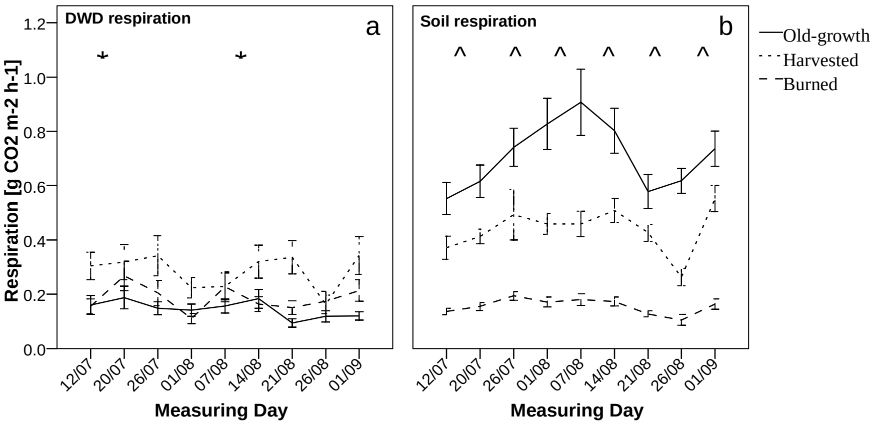


Figure 3



Tables

Table 1. List of abbreviations.

Abbreviation	Explanation
B	Burned stand type
C	Carbon
CO_2	Carbon dioxide
D_{DWD}	DWD density
H	Harvested stand type
OLT	Organic layer thickness [cm]
OG	Old-growth stand type
Ψ_{OL}	Organic layer moisture potential [cbar]
R_{S}	Soil respiration [g CO_2 m^{-2} h^{-1}]
R_{DWD}	WD respiration [g CO_2 m^{-2} h^{-1}]
RH%	Relative humidity [%]
T_{Air}	Air temperature [˚C]
T_{OL3}	Organic layer temperature below log (3 cm) [˚C]
T_{OL10}	Organic layer temperature (10 cm) [˚C]
$T_{\mathrm{WDsurface}}$	DWD surface temperature [˚C]
T_{DWDtop}	DWD top sapwood temperature (2 cm) [˚C]
T_{DWDheart}	DWD heartwood temperature (7 cm) [˚C]
$T_{\mathrm{DWDbottom}}$	DWD bottom sapwood temperature (2 cm) [˚C]
u_{DWD}	Gravimetric DWD moisture content [%]
DWD	Downed woody debris

Table 2. Pair-wise correlations* between a) air, downed woody debris and organic layer temperatures and b) relative humidity, downed woody debris moisture content, and organic layer moisture potential and thickness.

a)	Variables	Air temperature [˚C]	DWD temperature [˚C]				Organic layer temperature [˚C]	
			Surface	Top sapwood	Heart-wood	Bottom sapwood	3 cm	10 cm
	Air temperature [˚C]	1	.873 ‡	.821 ‡	.769 ‡	.743 ‡	.547 ‡	.483 ‡
DWD temperature [˚C]	Surface	.873 ‡	1	.924 ‡	.821 ‡	.797 ‡	.595 ‡	.505 ‡
	Top sapwood	.821 ‡	.924 ‡	1	.936 ‡	.899 ‡	.677 ‡	.581 ‡
	Heartwood	.769 ‡	.821 ‡	.936 ‡	1	.953 ‡	.715 ‡	.615 ‡
	Bottom sapwood	.743 ‡	.797 ‡	.899 ‡	.953 ‡	1	.778 ‡	.665 ‡
Organic layer temperature [˚C]	3 cm	.547 ‡	.595 ‡	.677 ‡	.715 ‡	.778 ‡	1	.826 ‡
	10 cm	.483 ‡	.505 ‡	.581 ‡	.615 ‡	.665 ‡	.826 ‡	1

b)	Variables	RH [%]	DWD moisture content [%]	Organic layer	
				Moisture potential [cbar]	Thickness [cm]
	RH [%]	1	.259 ‡	.399 ‡	.092
	DWD moisture content [%]	.259 ‡	1	.377 ‡	.384 †
Organic layer	Moisture potential [cbar]	.399 ‡	.377 ‡	1	.524 †
	Thickness [cm]	.092	.384 †	.524 †	1

* Correlation strength given by Spearman’s *ρ*.
† Significant at α = 0.001.
‡ Significant at α = 0.01.

Table 3. a) Downed woody debris volume (Hagemann et al. 2009) and estimated surface area; and b) per-hectare values of soil and downed woody debris respiration accounting for total downed woody debris surface area.

a)		DWD Volume [m^3 ha^{-1}] [a]			DWD surface area [m^2 ha^{-1}] [b]		
Diameter class [cm] [c]	Average [d] diameter [cm]	Harvested	Burned	Old–growth	Harvested	Burned	Old–growth
20.0–≤37.0	27.5	8.1 (1.0–17.9)	6.0 (3.4–8.9)	8.3 (4.3–12.7)	118 (15–260)	87 (49–129)	121 (63–185)
10.0–<20.0	15.0	22.3 (17.1–27.8)	46.2 (36.4–56.5)	23.3 (17.3–29.6)	595 (456–741)	1232 (971–1507)	621 (461–789)
>7.5–<10.0	8.8	3.9 (3.5–4.4)	9.9 (7.1–12.9)	3.9 (2.2–5.8)	177 (159–200)	450 (323–589)	177 (100–264)
>5.0–7.5	6.3	6.9 (5.7–8.2)	8.1 (7.1–9.2)	2.3 (0.8–4.1)	438 (362–521)	514 (451–584)	146 (51–260)
>3.0–5.0	4.1	4.7 (3.3–6.1)	5.3 (3.7–6.9)	1.5 (0.7–2.3)	459 (322–595)	517 (361–673)	146 (68–224)
>1.0–3.0	2.1	9.0 (8.0–10.1)	4.9 (3.5–6.5)	2.4 (1.7–3.1)	1714 (1524–1924)	933 (667–1238)	457 (324–590)
≤1.0	0.5	13.7 (12.7–14.6)	3.6 (3.2–4.0)	3.1 (2.5–3.8)	10960 (10160–11680)	2880 (2560–3200)	2480 (2000–3040)
Piles (≤30.0)	15.0	28.1 (19.0–38.1)	7.7 (2.3–14.2)	0.6 (0.2–1.0)	749 (507–1016)	205 (61–379)	16 (5–37)
Total		*144.0 (126.1–162.5)*	*91.5 (83.3–100.0)*	*46.9 (34.8–59.8)*	*15210 (13504–16937)*	*6819 (5443–8297)*	*4165 (3072–5380)*

b)	Soil respiration [kg CO_2 ha^{-1} h^{-1}]			DWD respiration [kg CO_2 ha^{-1} h^{-1}]		
Measurement date	Harvested	Burned	Old–growth	Harvested	Burned	Old–growth
12/07	3.7 (2.9–4.6)	1.4 (0.3–2.2)	5.5 (4.7–6.4)	4.7 (4.2–5.3)	1.1 (0.9–1.3)	0.7 (0.5–0.9)
20/07	4.1 (3.3–5.0)	1.6 (0.8–2.4)	6.2 (5.4–7.0)	4.9 (4.3–5.4)	1.8 (1.5–2.2)	0.8 (0.6–1.0)
26/07	5.0 (3.5–6.3)	1.9 (0.5–3.4)	7.4 (6.0–8.8)	5.2 (4.6–5.8)	1.4 (1.1–1.7)	0.6 (0.5–0.8)
01/08	4.6 (3.4–5.8)	1.7 (0.5–2.9)	8.3 (7.1–9.5)	3.3 (3.0–3.7)	0.8 (0.6–0.9)	0.6 (0.4–0.8)
07/08	4.6 (3.0–6.2)	1.8 (0.2–3.4)	9.1 (7.5–10.7)	3.5 (3.1–3.9)	1.6 (1.3–1.9)	0.7 (0.5–0.9)
14/08	5.1 (3.9–6.2)	1.7 (0.8–2.9)	8.0 (6.9–9.2)	4.9 (4.3–5.4)	1.1 (0.9–1.3)	0.7 (0.6–1.0)
21/08	4.3 (3.4–5.1)	1.3 (0.4–2.1)	5.8 (5.0–6.6)	5.2 (4.6–5.8)	1.0 (0.8–1.2)	0.4 (0.3–0.5)
26/08	2.6 (2.0–3.3)	1.1 (0.4–1.7)	6.2 (5.5–6.9)	2.4 (2.2–2.7)	1.2 (1.0–1.5)	0.5 (0.4–0.6)
01/09	5.5 (4.5–6.5)	1.6 (0.6–2.6)	7.4 (6.4–8.4)	5.2 (4.6–5.8)	1.5 (1.2–1.8)	0.5 (0.4–0.6)

Note: 95% confidence intervals in parentheses

[a] Data from Table 6 in Hagemann et al. (2009)

[b] DWD surface per diameter class calculated based on total volume and average diameter assuming cylindrical shape

[c] DWD diameter class (Hagemann et al. 2009); largest measured diameter 37 cm

[d] Assumed average diameter for each diameter class

Table 4. Summary statistics for (a) factor analysis showing component matrix and explained variance, and (b) hierarchical nested linear mixed model (LMM) analysis describing the influence of the listed variables on downed woody debris respiration.

(a) Factor analysis	**Component**		**Communalities**
Variable	**1**	**2**	**Extraction**
Air temperature T_{Air}	0.870	0.255	0.822
DWD temperature			
$T_{DWDsurface}$	0.896	0.245	0.862
T_{DWDtop}	0.946	0.166	0.923
$T_{DWDheart}$	0.942		0.897
$T_{DWDbottom}$	0.951		0.906
Organic layer temperature			
T_{OL3}	0.868		0.758
T_{OL10}	0.781	-0.161	0.637
Organic layer moisture potential Ψ_{OL}	0.633	-0.208	0.443
Relative humidity *RH%*	-0.781	-0.202	0.651
DWD moisture content u_{DWD}	-0.393	0.842	0.864
DWD density D_{DWD}	0.256	-0.879	0.839

	Variance		
Component	**Total**	**%**	**Cumulative %**
1	6.841	62.2	62.2
2	1.761	16.0	78.2

(b) LMM analysis

Variable	**FT***	***F***	**Wald *Z***	***P***	**Variance [%]**
Intercept		62.227	na[†]	≤0.001 [‡]	
Stand type	F	7.858	na[†]	0.043 [‡]	
Site(Stand type)	R	na[†]	1.120	0.263	7.5
Plot(Site)	R	na[†]	2.533	0.011 [‡]	35.0
Measuring day	F_{rep}	4.732	na[†]	0.031 [‡]	
Measuring time	F	36.341	na[†]	≤0.001 [‡]	
T_{DWDtop}	F	19.227	na[†]	≤0.001 [‡]	
$T_{DWDbottom}$	F	24.536	na[†]	≤0.001 [‡]	
u_{DWD}	F	76.321	na[†]	≤0.001 [‡]	
D_{DWD}	F	16.207	na[†]	≤0.001 [‡]	
Error					57.5

Note for (b): Stand type, measuring day (repeated), measuring time, DWD top sap temperature (T_{DWDtop}), DWD bottom sap temperature ($T_{DWDbottom}$), DWD moisture content (u_{DWD}), and DWD density (D_{DWD}) are fixed factors; site nested within stand type and plot nested within site are random factors.

* FT = factor type; fixed (F) and random (R) factors.

[†] The statistic is not applicable to this factor type.

[‡] Significant at α = 0.05.

Table 5. Summary statistics for (a) factor analysis showing component matrix and explained variance, and (b) hierarchical nested linear mixed model (LMM) analysis describing the influence of the listed variables on soil respiration.

(a) Factor analysis	**Component**		**Communalities**
Variable	**1**	**2**	**Extraction**
Air temperature T_{Air}	0.818	0.391	0.821
Organic layer temperature			
T_{OL3}	0.881	0.020	0.776
T_{OL10}	0.844	-0.022	0.713
Organic layer moisture potential Ψ_{OL}	0.766	-0.415	0.760
Relative humidity *RH%*	-0.751	-0.388	0.715
Organic layer thickness *OLT*	-0.346	0.845	0.834

	Variance		
Component	**Total**	**%**	**Cumulative %**
1	3.428	57.1	57.1
2	1.191	19.9	77.0

(b) LMM analysis

Variable	**FT***	***F***	**Wald *Z***	***P***	**Variance [%]**
Intercept		242.332	na†	≤0.001 ‡	
Stand type	F	42.219	na†	≤0.001 ‡	
Site(Stand type)	R	na†	1.370	0.171	10.7
Plot(Site)	R	na†	1.995	0.047 ‡	7.4
Measuring day	F_{rep}	0.000	na†	0.992	
Measuring time	F	5.581	na†	0.019 ‡	
T_{Air}	F	18.886	na†	≤0.001 ‡	
T_{OL3}	F	7.378	na†	0.007 ‡	
T_{OL10}	F	9.182	na†	0.003 ‡	
Ψ_{OL}	F	0.013	na†	0.909	
RH%	F	13.455	na†	≤0.001 ‡	
OLT	F	2.309	na†	0.130	
T_{OL10} * Ψ_{OL}	F	5.717	na†	0.018 ‡	
T_{OL10} * *OLT*	F	5.681	na†	0.018 ‡	
Error					81.9

Note for (b): Stand type, measuring day (repeated), measuring time, air temperature (T_{Air}), organic layer temperature (T_{OL3} & T_{OL10}), organic layer moisture potential (Ψ_{OL}), relative humidity (*RH%*), and organic layer thickness (*OLT*) are fixed factors; site nested within stand type and plot nested within site are random factors.

* FT = factor type; fixed (F) and random (R) factors.

† The statistic is not applicable to this factor type.

‡ Significant at α = 0.05.

4.5 Measured and Modelled Carbon Stocks

Carbon dynamics of DOM, organic layer, and mineral soil in small-treed, cool and humid boreal forests such as Labrador black spruce are expected to differ from those of drier or warmer boreal forests (Section 2.2.1). Although deadwood abundance and aboveground residence times in Labrador were similar to other boreal forests (Section 4.3), processes such as paludification (Simard et al. 2009) and the burial of WD by overgrowing moss (Hagemann et al. 2009) are likely more pronounced in regions with low average temperatures, vigorous moss layers, and long FRI. The applicability of C budget models particularly to northern boreal forests remains unclear despite efforts to comprehensively model post-disturbance boreal forest C stocks at the stand-level, because studies generally focussed on regional to large-scale representation of C stocks and fluxes (Beer et al. 2006), one disturbance type (Balshi et al. 2007), or a specific C pool (Ju and Chen 2008).

The biomass and C content data collected in Labrador black spruce using the NFI Ground Sampling Guidelines (Natural Resources Canada 2010a) allow estimates of C stored in live trees, aboveground and belowground deadwood, organic layer, and mineral soil, and permits estimates of the effect of disturbance history and time since disturbance on these C pools. In addition, measured C stocks of the different strata can be mapped to CBM-CFS3 modelled pools thus providing a unique opportunity to evaluate and, if required, calibrate the CBM-CFS3 to northern boreal forests.

4.5.1 Hagemann U, Moroni M, Shaw C, Makeschin F, and Kurz W. 2010. Comparing measured and modelled forest C stocks in high-boreal forests of harvest and natural- disturbance origin in Labrador, Canada. Ecol. Model. 221: 825–839

Extended Abstract

Live-tree C stocks increased with tree age from 0.4 Mg C ha^{-1} in the recently harvested to 46.9 Mg C ha^{-1} in the old-growth stratum, and are in the lower range of values reported for the closed-canopy boreal forest. Snags C stocks in the gap-driven old-growth stratum amounted to 5.5 Mg C ha^{-1}, and exceeded those of harvested and middle-aged burned strata, where few snags were created by the post-harvest death of uncut trees or most fire-generated snags had collapsed, respectively. Woody debris was the largest aboveground deadwood C pool (0.8–25.8 Mg C ha^{-1}) and significantly decreased with time since harvest. Buried deadwood C stocks were highest in the old-growth stratum (18.2 Mg C ha^{-1}), and ranked higher than aboveground WD C pools in all but the recently harvested and middle-aged burned strata. Organic layer C stocks (30.4–47.4 Mg C ha^{-1}) were within the range reported for other boreal forests, but mineral soil C stocks (121.5–208.1 Mg C ha^{-1}) were considerably higher than observed in drier or warmer upland boreal forests and comparable to values reported for poorly-drained forested Podzol and peatland sites. Buried deadwood, organic layer, mineral soil, and total ecosystem C (185.6–279.7 Mg C ha^{-1}) showed no trend with disturbance history or forest age.

Although the CBM-CFS3 represented measured live-tree C dynamics in all strata well, adjustments to the volume-to-biomass conversion and partitioning parameters were required for the non-merchantable and branch C pools to accurately capture live-tree C stocks in the studied black spruce ecosystem. Default CBM-CFS3 parameters overestimated non-merchantable biomass particularly in the old-growth stratum, where tree productivity and regeneration decline as a result of paludification, and may not be appropriate for all regions due to allometric crown plasticity and within-species variability. Both yield curves and VBC parameters must therefore be considered when modelling forest C stocks using CBM-CFS3, as uncertainty of live-tree C estimates will affect all DOM C pools.

Default CBM-CFS3 modelled snag and WD C dynamics reflected the expected decrease with time since fire or harvest, respectively, but measured snag fall rates and old-growth $>$10 cm WD stocks were considerably underestimated. Accuracy of the modelled estimates of dead organic matter and subsequently soil C pools was improved relative to regional default parameters by increased snag fall (0.10 yr^{-1}) and $>$10 cm WD base decay (0.06 yr^{-1}) rates.

The incorporation of BW and bryophyte dynamics into the CBM-CFS3 requires structural changes to the model. Recommendations are to (a) develop a module to account for the C dynamics of a bryophyte pool that provides parameters to express the physical burial of WD and impacts on its decay, or – in the absence of a bryophyte module – either (b) calibrate a $>$10 cm WD to organic layer C pool transfer rate based on field-measured rates of moss growth and WD burial and modify organic layer base decay rates in cool humid ecosystems based on field-measured decay rates of BW, or (c) introduce a belowground medium (i.e., BW) C pool into the CBM-CFS3 to represent the lower decay rates of BW.

As the CBM-CFS3 was initially designed for well-drained upland forests, the uncertainty of modelled organic layer and mineral soil C stocks increases with increasing bryophyte productivity and average soil moisture levels. Modelled estimates of organic layer C stocks in Labrador black spruce improved after reducing the default organic layer base decay rate to 0.0075 yr^{-1}, reflecting the combination of decay-resistant feathermoss and sphagnum litter and wood-derived lignified litter typical of boreal forests. Modelled mineral soil C estimates were improved by applying a preliminary belowground slow C pool base decay rate (0.00207 yr^{-1}) optimized for the soil type of the studied sites, Humo-Ferric Podzols, indicating that the incorporation of soil type-specific decay rates will likely improve the CBM-CFS3 estimates of mineral soil C stocks.

The CBM-CFS3 modifications recommended above will need to be tested further using new plot-level data collected as part of Canada's NFI. However, the NFI only measures $>$10 cm BW and provides no data on bryophyte dynamics, making it difficult to adequately capture BW and bryophyte-dominated organic layer dynamics in cool wet boreal forests.

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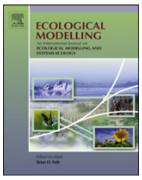

Comparing measured and modelled forest carbon stocks in high-boreal forests of harvest and natural-disturbance origin in Labrador, Canada

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Organic layer

ABSTRACT

Understanding the effects of disturbance regimes on carbon (C) stocks and stock changes is a prerequisite to estimating forest C stocks and fluxes. Live-tree, dead-tree, woody debris (WD), stump, buried wood, organic layer, and mineral soil C stock data were collected from high-boreal black spruce (*Picea mariana* (Mill.) B.S.P.) stands of harvest and fire origin and compared to values predicted by the Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3); the core model of Canada's National Forest Carbon Monitoring, Accounting and Reporting System. Data comparing the effect of natural and anthropogenic disturbance history on forest C stocks are limited, but needed to evaluate models such as the CBM-CFS3. Results showed that adjustments to the CBM-CFS3 volume-to-biomass conversion and partitioning parameters were required for the non-merchantable and branch C pools to accurately capture live-tree C stocks in the studied black spruce ecosystems. Accuracy of the CBM-CFS3 modelled estimates of dead organic matter and soil C pools was improved relative to regional default parameters by increased snag fall and >10 cm WD base decay rates. The model evaluation process also highlighted the importance of developing a bryophyte module to account for bryophyte C dynamics and the physical burial of woody debris by bryophytes. Modelled mineral soil C estimates were improved by applying a preliminary belowground slow C pool base decay rate optimized for the soil type of the studied sites, Humo-Ferric Podzols.

1. Introduction

Forests contain large amounts of carbon (C) in biomass, dead organic matter (DOM), and soil and contribute to significant annual C exchanges with the atmosphere (Denman et al., 2007). The importance of Canada's extensive forest resource to the global C cycle is being recognized, and efforts are being made to quantify the biomass resource and its C dynamics (e.g., Kurz and Apps, 1999; Chen et al., 2000; Kurz et al., 2008, 2009). As a signatory to the United Nations Framework Convention on Climate Change (UNFCCC, 1992) Canada must report on emissions and removals of carbon dioxide (CO_2) and non-CO_2 greenhouse gases in the managed forest.

The Carbon Budget Model of the Canadian Forest Sector (CBM-CFS3) is the core model of Canada's National Forest Carbon Monitoring, Accounting and Reporting System (NFCMARS, Kurz and Apps, 2006). The CBM-CFS3 simulates the impacts of disturbances, including harvesting, insect outbreaks, and fire, on forest C stocks (Kurz and Apps, 1999; Kurz et al., 2009). Understanding the effects of different disturbance regimes on C stocks and stock changes is a prerequisite for modelling Canadian boreal forest dynamics (Li and Apps, 1995) and for estimating forest C stocks and fluxes (Kurz et al., 1998). Data on the effects of natural and anthropogenic disturbance history on forest DOM and soil C stocks are limited, however, in particular for the northern boreal forest.

Small-treed, short-lived northern boreal forests such as high-boreal Labrador black spruce (*Picea mariana* (Mill.) B.S.P.) forests cover large areas throughout the Canadian and circumpolar boreal region and—in the form of oroboreal forests—in mountain ranges, but dead wood and C dynamics in these forests have received relatively little attention so far. Studies of boreal and oroboreal forest C dynamics have mostly focused on one disturbance type (e.g., post-fire; Manies et al., 2005) or one stage of development (e.g., mature or old growth; Harvey et al., 1981; Thompson et al., 2003; Zielonka,

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2006), or investigated specific DOM C pools such as woody debris (Bond-Lamberty et al., 2003), snags (Smith et al., 2008), or dead wood (Moroni, 2006). Dead organic matter, organic layer, and mineral soil C dynamics in cool and humid northern boreal forests such as in central Labrador are expected to differ from those of drier or warmer boreal forests, because processes such as woody debris (WD) burial within the organic layer by overgrowing moss (Hagemann et al., 2009) and paludification (Simard et al., 2009) are more pronounced in regions with low average temperatures, vigorous moss layers, and long fire-return intervals (FRI). Research is thus required to examine the impact of disturbance history and time since disturbance using a comprehensive data set of biomass, DOM, and mineral soil C of high-boreal forests, to develop forest management strategies aimed at decreasing C sources and increasing C sinks (Canadell et al., 2007), and to evaluate models such as the CBM-CFS3 for northern boreal forest ecosystems.

To date, few efforts have been made to comprehensively model boreal forest C stocks at the stand-level after different disturbances. Studies generally focussed on a regional to large-scale representation of C stocks and fluxes (Beer et al., 2006; Balshi et al., 2007), one disturbance type (Jiang et al., 2002; Balshi et al., 2007), or a specific C pool such as organic layer or soil C (Yurova and Lankreijer, 2007; Ju and Chen, 2008). However, the applicability of models to the northern boreal forest remains unclear. The dataset of this study provides a unique opportunity to evaluate the performance of the CBM-CFS3 in high-boreal Labrador black spruce forests for three reasons. First, the sampling design focused on black spruce, a species of major economic and ecological significance in Labrador and throughout the North American boreal forests. Second, it assessed impacts of two dominant forest disturbance types in Labrador (harvest (H) and burned (B)). The major anthropogenic disturbance in Labrador black spruce is clearcut harvesting, with a total cut area of roughly 21,000 ha in the central region since 1969 (Roberts et al., 2006). The major natural disturbance in Labrador is wildfire (Wilton, 1964), with estimates of the FRI ranging from 300 to 500 years—longer than for most other boreal forests (Foster, 1984). And third, the very detailed sampling design enabled comparison of most CBM-CFS3 pools to measured data, thus allowing for identification of model components that might be improved to increase the model's accuracy when applied to northern boreal forest ecosystems.

The objectives of the research reported here were to (1) characterize forest C dynamics of central Labrador high-boreal black spruce forest regrown after clearcut harvesting and to contrast C stocks in harvested sites with those in old-growth stands aged >140 years and with stands burned 21 years before measurement, and (2) compare field-measured C stocks with those predicted using the CBM-CFS3 with emphasis on (a) the impact of harvesting and wildfire on forest C stocks, (b) changes in forest C pools with time since disturbance, and (c) identification of model components that could be modified to more accurately reflect C dynamics of these forest ecosystems.

2. Materials and methods

2.1. Field study

The field study was conducted in central Labrador in the Lake Melville Ecoregion, which represents the eastern extent of the Boreal Shield Ecozone and is a narrow extension of the boreal forest into the Taiga Shield Ecozone (Ecoregions Working Group, 1989). Study sites experience mean annual temperatures (MAT) of −2.4 °C to −1.0 °C (Table 1), and receive approximately 1000 mm of precipitation evenly distributed throughout the year, making it one of the wettest North American boreal forests (Foster, 1985; Environment Canada, 2008). Soils are mainly Humo-Ferric and juvenile Ferro-Humic Podzols (Soil Classification Working Group, 1998). An overview of the field study design is described below. For details, please refer to Hagemann et al. (2009).

2.1.1. Site selection

Sites were selected to represent five populations, hereafter strata, classified by disturbance type (harvest (H), burned (B), or unknown origin (U)) and stand age (recently disturbed (D), young (Y), middle-aged (M), and old (O)). Three sampling sites were located for each of the five strata for a total of 15 sites (Fig. 1; Table 1); all located within 50 km north to northwest of Goose Bay. Because past disturbances have the potential to leave a legacy of

Table 1
Characteristics of Labrador black spruce sites.

	Disturbance history/stand age class[a]				
Variables	H/D	H/Y	H/M	B/Y	U/O
Year of last disturbance	2005	1989	1970–72	1985	n.a.[b]
Forest age (years)					
Pre-disturbance[c]	>140	>140	>140	>140	n.a.[b]
Current[c]	n.a.[b]	15–16	30–32	n.a.[b]	146–204
Forest type					
Pre-disturbance[c]	bS842M/P[d]	bS842M[d]	bS842M[d]	bS842M[d]	n.a.[b]
Current[c]	n.a.[e]	n.a.[e]	bSbF110M[f]	Scs[e]	bS842M[d]
Stand characteristics					
Median DBH [cm]	6.9 ± 3.5	7.9 ± 4.2	10.8 ± 0.3	0.0 ± 0.0	14.0 ± 0.7
Mean tree height[g] [m]	6.1 ± 1.8	5.1 ± 2.4	7.6 ± 0.4	0.0 ± 0.0	11.0 ± 0.4
Basal area $[m^2\ ha^{-1}]$	0.1 ± 0.1	0.1 ± 0.0	4.2 ± 0.7	0.0 ± 0.0	25.0 ± 2.6
Merchantable volume $[m^3\ ha^{-1}]$	0.0 ± 0.0	0.3 ± 0.3	16.2 ± 4.8	0.0 ± 0.0	130.2 ± 22.3
Climate and topography					
Mean annual temp.[h] [°C]	−2.1 to −1.1	−2.4 to −2.1	−1.2 to −1.0	−1.6 to −1.3	−2.2 to −1.8
Elevation [m asl]	81–281	230–321	100–134	99–194	161–257

[a] Disturbance history – clear-cut harvest (H), burned (B), unknown origin (U); stand age class – recently disturbed (D), young-aged (Y), middle-aged (M), old-aged (O).
[b] Unknown or regeneration too small for classification.
[c] Newfoundland and Labrador forest inventory data (NL Provincial Forest Service, Data Dictionary for District Library).
[d] >75% black spruce; older than 140 yrs; average height 12–15m; crown closure 50–75%; medium (M) or poor (P) site productivity.
[e] No current forest type classification. Scs = Scrub.
[f] >50% black spruce with >25% balsam fir; older than 20 yrs; average height <6m; crown closure <25%, medium site productivity.
[g] For all trees with DBH >9 cm.
[h] Site-specific data; refer to McKenney et al. (2007).

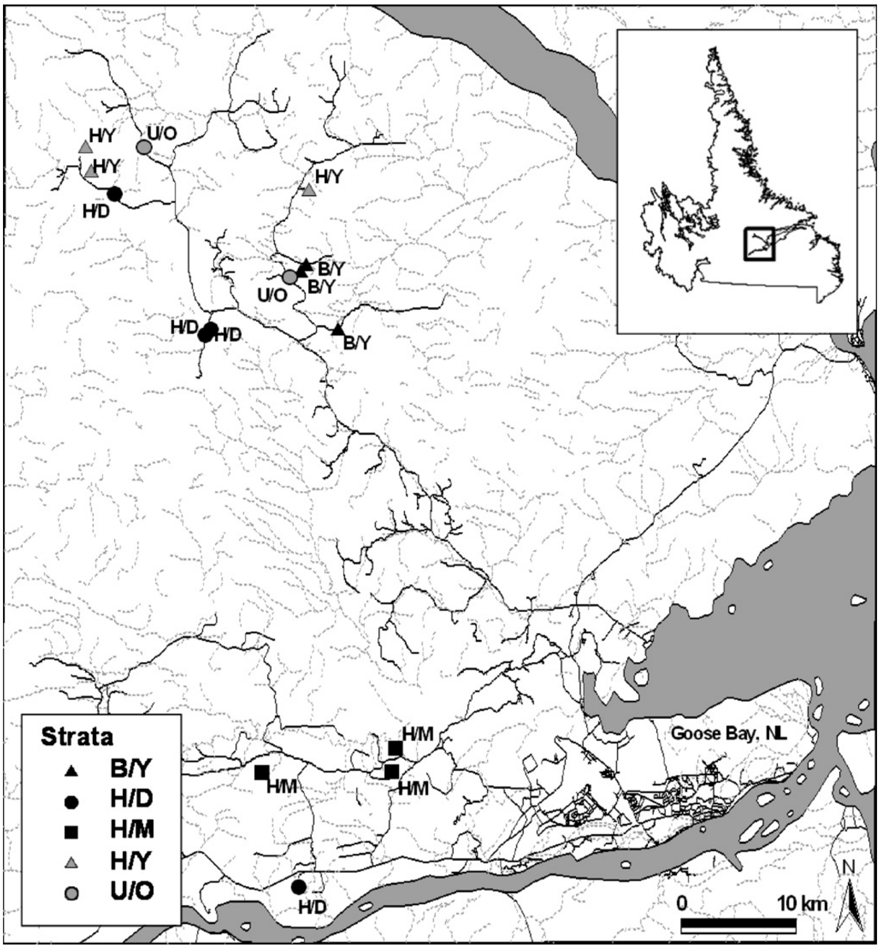

Fig. 1. Distribution of the Labrador study sites by strata. H/D: 1 year after harvest; H/Y: 17 years after harvest; H/M: 36–36 years after harvest; B/Y: 21 years after fire; U/O: old-growth of unknown origin.

dead wood in the current rotation (Krankina and Harmon, 1994), all recently disturbed, young, and middle-aged sites were selected to represent stands that were old-growth spruce-dominated forests at the time of the last stand-replacing disturbance, and had regenerated or were regenerating to stands dominated by spruce. At the time of measurement, regeneration had failed in the young burned stratum (B/Y), but stands were expected to eventually regenerate to black spruce-dominated stands (Roberts et al., 2006).

Harvested sites were selected to form a chronosequence comprising nine sites: (1) three harvested 1 year before measurement (H/D); (2) three harvested 17 years before measurement (H/Y); and (3) three harvested 34–36 years before measurement (H/M). No suitable sites were found for a corresponding post-fire chronosequence, thus post-fire measurements were restricted to sites temporally equivalent to the H/Y sites: three sites killed by fire 21 years before measurement (B/Y). Sites regenerating after harvesting and fire are referred to as harvested and burned sites, respectively.

Old-growth stands and, for disturbed strata, stands of the pre-disturbance rotation were classified as the most common productive forest type in Labrador (bS842M; Government of Newfoundland and Labrador, 2006a). This forest type is dominated by black spruce (>75%) older than 140 years with an average height of 12–15 m, crown closure of 50–75%, and of medium productivity (for merchantable yield). This criterion could not be met at the H/D Churchill River site, which supports a stand of type bS842 that is a spatial mix of medium and poor site-productivity classes (Table 1). Average live-tree diameter at breast height (DBH), height, basal area, and merchantable volume for all strata are presented in Table 1. Harvested strata were either regenerating to or were expected to regenerate to black spruce-dominated forests (Roberts et al., 2006).

Where pre-disturbance stand-type data were unavailable (B/Y), the stand type was assessed based on the knowledge of local forestry professionals, on site-specific relief and vegetation, soil type, and characteristics of adjacent stands. Stand age was determined from increment-core ring counts at the stem base. Harvesting removed all stems with a DBH ≥9 cm to a top diameter of 8 cm, by chainsaw in the H/Y and H/M sites, and by short-wood mechanical harvester in the H/D sites. All fires were stand replacing and the sites were not salvage logged.

2.1.2. Sampling design

All field measurements were conducted from June to September 2006. The plot design and field measurements were based on the National Forest Inventory (NFI) Ground Sampling Guidelines (Natural Resources Canada, 2009). Four sample plots were located randomly within each site. Each plot comprised two concentric circular subplots (radius 11.28 m and 3.99 m, respectively) with two 40-m line transects, perpendicular to each other, crossing at their mid-point at the plot center. At the end of one randomly selected transect, a square subplot (1 m^2) was established.

Data on live-tree, mineral, and organic soil horizon C were collected concurrent with dead wood data reported by Hagemann et al. (2009). Diameter and height of live trees and snags (dead standing trees) with DBH $\geq$9 cm were measured within the 11.28-m radius circular subplot. Diameter and height of live trees and snags with DBH <9 cm and stump (<1.3 m rooted bole portion of dead trees) height and top diameter inside bark were measured within the 3.99-m radius circular subplot. Live individual-tree aboveground biomass was estimated from regional NFI biomass equations for Ecozone 6 differentiated by site productivity class based on species, tree height, and DBH (Lambert et al., 2005). Live-tree C stocks were estimated by multiplying live-tree oven-dry biomass by 0.5 (Matthews, 1993; Lamlom and Savidge, 2003). Snag biomass was estimated from regional NFI biomass equations (Lambert et al., 2005; Natural Resources Canada, 2005, unpublished report) and corrected for dead wood density based on decay class (Hagemann et al., 2009). Where snag tops had fallen, intact snag heights were estimated, and the proportion of snag biomass remaining was determined from stem volume distribution equations (Honer, 1965). Stump volume was calculated assuming a cylindrical stump shape (Natural Resources Canada, 2009) and converted to biomass by assigning dead wood density by decay class (Hagemann et al., 2009). Carbon stocks of snags and stumps were estimated by multiplying oven-dry biomass by 0.5 (Matthews, 1993; Lamlom and Savidge, 2003). For a more detailed description of snag, stump, and WD estimation see Hagemann et al. (2009).

The diameters of WD were measured at their point of intersection along the 40-m transects. Volumes of WD were calculated using the line intersect method equation 8 (Marshall et al., 2000), and biomass was estimated by assigning dead wood densities by species and decay class. Woody debris <1 cm in diameter was sampled in the 1-m^2 subplot (Hagemann et al., 2009). Carbon stocks of snags, stumps, and WD were estimated by multiplying oven-dry biomass by 0.5, for <1 cm WD, laboratory-determined C contents were used (0.57 ± 0.002%). All C analysis was done using a LECO CNS-2000 combustion analyzer following the method of LECO Corporation (2003).

Thickness of the soil organic horizons and buried dead wood (BW; WD incorporated more than 50% into the organic layer) were measured at 2-m intervals along each transect by driving a shovel into the surface of the forest floor. Woody debris was defined as BW if it was more than half buried in the organic layer. The area of the plot occupied by BW or organic horizons was determined from the proportion of 2-m observations that encountered these tissues. The volume of BW or soil organic horizons was estimated from the average thickness of each multiplied by the area they occupied in the plot. Volume of BW was multiplied by species and decay class specific densities (Hagemann et al., 2009) to estimate BW biomass. Half of the BW biomass was assumed to be C. Organic horizon bulk density was estimated from the volume and oven-dry mass of a sample taken from a 20 × 20 cm area to the top of the mineral soil in the 1-m^2 subplot. Organic horizon samples were dried at 55 °C for 4 days, sub-sampled, and passed through an 850-μm mesh before C analysis (LECO).

From each site, 0.75–1.5 dm^3 soil samples, which included coarse fragments (>2 mm diameter), were taken from 0 to 15, 15 to 30, and 30 to 45 cm depths. Depth samples were taken from all four plots at 0–15 cm; from two randomly selected plots at 15–30 cm, and from one randomly selected plot at 30–45 cm. The volume of each hole excavated during soil sampling was measured by placing a plastic bag into the hole and measuring the volume of glass beads required to fill the hole. Mineral soil samples were air dried and passed through a 2-mm mesh, dried at 55 °C for 4 days, and weighed. Bulk density of <2 mm mineral soil was estimated based on <2 mm dry weight and the volume excavated. A sub-sample of <2 mm mineral soil was passed through an 850-μm mesh before C analysis (LECO).

2.2. Carbon Budget Model of the Canadian Forest Sector 3 (CBM-CFS3)

2.2.1. Overview

Here, we provide an overview of the CBM-CFS3, a stand- and landscape-level model of forest dynamics that tracks C stocks, stock changes, and emissions and removals of CO_2, methane (CH_4), and carbon monoxide (CO) (Kurz et al., 1992, 2002; Kurz and Apps, 1999). The CBM-CFS3 (version 1.0) used in this analysis is a substantially advanced version of the model that, among other changes, includes a detailed presentation of DOM dynamics (Kurz et al., 2009). To meet the requirements of an operational-scale forest C budget model (Kurz et al., 2002), the model has been made more accessible through a graphical user interface, data pre- and post-processing tools, and a detailed user's guide (Kull et al., 2006). The model and documentation are available on the internet at www.carbon.cfs.nrcan.gc.ca. A detailed description and a conceptual diagram of the model are provided in Kurz et al. (2009).

Biomass C dynamics in the CBM-CFS3 are simulated in annual time steps using yield curves (defining merchantable volume as a function of stand age) that are provided by the user. Merchantable volume is converted into aboveground biomass components based on the volume-to-biomass conversion (VBC) equation used to estimate Canada's national forest biomass (Boudewyn et al., 2007). Belowground biomass is predicted from aboveground biomass using stand-level regression equations for softwood and hardwood species (Li et al., 2003).

To improve the representation of C dynamics in dead standing trees, four additional C pools have been added to the earlier version of the model (Kurz and Apps, 1999). These contain standing dead stemwood (snags) and the dead branches associated with standing dead trees for the softwood and the hardwood stand components (Kurz et al., 2009). Moreover, to facilitate comparison between modelled and measured DOM and soil C pools, the model's DOM pools have been partitioned into above- and belowground components (along the interface between the forest floor and the mineral soil).

As in the earlier versions of the model, each biomass component can be transferred to DOM pools through litterfall, tree mortality, and disturbance impacts. Litterfall and other turnover rates for each biomass pool are defined by regional parameter sets. Annual biomass turnover rates are used to represent mortality that occurs for most stand development to the point of stand break-up. When the merchantable volume over age curve indicates declining volume at higher stand ages (stand break-up), biomass transfer to DOM pools is the sum of biomass loss (declining volume) plus annual turnover. Disturbance impacts of each disturbance type are modelled through "disturbance matrices" (Kurz et al., 1992) that define the impacts of each disturbance type for each biomass and DOM pool in the stand. For example, stand-replacing wildfire consumes some biomass pools, kills the remainder of the biomass (and transfers it to the DOM pools), and releases greenhouse gases (CO_2, CH_4, and CO) to the atmosphere through the partial combustion of biomass and DOM pools.

2.2.2. Initialization

The CBM-CFS3 uses a spin-up procedure (Kurz and Apps, 1999; Kurz et al., 2009) to estimate the quantity of C in soil and DOM pools before simulating scenarios. It requires user-specified assumptions

Table 2
'Default' CBM-CFS3 parameters used (without parentheses) and 'Modified B' parameters tested (in parentheses) in dead organic matter (DOM) dynamics simulations of the black spruce study sites.

CBM-CFS3 C pool	Decay parameters					Physical transfer parameters	
	Base decay rate (yr^{-1})	Q_{10}	P_{atm}	P_t	Pool receiving, P_t	Transfer rate (yr^{-1})	Pool receiving transfer
Snag stems	0.0187	2	0.83	0.17	AG slow	0.032 (0.10[a])	Medium
Snag branches	0.0718	2	0.83	0.17	AG slow	0.10 (0.20[b])	AG fast
Medium	0.0374 (0.06[a])	2	0.83 (0.70)	0.17 (0.30)	AG slow	N/A	N/A
AG fast	0.1435	2	0.83	0.17	AG slow	N/A	N/A
AG very fast	0.355	2.65	0.815	0.185	AG slow	N/A	N/A
AG slow	0.015 (0.0075)	2.65	1.0	0.0	N/A	0.006	BG slow
BG fast	0.1435	2	0.83	0.17	BG slow	N/A	N/A
BG very fast	0.5	2	0.83	0.17	BG slow	N/A	N/A
BG slow	0.0033 (0.00207)	1	1.0	0.0	N/A	N/A	N/A

Decomposition parameters include the base decay rate at a temperature of 10 °C, sensitivity to temperature (Q_{10}), and the proportion of decay C released to the atmosphere (P_{atm}) versus transferred to a slow DOM pool (P_t), where $P_{atm} + P_t = 1$. AG = aboveground, BG = belowground, N/A = not applicable.

[a] Recommended by Moroni et al. (submitted for publication) and this study.

[b] Recommended by Moroni et al. (submitted for publication), but not by this study.

about historic disturbance-return intervals, the type of disturbance occurring during the spin-up procedure, and the type of the last disturbance that preceded the establishment of the current stand. To initialize the DOM pools for the simulations in this study, we assumed a 300-year historic FRI. Stands were assumed to follow growth curves for previous rotation forest types where known, and for current rotation forest type where the previous rotation forest type was not known (Table 1).

During the spin-up procedure, stands were grown to the age of the disturbance-return interval (300 years), and disturbed using the stand's historic disturbance type. At the end of each disturbance-return interval, the CBM-CFS3 compares the slow pool DOM C stocks between the current and previous rotations. If the difference in the stocks is <1%, then the DOM C stocks are assumed to be in a quasi-equilibrium state determined by inputs (which are a function of net primary productivity, site productivity, disturbance type, and species) and losses from decomposition (rates are a function of MAT) and disturbances (direct losses only from wildfires). Once this equilibrium is reached, the CBM-CFS3 simulates one more rotation with the known disturbance history.

In this study, where the forest type and age before the last stand-replacing disturbance were known, the CBM-CFS3 simulated the previous rotation to the age of disturbance and applied the last known disturbance to the stand. The CBM-CFS3 then simulated forest growth of the current stand to the age of stand measurement. Where the previous rotation length was unknown, the final 300-year rotation from the historic DOM C estimation was assumed to be the previous rotation, and the stand was simulated from the last disturbance to the current age.

2.2.3. *Model simulations, assumptions, and parameterization*

In this study, the model was applied to single theoretical stands 1 ha in size, each representative of one of the 15 sites in the field study. The Labrador administrative boundary and the Boreal Shield East Ecozone were selected during data import, providing default parameters for decay rates, litter fall rates, snag fall rates (Table 2), disturbance matrices, and VBC parameters. Growth curves specific to forest type and site productivity class were taken from the Department of Natural Resources (Government of Newfoundland and Labrador, 2006b). The field-measured percentages of black spruce and balsam fir (*Abies balsamea* (L.) Mill.) were used to guide yield curve selection, and stands were modelled identifying black spruce as the lead species. For stand ages exceeding the existing growth curves, the volume of the last available age class (190–200 years) was maintained, assuming the forest continues under a gap-replacement system (McCarthy, 2001). The historical disturbance type used for model initialization was assumed to be 100% fire mortality for all sites that were assumed to regenerate to black spruce-dominated forest types with a regeneration delay of 20 years. All disturbance types simulated (historic and last) were assumed to be stand replacing.

Four modifications were made to the regional default settings so the model would better represent conditions at the scale of the sites. First, 1970–2001 MAT values were estimated by McKenney et al. (2007) rather than using the single regional default value of 3.4° C; second, the post-fire regeneration delay was set to 20 years, because black spruce regeneration in Labrador establishes slower than in central and western Canada (Foster, 1985), usually where snags have been uprooted (Simon and Schwab, 2005), and most snags had fallen in the B/Y stratum (Hagemann et al., 2009); third, the regional default FRI was changed from 125 years (Kull et al., 2006) to 300 years (Foster, 1984; McRae et al., 2001); and four, the parameters used to predict biomass components were modified to better reflect measured biomass components. The rationale and analyses leading to the latter two modifications are provided in Sections 3 and 4.

Three sets of model simulations were executed: one set using the model's default parameters for the Boreal Shield East Ecozone in Labrador, a FRI of 300 years, and a 20-year regeneration delay after fire ('Default'; Table 2); one set using the 'Default' parameters along with the previously described VBC parameter changes, FRI, and regeneration delay modifications ('Modified A' parameter set); and another set to test if modelled estimates could be improved by using an alternative parameter set that included all the changes described for 'Modified A', plus modified fall rates for snag stem and snag branches, and modified base decay rates of WD C pools recommended by previously published C modelling studies, plus modifications to account for the contribution of BW based on results from this study ('Modified B' parameter set; Table 2). Further rationale for the 'Modified B' modifications is developed in the results section, where these changes and their implications are described.

2.3. *Statistical analyses*

2.3.1. *Field data*

No departures from normality were observed for C stock data within data grouped by stratum and C pool (Shapiro–Wilk test). Differences in C stocks among or within site types were determined using one-way nested ANOVA with site type or C pool as a fixed factor, site as a random factor, and plot nested within site. Where differences were significant ($P < 0.05$), pair-wise comparisons were tested for significance using the Games–Howell test. Statistical analysis was carried out using SPSS, release 15.0.1 (SPSS Inc.).

2.3.2. Comparison between field-measured and CBM-CFS3-modelled C pools

Before comparing output from the CBM-CFS3 to measured estimates, the field data reported here and in Hagemann et al. (2009) were combined and used to recalculate pools that could be directly compared to the CBM-CFS3 pools (Table 3). Therefore, comparisons of measured and modelled C pools are based on pools defined in the CBM-CFS3, and should not be confused with field-measured pools (Table 4) that were defined for the purposes of the field study.

Statistical model evaluation was based on four goodness-of-fit (GOF) statistics (Smith and Smith, 2007) and Theil's unequality coefficient (Theil, 1966). These statistics were used to assess model accuracy for nine pools by comparing field estimates with those from the CBM-CFS3 simulations using 'Default', 'Modified A', and 'Modified B' parameter sets. The correlation r was calculated to assess the degree of association between modelled and measured estimates. The correlation was considered significant if the F-value for r was greater than the critical $F_{(p=0.05)}$. The mean difference M and the percent relative error E were calculated to assess model bias. The bias was considered significant if $t_M > t_{(p=0.05)}$ or $E > E_{(95\%)}$, respectively (Smith and Smith, 2007). The *LOFIT* (lack-of-fit) statistic was calculated based on our replicate field data to evaluate differences between model estimates and measurements excluding variability due to field measurements. To determine its significance the *LOFIT F*-value was calculated and compared with the critical $F_{(p=0.05)}$. The lack of fit between modelled and measured values was considered not significant if the *LOFIT F*-value was less than the critical F. The value of Theil's inequality coefficient U can range from 0 (perfect fit) to greater than 1 (lack of model fit; Theil, 1966).

'Modified B' parameters were applied where any of the GOF and inequality statistics indicated a significant error, bias, or inequality, to determine if modelled estimates could be improved with minimal adjustment. Once parameters were altered, GOF and inequality statistics were run again on all pools to determine if model accuracy was improved (Table 2).

3. Results

3.1. Field-measured C stocks

Live-tree C stocks significantly increased with tree age from 0.4 Mg ha^{-1} (H/D) to 46.9 Mg ha^{-1} (U/O; Table 4), reaching 19% of old-growth levels 34–36 years after harvest. In the old-growth stratum (U/O), live trees were the largest non-soil C pool. The burned stratum contained no measurable live-tree C stocks 21 years after disturbance, indicating that a long post-fire regeneration delay is applicable to the study region, whereas stands regenerate faster after harvest (H/Y; H/M). Hardwood C stocks were negligible in all strata.

Woody debris was the largest dead wood (WD, snags, stumps, and BW) C pool in the H/D and B/Y strata, and significantly decreased with time since harvest (H/D > H/Y > H/M; Table 4). Seventeen to 21 years after disturbance, the H/Y stratum contained less WD C than the B/Y stratum. Woody debris C stocks in all strata were dominated by small-diameter (<20 cm) WD (Hagemann et al., 2009).

The U/O stratum contained the highest snag C stocks (Table 4). The H/D, H/Y, H/M strata, regardless of age, contained significantly less snag C than the B/Y stratum. The contribution of snags to total dead wood C stocks significantly increased from 1% in the recently harvested stratum to 46% in the old-growth stratum. Stumps contributed as much as 25% to total dead wood C stocks, but never exceeded 1.4 Mg ha^{-1}. The highest stump C stocks were observed in the H/D and H/Y strata.

Buried dead wood C stocks were highest in the old-growth stratum, and ranked higher than aboveground WD C pools in all but the H/D and B/Y strata (Table 4). Most strata contained more C in the organic layer than in any other pool except mineral soil, with the exceptions of the U/O and H/D strata, where the size of the live-tree and WD C pools was similar to the organic layer C stocks (Table 4). Mineral soil was by far the largest C pool in all strata, exceeding all other C pools by a factor of 3.5–5.1 (Table 4). There were no obvious trends in BW, organic layer, mineral soil, and total ecosystem C with disturbance history or forest age; however, mineral soil, organic layer, and total ecosystem C stocks were lowest in H/D sites (Table 4).

3.2. Comparison of field-measured and CBM-CFS3 estimated ecosystem C pools

3.2.1. 'Default' CBM-CFS3 initialization, fire-return interval, and biomass C calibration

In order to determine the sensitivity of DOM initialization to using a 125- (CBM-CFS3 default), 300-, or 500-year FRI (range of regional FRI), we compared 'Default' estimates of ecosystem C pools resulting from each FRI. Most 'Default' C pools were relatively insensitive to changing the FRI from 125 to 300 years,

Table 3
Mapping of CBM-CFS3 C pools to measured C pools and recommended modifications.

CBM-CFS3 pools[a]	Measured pools
Live biomass pools	
Softwood merch. + bark, other wood + bark, foliage	Softwood aboveground live biomass
Softwood fine + coarse roots	*Not measured*
Hardwood merch. + bark, other wood + bark, foliage	Hardwood aboveground live biomass
Hardwood fine + coarse roots	*Not measured*
Dead organic matter (DOM) pools	
Snag stems	>9 cm DBH snag stems + bark
Snag branches	≤9 cm DBH snags + bark, snag branches, tops + butt ends
Aboveground very fast and slow	Organic L, F, H, and O^2 horizons incl. dead fine roots
Aboveground fast	≤10 cm woody debris and stumps
Medium	>10 cm woody debris and buried DW
Below ground very fast and slow	Mineral soil to 45 cm depth incl. dead fine roots
Below ground fast	Dead coarse roots; *not measured*
Recommended modifications of DOM pools	
Aboveground very fast and slow	Organic L, F, H, + O[b] horizons and buried DW
Medium	>10 cm woody debris

The CBM-CFS3 does not simulate non-woody vegetation or shrubs.

[a] For detailed description of CBM-CFS3 pools refer to Kurz et al. (2009).

[b] Soil Classification Working Group (1998).

Table 4
Carbon content (Mg ha^{-1}) of black spruce study sites.

Measured C pools		Strata				
		H/D	H/Y	H/M	B/Y	U/O
Live biomass						
Live tree dbh	≥9 cm	0.2 (0.2) a	0.2 (0.1) a	6.7 (1.8) b	0.0 (0.0) a	46.4 (8.4) c
	<9 cm	0.2 (0.0) c	0.4 (0.1) c	2.0 (0.3) b	0.0 (0.0) a	0.5 (0.2) c
	Total live tree	**0.4 (0.2) ab A**	**0.5 (0.2) b A**	**8.7 (1.8) c C**	**0.0 (0.0) a A**	**46.9 (8.5) d C**
DOM						
	Snags	**0.2 (0.0) a A**	**0.3 (0.1) a A**	**0.1 (0.0) a A**	**2.2 (0.8) b B**	**5.5 (1.1) c B**
	Woody debris	**25.8 (1.4) d C**	**8.4 (2.0) b C**	**0.8 (0.2) a B**	**14.1 (0.8) c C**	**6.4 (0.8) b B**
	Stumps	**1.4 (0.3) b B**	**1.3 (0.1) b B**	**0.3 (0.2) a AB**	**0.3 (0.1) a A**	**0.1 (0.1) a A**
	Buried dead wood	**5.8 (2.9) a AB**	**9.6 (3.3) a BC**	**5.8 (1.4) a BC**	**4.7 (2.1) a AB**	**18.2 (8.2) a B**
	Organic layer	**30.4 (4.2) a C**	**46.8 (6.0) bc D**	**47.4 (3.4) b D**	**32.8 (3.1) ac D**	**39.8 (1.0) bc C**
	Mineral soil[a]	**121.5 (18.7) a D**	**208.1 (38.4) b E**	**186.4 (20.5) b E**	**168.4 (19.3) ab E**	**162.7 (37.5) ab D**
Total ecosystem	185.6 (20.2)[a]	275.0 (33.9) b	249.7 (20.4) b		222.4 (22.9) ab	279.7 (54.8) b

[a] 0–45 cm depth.

Note: Standard error in parentheses; lower case letters denote significant differences within rows; capital letters denote significant differences between bolded numerals within columns; nested ANOVA; $n = 3$, $k = 5$, $s = 4$, *post-hoc* Games-Howell; $P < 0.05$. Strata—H/D: 1 year after harvest; H/Y: 17 years after harvest; H/M: 36–36 years after harvest; B/Y: 21 years after fire; U/O: old-growth of unknown origin.

but modelled mineral soil (belowground very fast plus slow) and total ecosystem C pool estimates increased 7–12% and 3.8–4.6%, respectively (Table 5). However, changing the FRI from 300 to 500 years resulted in an insignificant increase of the modelled mineral soil and total ecosystem C pools (≤2.0%; Table 5). Therefore, we used a 300-year FRI for all subsequent model runs, because it more accurately reflects the regional FRI (Roberts et al., 2006) and measured mineral soil and total ecosystem C pools.

'Default' estimates of some live-tree components exceeded measured stocks in H/M and U/O strata, where considerable amounts of live-tree C were observed. The overestimated live-tree C was mainly due to the high modelled estimates for the non-merchantable ('other wood and bark'), branch, and foliage C sub-pools of the live-tree C pool (Fig. 2). A significant overestimate of the live biomass C pools could result in errors in the estimation of DOM pools. Therefore, before comparing DOM and soil C pools, we modified five 'Default' stand-level VBC parameters (Boudewyn et al., 2007) affecting mainly non-merchantable stem wood, branch, and foliage biomass, to yield live-tree C pool estimates similar to those we calculated based on individual-tree field measurements and individual-tree biomass component equations (Lambert et al., 2005) summed to give stand-level estimates (Table 6). These modified VBC parameters were used in all subsequent model runs, identified as 'Modified A' and 'Modified B'.

3.2.2. *'Modified A' CBM-CFS3-modelled C stocks*

Measured live-tree C stocks and dynamics were well captured by 'Modified A' estimates, in particular the increase in live-tree C after harvest, as well as the absence of live-tree C 21 years after fire due to the regeneration delay of 20 years observed for burned sites in Labrador (Tables 6 and 8). Modifications of the VBC parameters decreased live-tree C stocks (Fig. 2), thus reflecting observed black spruce allometry in Labrador, and error (*LOFIT*), bias (*M*, *E*), and inequality (*U*) statistics were improved compared with 'Default' (Table 8). Modifications to the VBC parameters particularly decreased estimates of non-merchantable C and subsequently branch C, resulting in a reduced C transfer to the snag branch, ≤10 cm WD (aboveground fast), organic layer (aboveground very fast and slow), and mineral soil (belowground very fast and slow) C pools (Table 7), as expected. Although 'Modified A' belowground C stocks were significantly underestimating measured mineral soil C stocks, 'Modified A' estimated snag branch, ≤10 cm WD, and organic layer C stocks captured the measured data better than the 'Default' estimates, as reflected by a reduction of error (*LOFIT*), bias (*E*), and inequality (*U*; Table 8).

Measured and 'Modified A' snag stem C stocks were well correlated in all strata except the B/Y stratum, indicating that CBM-CFS3 generally captured the collapse of snags as indicated by high B/Y >10 cm WD C stocks (Table 7). However, modelled B/Y snag stem C stocks considerably exceeded measured snag stem C stocks (Tables 7 and 8), indicating that the CBM-CFS3 default snag fall

Table 5
'Default' CBM-CFS3 modelled estimates of the belowground very fast + slow C pool (Mg ha^{-1}) for 125-year (default), 300-year and 500-year fire return intervals (FRI).

	Strata				
Modelled C pool [Mg ha^{-1}]	H/D	H/Y	H/M	B/Y	U/O
Belowground very fast and slow DOM					
FRI 125	122.2 (2.1)	122.2 (0.5)	117.9 (0.6)	116.2 (0.3)	103.6 (2.9)
FRI 300	132.4 (2.7)	132.4 (0.6)	126.5 (0.8)	124.9 (0.4)	116.3 (2.7)
FRI 500	134.4 (3.0)	134.4 (0.6)	128.1 (0.9)	126.3 (0.4)	118.6 (2.7)
Difference[a]	*+1.5%*	*+1.6%*	*+1.2%*	*+1.1%*	*+2.0%*
Total ecosystem					
FRI 125	271.8 (7.4)	220.7 (0.9)	201.6 (2.4)	199.0 (0.7)	278.7 (4.4)
FRI 300	282.1 (8.0)	230.9 (1.0)	210.2 (2.5)	207.7 (0.7)	291.6 (4.2)
FRI 500	284.0 (8.3)	233.0 (1.1)	211.8 (2.6)	209.1 (0.8)	293.9 (4.1)
Difference[a]	*+0.7%*	*+0.9%*	*+0.7%*	*+0.7%*	*+0.8%*

[a] Difference between FRI 300 and FRI 500.

Note—H/D: 1 year after harvest; H/Y: 17 years after harvest; H/M: 36–36 years after harvest; B/Y: 21 years after fire; U/O: old-growth of unknown origin.

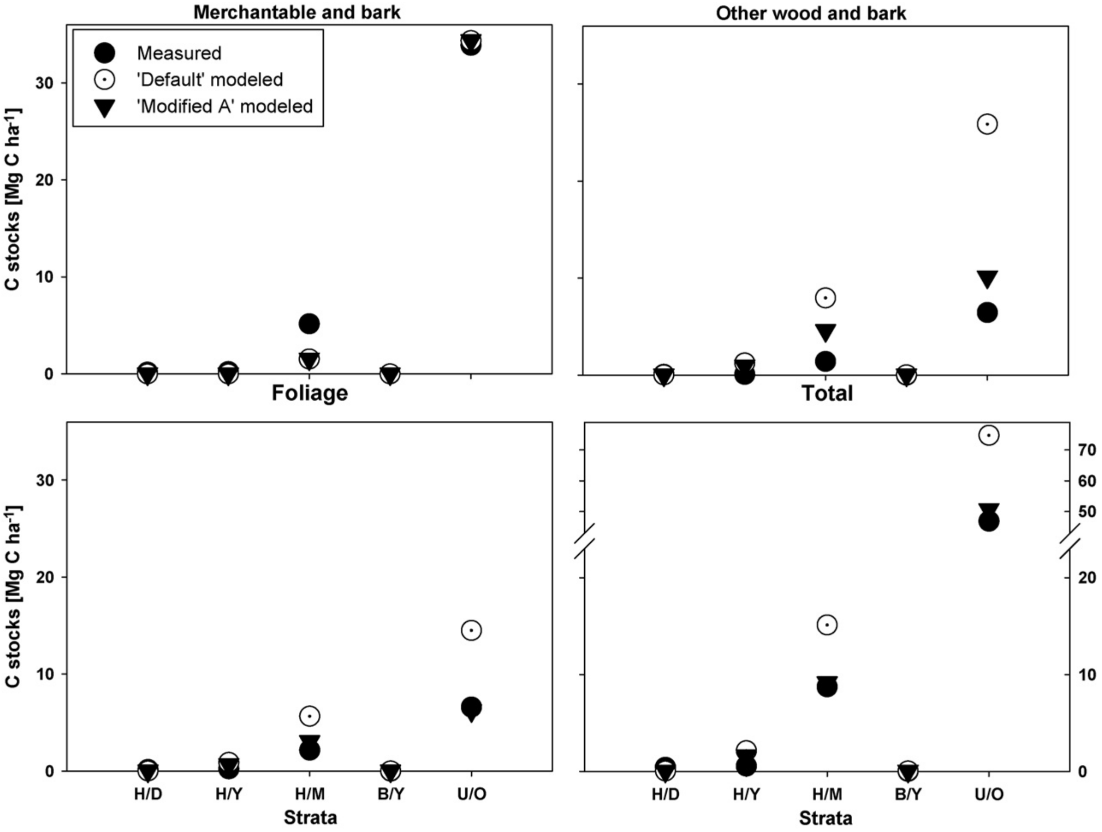

Fig. 2. Total live softwood and CBM-CFS3 live softwood sub-pool C stocks estimated from field measurements and from CBM-CFS3 using 'Default' and 'Modified A' parameters. Please note axis break for total live softwood C stocks. Strata: H/D: 1 year after harvest; H/Y: 17 years after harvest; H/M: 36–36 years after harvest; B/Y: 21 years after fire; U/O: old-growth of unknown origin.

rate of 0.032 yr^{-1} underestimates the measured snag fall rate. We therefore increased the CBM-CFS3 snag and snag branch fall rates to 0.1 yr^{-1} and 0.2 yr^{-1}, respectively ('Modified B'; Moroni et al., submitted for publication). Snag fall rates of 0.111 yr^{-1} (Manies et al., 2005) and 0.094 yr^{-1} (Carrasco et al., 2006) have previously been used in boreal forest C modelling.

'Modified A' and measured ≤10 cm WD (aboveground fast) C stocks decreased with time since harvest (H/D > H/Y > H/M;

Table 6
Original 'Default' (Boudewyn et al., 2007) and 'Modified A' (in bold) volume-to-biomass conversion and extension parameters for black spruce in Ecozone 6, Newfoundland and Labrador.

	Parameter	'Default' Original value	'Modified A' Modified value
Merchantable stem wood biomass model	a	0.82921	n/c[a]
	b	0.88429	n/c[a]
Non-merchantable stem wood biomass model	a	8.53874	**38.53874**
	b	−0.82173	**−1.68217**
	k	1.01392	n/c[a]
	cap	5.12500	n/c[a]
Sapling biomass model	a	0.29205	n/c[a]
	b	−1.19977	n/c[a]
	k	1.00083	n/c[a]
	cap	1.01500	n/c[a]
Proportion model	a1	−1.50326	n/c[a]
	a2	−0.00014	n/c[a]
	a3	−0.06497	n/c[a]
	b1	−0.36910	n/c[a]
	b2	0.00102	n/c[a]
	b3	−0.18018	**−0.28018**
	c1	0.86531	**0.79531**
	c2	0.00052	n/c[a]
	c3	−0.39713	**−0.49713**

[a] No change.

Table 7
Mean C pool stocks (Mg C ha^{-1}) estimated by field-measurements and by CBM-CFS3 using ‘Default’, ‘Modified A’[a], and ‘Modified B’[b] parameter sets (stratum abbreviation in parentheses).

		Originating disturbance									
		Harvest (H)						Burned (B)		Unknown (U)	
		Years since last disturbance						Years since last disturbance		Stand age	
		1 (H/D)		17 (H/Y)		34–36 (H/M)		21 (B/Y)		146–204 (U/O)	
C Pools	Estimate	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Live tree biomass	Measured	0.4	(0.2)	0.5	(0.2)	8.7	(1.8)	0.0	(0.0)	46.9	(8.5)
	Modelled (‘Default’)	0.0	(0.0)	2.1	(0.1)	15.1	(1.4)	0.0	(0.0)	74.7	(2.2)
	Modelled (‘Modified A’)[c]	0.0	(0.0)	1.6	(0.1)	9.2	(0.7)	0.0	(0.0)	50.7	(2.0)
Snag stems	Measured	0.1	(0.1)	0.3	(0.1)	0.1	(0.0)	2.0	(0.8)	5.1	(1.1)
	Modelled (‘Default’)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	12.1	(0.0)	5.3	(0.5)
	Modelled (‘Modified A’)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	12.1	(0.0)	5.4	(0.6)
	Modelled (‘Modified B’)[c]	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	2.6	(0.0)	2.0	(0.0)
Snag branches	Measured	0.1	(0.0)	0.0	(0.0)	0.0	(0.0)	0.2	(0.1)	0.4	(0.1)
	Modelled (‘Default’)	0.0	(0.0)	0.0	(0.0)	0.4	(0.0)	1.0	(0.0)	2.0	(0.1)
	Modelled (‘Modified A’)	0.0	(0.0)	0.0	(0.0)	0.2	(0.0)	0.4	(0.0)	0.8	(0.0)
	Modelled (‘Modified B’)[d]	0.0	(0.0)	0.0	(0.0)	0.2	(0.0)	0.0	(0.0)	0.4	(0.0)
Medium DOM (>10 cm WD)	Measured	10.5	(2.7)	12.9	(3.3)	6.0	(1.4)	12.4	(1.5)	22.4	(8.1)
	Modelled (‘Default’)	12.9	(0.7)	10.6	(0.1)	7.1	(0.1)	16.5	(0.1)	9.0	(1.0)
	Modelled (‘Modified A’)	13.0	(0.6)	10.7	(0.1)	7.2	(0.1)	16.6	(0.1)	9.2	(1.1)
	Measured (‘Remapped’)[c]	4.7	(1.2)	3.3	(0.4)	0.2	(0.0)	7.7	(0.6)	4.2	(0.7)
	Modelled (‘Modified B’)[c]	7.7	(0.4)	5.5	(0.0)	3.1	(0.1)	18.8	(0.1)	7.2	(1.2)
AG fast DOM (≤10 cm WD)	Measured	22.5	(1.9)	6.5	(2.2)	1.0	(0.4)	6.7	(0.6)	2.3	(0.3)
	Modelled (‘Default’)	37.8	(1.3)	15.7	(0.2)	6.1	(0.1)	6.2	(0.1)	15.1	(0.2)
	Modelled (‘Modified A’)	14.8	(0.6)	6.2	(0.1)	2.8	(0.0)	2.3	(0.0)	6.0	(0.1)
AG very fast + slow DOM (organic layer)	Measured	30.4	(4.2)	46.7	(6.0)	47.4	(3.4)	32.8	(3.1)	39.8	(1.0)
	Modelled (‘Default’)	82.6	(2.6)	63.3	(0.3)	52.9	(0.5)	42.9	(0.2)	64.5	(2.5)
	Modelled (‘Modified A’)	46.0	(1.5)	35.3	(0.2)	29.8	(0.2)	24.5	(0.1)	36.4	(0.5)
	Measured (‘Remapped’)[c]	36.3	(4.1)	56.3	(5.1)	53.3	(2.0)	37.5	(3.6)	58.0	(8.8)
	Modelled (‘Modified B’)[c]	57.4	(1.6)	46.8	(0.2)	40.5	(0.3)	36.0	(0.1)	46.0	(0.9)
BG very fast + slow DOM (mineral soil)	Measured	121.5	(18.7)	208.1	(38.4)	186.4	(20.5)	168.4	(19.3)	162.7	(37.5)
	Modelled (‘Default’)	132.4	(2.7)	132.4	(0.6)	126.5	(0.8)	124.9	(0.4)	116.3	(2.7)
	Modelled (‘Modified A’)	87.5	(1.8)	86.3	(0.4)	82.3	(0.5)	81.5	(0.2)	76.8	(1.5)
	Modelled (‘Modified B’)[c]	169.9	(3.3)	169.5	(0.7)	163.4	(1.0)	161.7	(0.3)	156.0	(1.5)
Total ecosystem	Measured	185.6	(20.2)	275.0	(33.9)	249.7	(20. 6)	222.4	(22.9)	279.7	(53.5)
	Modelled (‘Default’)	282.1	(8.0)	230.9	(1.0)	210.2	(2.5)	207.7	(0.7)	291.6	(4.2)
	Modelled (‘Modified A’)	171.9	(5.1)	144.6	(0.7)	132.8	(1.3)	140.0	(0.5)	188.4	(1.5)
	Modelled (‘Modified B’)	255.7	(6.3)	228.2	(1.0)	218.1	(1.9)	221.4	(0.5)	267.4	(1.6)

In all cases except Medium and AG very fast + slow DOM measured values are compared with modelled ‘Default’, ‘Modified A’ and ‘Modified B’ values. For the Medium and AG very fast + slow DOM measured values are compared with modelled ‘Default’ and ‘Modified A’ values, and then measured ‘Remapped’ values are compared with ‘Modified B’ values.

[a] Changed volume-to-biomass conversion and expansion parameters as indicated in Table 6.

[b] Changed volume-to-biomass conversion and expansion parameters as indicated in Table 6; changed transfer rates: snag stem fall 0.1 yr^{-1}, snag branch fall 0.2 yr^{-1}, medium to AG slow 0.30 yr^{-1} (Table 2); changed base decay rates: medium 0.06 yr^{-1}, AG slow 0.0075 yr^{-1}, BG slow 0.00207 yr^{-1} (Table 2).

[c] Change recommended.

[d] Change not recommended.

Note—H/D: 1 year after harvest; H/Y: 17 years after harvest; H/M: 36–36 years after harvest; B/Y: 21 years after fire; U/O: old-growth of unknown origin.

Table 7), but measured amounts of ≤10 cm WD C were considerably underestimated in the H/D stratum. ‘Modified A’ >10 cm WD (medium) C stocks also decreased after harvest, but measured >10 cm WD C stocks showed no consistent trend with time since disturbance (Table 7). Goodness-of-fit statistics indicated no correlation between measured and ‘Modified A’ values for the medium C pool (Table 8), largely because measured old-growth (U/O) medium C stocks were considerably underestimated by the ‘Modified A’ CBM-CFS3 (Table 7), where burial of WD is particularly prevalent due to a continuous ground cover of vital bryophytes (Hagemann et al., 2009). Buried dead wood is embedded in the organic layer, but, by default, the CBM-CFS3 includes any >10 cm BW in the medium C pool, assuming it belongs to the coarse WD pool (Table 3; Kurz et al., 2009). To test the potential impact of the WD burial process in the current model structure, we remapped measured BW C stocks (‘Remapped’; Table 7), i.e. we deducted the measured BW C stocks from the >10 cm WD (medium) C pool and added it to the organic layer (aboveground slow) C pool.

Measured ‘Remapped’ and ‘Modified A’ medium C stocks were highly correlated (Tables 7 and 8), and showed a decrease with time since harvest as well as large amounts of >10 cm WD 21 years after fire. However, ‘Modified A’ CBM-CFS3 considerably overestimated measured ‘Remapped’ medium C stocks in all strata (Table 7), indicating that the CBM-CFS3 default medium C pool base decay rate of 0.0374 yr^{-1} (at 10 °C) possibly underestimates the >10 cm WD decay rate. We therefore increased the medium C pool base decay rate to 0.06 yr^{-1} (‘Modified B’) recommended by Moroni et al. (submitted for publication) for Newfoundland black spruce. This rate is at the upper range of the rates observed by Bond-Lamberty et al. (2003) and corresponds to a 6% reduction of >10 cm WD C per year. The current model structure does not have a bryophyte C pool (and associated inputs/outputs/production/decay) making it

Table 8
Goodness-of-fit and inequality statistics for live tree, DOM, soil, and total ecosystem C pools ($n = 3$).

		Error (*LOFIT*)		Bias						
Parameter set	CBM-CFS3 C pool			Mean difference (M)		Relative error (E)		Correlation (r)		Theil's inequality coefficient
		LOFIT	F^a	M	T^b	E	95% CI	r	F^c	U^d
Default'	Live tree biomass	2451	0.13	−7.1	1.33	−62	241.94	*1.00	4671.87	0.12
	Snag stems	311	1.23	−2.0	0.95	−129	330.07	0.52	1.14	0.57
	Snag branches	*10	5.52	−0.5	1.77	−396	400.48	*0.97	55.17	3.65
	>10 cm WD	1058	0.08	5.0	1.52	31	316.78	0.26	0.21	0.13
	≤10 cm WD	1523	0.33	−8.4	2.99	−107	174.63	*0.91	14.09	0.26
	Organic layer	11,197	0.18	−21.8	2.64	−55	114.10	−0.26	0.22	0.12
	Mineral soil	40,474	0.03	*42.9	4280.82	25	201.65	0.02	0.00	0.04
	Total ecosystem	39,515	0.02	−2.0	0.08	−1	158.36	−0.05	0.01	0.01
'Modified A'	Live tree biomass	47	0.00	−1.0	1.35	−9	241.94	*1.00	4579.04	0.05
	Snag stems	311	1.23	−2.0	0.97	−131	330.08	0.54	1.21	0.57
	Snag branches	1	0.39	−0.2	1.93	−110	400.48	*0.94	24.78	1.92
	>10 cm WD	616	0.07	1.5	0.49	12	316.78	0.02	0.00	0.09
	≤10 cm WD	285	0.06	1.4	0.66	18	174.63	*0.90	13.13	0.11
	Organic layer	2298	0.04	5.0	0.89	13	114.10	−0.27	0.24	0.06
	Mineral soil	12,5227	0.11	*86.5	5.89	51	201.65	−0.10	0.03	0.05
	Total ecosystem	13,7981	0.06	*87.0	4.30	36	158.37	0.02	0.00	0.04
'Modified B'	Live tree biomass	47	0.00	−1.0	1.35	−9	241.94	*1.00	4579.04	0.05
	Snag stems	31	0.12	0.6	0.91	39	330.08	0.75	3.84	0.31
	Snag branches	0	0.10	0.0	0.06	2	400.48	0.76	4.16	0.29
	>10 cm WD	462	0.54	−4.4	2.64	−110	184.52	*0.91	15.29	0.45
	≤10 cm WD	285	0.06	1.4	0.66	18	174.63	*0.90	13.13	0.11
	Organic layer	2536	0.03	3.0	0.47	6	124.18	−0.15	0.07	0.03
	Mineral soil	13,367	0.01	5.3	0.36	3	201.65	−0.03	0.00	0.01
	Total ecosystem	24,792	0.01	4.3	0.21	2	158.37	−0.01	0.00	0.01

[*] Statistical significance at $P \leq 0.05$ for *LOFIT*, *M*, and *r*.
[a] Critical *F*-value = 2.95.
[b] Critical *t*-value = 3.18.
[c] Critical *F*-value = 10.13.
[d] $U = 0$ indicates a perfect model; $U > 1$ indicates lack of model fit.

impossible to accurately test burial of WD by bryophytes. Currently, an amount of C determined by the pool's decay rate is removed from the medium (>10 cm WD) C pool. By default, 83% of that amount is released to the atmosphere (i.e., decayed) and 17% is transferred to the aboveground slow C pool (Table 2). As a surrogate for the process of WD burial we increased the transfer of C from the medium C pool to the organic later from 17% to 30% ('Modified B').

'Modified A' organic layer C stocks slowly decreased after harvest, although there was no trend in the measured data with time since harvest (Table 7). Measured organic layer C stocks of the H/D stratum were lower than those observed in all other strata, whereas the CBM-CFS3 predicted H/D to have the highest organic layer C stocks. 'Modified A' and measured organic layer C stocks were uncorrelated (Table 8), and 'Modified A' organic layer C stocks were up to 37% lower than measured values in most strata (Table 7), indicating that the decomposition of mainly wood- and bryophyte-derived organic layer material is overestimated by the CBM-CFS3 default aboveground slow C base decay rate. Therefore, we reduced the aboveground slow base decay rate to 50% of default ($0.0075\,\mathrm{yr}^{-1}$; Table 2), which falls in the lower range of the shallow C pool decay rate ($0.004–0.0182\,\mathrm{yr}^{-1}$) reported by Harden et al. (2000) and Manies et al. (2005).

'Modified A' mineral soil C stocks were predicted to slowly decrease with time since harvest, with no trend observable for the measured data (Table 7). 'Modified A' and measured mineral soil C stocks were uncorrelated, and GOF statistics showed a significant bias (*M*) (Table 8). 'Modified A' mineral soil C stocks in all strata were 27–58% lower than measured values, suggesting either an underestimate of the aboveground slow to belowground slow transfer rate, a leaching process (out of the system) not accounted for by the CBM-CFS3, or an overestimate of the belowground slow base decay rate (default $0.0033\,\mathrm{yr}^{-1}$; Table 2). To reflect the pedogenesis of Humo-Ferric Podzols, the soil type of the study sites, we applied a belowground slow base decay rate of $0.00207\,\mathrm{yr}^{-1}$ optimized for this soil type ('Modified B'; Cindy Shaw, Canadian Forest Service, *personal communication*). As mineral soil C stocks dominated total ecosystem C stocks, 'Modified A' total ecosystem C stocks were also predicted to slowly decrease with time since harvest (Table 7). Statistics showed a lack of correlation between 'Modified A' and measured values as well as a significant bias (*M*) (Table 8).

3.3. *'Modified B' CBM-CFS3-modelled C stocks*

Following the increase of the snag stem and branch fall rates, 'Modified B' snag stem C stocks were reduced compared with previous parameter sets, and >10 cm WD (medium) C stocks of the B/Y stratum were increased due to higher snag fall rates (Table 7). Agreement between measured and 'Modified B' snag stem C estimates was improved, as indicated by lower *LOFIT*, *E*, and *U* values (Table 8). However, 'Modified B' old-growth snag stem C stocks underestimated measured U/O snag stem C stocks by $3.1\,\mathrm{Mg\,C\,ha}^{-1}$, and modelled snag branch C estimates and their respective statistics were not generally improved by the higher snag branch fall rate (Tables 7 and 8).

The increased medium C base decay and surrogate for medium to aboveground slow transfer rates improved the correlation between measured 'Remapped' and 'Modified B' >10 cm WD (medium) C stocks (Tables 7 and 8). 'Modified B' >10 cm WD C stocks in all strata were lower than estimated by 'Modified A', except for the B/Y stratum, where the expected decrease was masked by an increased transfer from the snag stem C pool due to the proposed higher snag fall rate.

The surrogate increased C transfer rate from the medium to the aboveground slow C pool also resulted in higher 'Modified A' aboveground very fast plus slow C stocks, but measured 'Remapped' organic layer C stocks were still underestimated by 34–44% for all strata (interim results; not shown in Table 8). Reducing the aboveground slow (organic layer) base decay rate increased 'Modified B' aboveground very fast plus slow C stocks to the magnitude of measured values (Table 7), but GOF and inequality statistics showed little improvement (*M*, *E*, *U*) and correlations remained poor (Table 8). Although measured organic layer C stocks showed no observable trend that the CBM-CFS3 could be expected to reflect, differences between measured and 'Modified B' values were particularly pronounced for the H/D and U/O strata. For H/D, this may result from the mix of site productivity classes at the Churchill River site, whereas for the old-growth stratum this may result from the high variability of measured BW C stocks (Table 4).

Modelled mineral soil C stocks increased following the reduction of the belowground slow base decay rate. Goodness-of-fit *LOFIT* and *M* statistics clearly improved for 'Modified B' mineral soil C stocks (Tables 7 and 8) when compared with 'Modified A' and 'Default' estimates, but the correlation between measured and 'Modified B' soil C values remained poor. Unlike measured values, 'Modified B' belowground slow C stocks decreased with time since disturbance. Estimates of total ecosystem C stocks improved in correspondence with 'Modified B' belowground slow C stocks, because total ecosystem C stocks are dominated by mineral soil C stocks.

4. Discussion

4.1. Field-measured C stocks

Measured live-tree C stocks of the old-growth stratum fall within the lower range of values reported for the closed-canopy boreal forest (Bhatti et al., 2003; Wang et al., 2003; McCarthy and Weetman, 2006). Measured U/O live-tree C stocks reflect maximum to equilibrium live-tree biomass, as live black spruce stand biomass peaks at ~125 years (Government of Newfoundland and Labrador, 2006b), then stabilizes at ~185 years when stands enter the gap dynamics phase (Harper et al., 2005).

Measured dead wood abundance in the humid high-boreal forests of Labrador was also in the lower range of values reported for old-growth and disturbed boreal forests composed of similar-sized trees (cf. Hagemann et al., 2009), e.g., in Manitoba (Bond-Lamberty et al., 2003; Manies et al., 2005), Quebec (Brais et al., 2005), and Newfoundland (Moroni, 2006). Snags constituted a minor C pool in gap-driven old-growth Labrador black spruce, similar to pre-senescent and senescent black spruce in Newfoundland (Moroni, 2006) and Quebec (Drapeau et al., 2002), but far less than reported for senescent balsam fir forests in Newfoundland (Moroni, 2006). Harvested strata contained little snag C retained from pre-disturbance stands or created as a result of the post-disturbance death of uncut trees, as previously observed (McRae et al., 2001; Pedlar et al., 2002). Unlike harvesting, wildfire generates large amounts of snags (McRae et al., 2001), but almost all snags had fallen 21 years after fire (B/Y). Previous studies indicate that snag longevity depends on tree size rather than climatic factors such as temperature and moisture (Moroni, 2006; Hagemann et al., 2009), and is thus similar in boreal and high-boreal forests, with most snags falling within 25–33 years after disturbance (Manies et al., 2005; Boulanger and Sirois, 2006; Moroni, 2006). Measured WD stocks 21 years after fire (B/Y) were dominated by large amounts of little decayed, medium-sized (>10 cm) logs (*data not shown*; Hagemann et al., 2009), and thus likely reflected maximum amounts of post-disturbance WD C resulting from the collapse of snags (Bond-Lamberty et al., 2003; Boulanger and Sirois, 2006; Hagemann et al., 2009).

Woody debris C stocks generated by clearcut harvesting (H/D) exceeded WD C stocks 21 years after fire, and were dominated by small-diameter WD remaining after harvest (Hagemann et al., 2009). Harvest-generated WD had almost completely decomposed or fragmented 34–36 years after harvest (H/M; Table 4), and is expected to completely disappear ~40–50 years after harvesting (Hagemann et al., 2009). Woody debris C stocks created by harvesting and natural disturbances are thus expected to converge at low levels after the disappearance of fire-generated WD ~70 years after disturbance (Moroni, 2006; Hagemann et al., 2009), because little dead wood—both WD and snags—is created in the course of self-thinning in the slow-growing, low-density young to mature black spruce forests of Labrador (Government of Newfoundland and Labrador, 2006b; Roberts et al., 2006). Newly created WD in the humid high-boreal forest is not only decreasing by decomposition and fragmentation but also by burial, thus further reducing aboveground WD C stocks compared to drier or warmer boreal forests.

The burial of WD by bryophytes is a process that has been observed by some studies in boreal and oroboreal coniferous forests (Harvey et al., 1981; Brais et al., 2005; Manies et al., 2005; Moroni, 2006), but it is neither well documented nor currently captured in forest C models (e.g., the CBM-CFS3; Kurz et al., 2009). In high-boreal Labrador black spruce, measured BW C stocks were equal to or higher than unburied WD C stocks in all but the H/D and B/Y strata (Table 4), and largely exceeded most values reported in the literature for boreal coniferous forests (0.1–7.5 Mg C ha^{-1}; Brais et al., 2005; Manies et al., 2005; Moroni, 2006). Larger amounts have only been observed in mountain Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands containing trees considerably larger than Labrador black spruce (volume of 370–430 m^3 ha^{-1}; Harvey et al., 1981). As production of new WD in Labrador black spruce is low, the large amounts of dead wood C buried within the organic layer of these forests are indicative of long-term accumulation of BW and of BW decay rates that are dramatically lower than decay rates of unburied WD, and possibly of the same magnitude as organic layer decay rates (Manies et al., 2005; Hagemann et al., 2009).

With the exception of WD burial, which seems to be more pronounced in high-boreal Labrador, post-disturbance dead wood dynamics were thus similar to those reported by other studies for sub-boreal and boreal forests (Bond-Lamberty et al., 2003; Brais et al., 2005; Manies et al., 2005; Moroni, 2006). Measured organic layer, mineral soil, and total ecosystem C pools did not show a clear influence of disturbance history (Table 4), but organic layer C stocks of the burned stratum tended to be lower than those of middle-aged and older harvested and old-growth sites. A reduction in organic layer C stocks after wildfire has been reported by several studies reviewed in McRae et al. (2001).

Measured organic layer, mineral soil, and total ecosystem C pools also showed no consistent trend with forest age. Possible trends in these C pools, e.g., as reported by Mattson and Swank (1989) or Diochon et al. (2009), may have been masked by site effects and the high spatial variability of organic layer and mineral soil C stocks (Conen et al., 2004; Diochon et al., 2009). For example, the significantly lower values observed in the recently harvested stratum for these pools are likely attributable to the spatial mix of medium and poor site productivity of the H/D Churchill River site, thus illustrating the influence of site productivity on net primary productivity, and subsequently biomass input into the DOM C pools (Kane et al., 2005). The influence of site productivity on organic layer and mineral soil C stocks thus likely masked any impact of disturbance history.

Organic layer C stocks were within the range reported for other boreal forests (Smith and Heath, 2002; Howard et al., 2004; Martin et al., 2005). Conversely, mineral soil C stocks in cool humid

Labrador contributed 58–76% to total ecosystem C stocks and were considerably higher than observed in other upland boreal forests in drier (mean annual precipitation 400–500 mm; Howard et al., 2004; Martin et al., 2005), or warmer (MAT 3.3–5.8 °C; Diochon et al., 2009; Moroni et al., submitted for publication) regions, but similar to values reported for black spruce on poorly drained sites throughout North America (Bhatti et al., 2002; Kane et al., 2005). Although soils at the study sites were classified as Humo-Ferric and juvenile Ferro-Humic Podzols (Soil Classification Working Group, 1998), their mineral soil C stocks (Table 4) are closer to estimates for Canadian Ferro-Humic ($182 \pm 17.4\,\mathrm{Mg\,C\,ha^{-1}}$) than Canadian Humo-Ferric ($97 \pm 5.0\,\mathrm{Mg\,C\,ha^{-1}}$) Podzols (Shaw et al., 2008). Low soil temperatures, high soil moisture levels, and pedogenic processes associated with Podzolic B horizon formation are known to favour accumulation of soil organic C (Kane et al., 2005; Simard et al., 2007; Shaw et al., 2008); hence higher than average mineral soil C stocks can be expected in forests with cool wet climates and Podzolic soils such as Labrador high-boreal black spruce, oceanic boreal forests (e.g., in Norway; Kjønass et al., 2000), or coniferous mountain forests (e.g., Tatra Mountains, Poland; Zielonka and Niklasson, 2001).

4.2. *'Default' CBM-CFS3 modelled C stocks*

Modelling C dynamics of Labrador black spruce with 'Default' parameters resulted in overestimates of some live-tree and WD C pools (Tables 3 and 6), possibly because the CBM-CFS3 currently does not account for the impact of successional paludification (Simard et al., 2007, 2009) and the VBC conversion parameters for Labrador (Boudewyn et al., 2007) overestimate non-merchantable and branch biomass. Paludification is a process that encompasses the gradual colonization of forests by peatmosses (*Sphagnum* spec.) followed by organic matter accumulation, a decrease in soil temperature, a rise in water table, and a subsequent decline in tree productivity and regeneration (Simard et al., 2009), which could account for the low amount of measured non-merchantable biomass in the old-growth stratum. Estimation of non-merchantable C pools based on the merchantable C pool should account for tree productivity, particularly in systems featuring a gradual productivity decline with stand age, such as small-diameter black spruce forests (Simard et al., 2007, 2009).

4.2.1. *Volume-to-biomass conversion parameters*

Overestimates of the "other wood and bark" C pool may be due to the overestimated non-merchantable C stocks or due to the allometric crown plasticity of black spruce (Raulier et al., 1996; Pereg and Payette, 1998; Bégin and Filion, 1999). In particular, biomass equations and VBC parameters applicable to medium-size merchantable trees in one region may not be appropriate (i) for trees in other regions as within-species variability may exceed between-species variability (Jenkins et al., 2003; Miao and Li, 2007), and (ii) for small (DBH <5 cm) and very large trees (Penner et al., 1997; Jenkins et al., 2003; Miao and Li, 2007). Overestimates of the "other wood and bark" C pool may be expected for other species exhibiting large variability in small-tree biomass estimates, such as trembling aspen (Miao and Li, 2007). During modelling, biomass production and allocation in selected sites must, therefore, be represented as accurately as possible; not only through appropriate choice of yield curves with respect to species and merchantable volume as suggested by Moroni et al. (submitted for publication), but also in terms of allometric equation applied to estimate stand-level biomass components such as non-merchantable and branch volume. Where detailed data are available, 'Default' biomass estimates of live-tree components could be checked against observed biomass components.

4.3. *'Modified A' and 'Modified B' CBM-CFS3 modelled C stocks*

4.3.1. *Snag stem and snag branch fall rate*

Large amounts of snags are generated after wildfire (McRae et al., 2001) and are expected to fall within 25–33 years in boreal forests (Boulanger and Sirois, 2006; Moroni, 2006). 'Modified A' and 'Default' parameters captured the creation and collapse of snags following wildfire, but underestimated the observed snag stem fall rate. Our field data thus support findings of Manies et al. (2005), Carrasco et al. (2006), and Moroni et al. (submitted for publication), that the default CBM-CFS3 snag stem fall rate of $0.032\,\mathrm{yr^{-1}}$ is too low for small-diameter boreal forests, at least after wildfire. Although snag stem dynamics were well captured by 'Modified B' parameters, measured U/O snag stem C stocks were underestimated by $3.1\,\mathrm{Mg\,C\,ha^{-1}}$; possibly because the higher post-fire snag stem fall rate is not applicable for snags originating from senescence during stand transition to the gap-dynamics phase (Lieffers et al., 2003; Harper et al., 2005), or because CBM-CFS3 parameters underestimate mortality in the gap-dynamics phase. Increasing the snag branch fall rate along with the snag stem fall rate did not improve modelled snag branch C estimates (Tables 7 and 8), because 'Default' snag branch C stocks were already reduced by 'Modified A' VBC parameters as a result of modified live-tree biomass distribution. An increased snag branch fall rate is thus not recommended for Labrador high-boreal black spruce.

4.3.2. *WD decay rates*

As snag stems and snag branches fall, C from the snag stem and branch pools is transferred to the aboveground DOM C pools (Kurz et al., 2009). Post-harvest dynamics of the aboveground fast C pool containing ≤10 cm WD and harvest-created stump C were fairly well captured by the default aboveground fast base decay rate of $0.1435\,\mathrm{yr^{-1}}$ (Table 2), which is similar to the decay rates observed for fine woody debris of pine and spruce in northern Finland ($0.066–0.128\,\mathrm{yr^{-1}}$; Vávřová et al., 2009). Increasing the aboveground fast base decay rate as recommended by Moroni et al. (submitted for publication) for Newfoundland is thus not considered appropriate for modelling the studied forests.

Unlike for ≤10 cm WD, 'Modified A' CBM-CFS3 did not accurately reflect >10 cm WD dynamics of the studied forests. After reducing >10 cm WD C stocks by measured BW C stocks, 'Remapped' and 'Modified A' medium C stocks generally reflected the decomposition, fragmentation, and burial of harvest residues as well as the post-fire collapse of snags (Bond-Lamberty et al., 2003; Boulanger and Sirois, 2006; Hagemann et al., 2009). However, the 'Modified A' CBM-CFS3 consistently overestimated measured >10 cm WD C stocks, which were better captured by an increased medium C pool base decay rate of $0.06\,\mathrm{yr^{-1}}$ (Moroni et al., submitted for publication). Decay rates of >10 cm WD in cool and humid high-boreal Labrador black spruce are thus at the upper range of rates observed in drier boreal regions, i.e. Manitoba (Bond-Lamberty et al., 2003). A change in the terminology of WD dynamics may be required for northern forests differentiating between 'decay rates' which describe mass or C loss by decay, fragmentation, and leaching, and 'reduction rates' which additionally include mass or C loss by WD burial.

4.3.3. *Buried dead wood*

The burial of WD results in an increased transfer of C from the medium (>10 cm WD) to the aboveground slow (organic layer) C pool relative to the decomposition process (Kurz et al., 2009). The increased annual transfer rate from the 'decayed' medium to the aboveground slow C pool applied in this study (30%) was merely used as a surrogate to test the concept of WD burial and is a rather conservative estimate given the enormous amounts of BW C (Hagemann et al., 2009). We are not recommending that this approach be used to represent WD burial by bryophytes in future modelling applications, because it would lead to potentially inaccurate and untested reductions in CO_2 emission estimates, particularly if applied to larger scales.

The burial of large amounts of WD observed in high-boreal Labrador may also occur in other cool and humid forests and may require special attention in forest C models. When incorporated into the organic layer by bryophytes, BW experiences a microclimate different from that of unburied WD. Decay rates of BW are thus expected to be significantly lower than decay rates of unburied WD (Manies et al., 2005; Hagemann et al., 2009). However, unlike the recommended parameter changes with respect to live-tree C estimates or snag fall rates, the incorporation of BW and bryophyte dynamics into the CBM-CFS3 requires structural changes to the model. We propose to (a) develop a module to account for the C dynamics of a bryophyte pool that provides parameters to express the physical burial of WD and impacts on its decay, or—in the absence of a bryophyte module—either (b) calibrate a medium to aboveground slow C pool transfer rate based on field-measured rates of moss growth and WD burial and modify aboveground slow base decay rates in cool humid ecosystems based on further knowledge about the decay dynamics of BW, or (c) introduce a belowground medium (i.e., BW) C pool into the CBM-CFS3 to represent the lower decay rates of buried wood.

Representation of BW in the CBM-CFS3 could be further improved by differentiating medium (>10 cm WD) to aboveground slow (organic layer) C pool transfer rates by disturbance type and time since disturbance. For example, fire can interrupt the burial of WD and the subsequent accumulation of BW for 30–70 years due to the consumption and slow recovery of the live moss layer, parts of the organic layer and the wood buried within it (Nguyen-Xuan et al., 2000; O'Neill et al., 2006). In contrast, clearcut harvesting has a lesser impact on organic layer and BW stocks (McRae et al., 2001), and feathermoss cover potentially recovers within 5 years after harvest (Palviainen et al., 2005).

4.3.4. *Organic layer decay rate*

CBM-CFS3 estimates of mainly wood- and bryophyte-derived organic layer C stocks improved after reducing the default aboveground slow base decay rate to $0.0075\,\mathrm{yr}^{-1}$ ('Modified B'; Table 2). This rate is within the range of decay rates estimated by Harden et al. (2000) and Manies et al. (2005) for black spruce-feathermoss stands in Manitoba and reflects the specific litter quality of boreal forests (Ise and Moorcroft, 2006): decay-resistant feathermoss and sphagnum litter (Ise and Moorcroft, 2006), and wood-derived lignified litter (Berg, 2000; Vávřová et al., 2009) of high bulk density. Large amounts of the organic layer and soil C stocks can be derived from wood: up to a third (10–31%) of the measured organic layer C in Labrador black spruce (Hagemann et al., 2009), and 39–74% of the deep C stocks in Manitoba black spruce (Harden et al., 2000). However, the CBM-CFS3 was designed for upland sites and currently does not include specific decomposition rates for slow-decaying BW and bryophyte-derived litter (Kurz et al., 2009). Moreover, currently available data on BW and bryophyte dynamics are insufficient to parameterize the CBM-CFS3 to adequately capture BW and bryophyte-dominated organic layer dynamics in cool wet boreal forests.

4.3.5. *Mineral soil decay rate*

The poor correlation between measured and 'Modified B' modelled mineral soil C stocks results from the lack of significant trends observed for the measured data. The remaining deviation between measured and 'Modified B' modelled mineral soil C stocks reflects the high site variability, the site productivity mix (H/D), and the generally small impact of harvesting and wildfire on the mineral soil C pool (Johnson and Curtis, 2001). Possibly, differences between measured and modelled mineral soil C stocks could also arise from the fact that CBM-CFS3 was designed for well-drained upland forests, and currently does not account for the accumulation of soil organic C in the course of successional paludification (Simard et al., 2007; Kurz et al., 2009).

The decrease of 'Modified B' estimates of mineral soil C stocks with time since disturbance (Table 7) indicates that paludification and the subsequent DOM C accumulation in Podzolic soils, particularly in the B horizon, is not accounted for by the CBM-CFS3. Reducing the default belowground slow base decay rate from $0.0033\,\mathrm{yr}^{-1}$ to a soil-type specific rate of $0.00207\,\mathrm{yr}^{-1}$ improved agreement between measured and 'Modified B' mineral soil C stocks. The decomposition rate of mineral soil C in humid high-boreal Labrador black spruce (Humo-Ferric Podzol) is thus at the lower range of deep C decay rates reported for drier, more continental black spruce-feathermoss stands (Gray Luvisol) in Manitoba ($0.002–0.004\,\mathrm{yr}^{-1}$; Harden et al., 2000; Manies et al., 2005). Considering the strong link between temperature, precipitation, soil moisture, geological parent material, and soil type, soil type-specific decay rates may generally improve the CBM-CFS3 estimates of mineral soil C stocks (Shaw et al., 2008).

New plot-level data collected as part of Canada's new National Forest Inventory (NFI; Natural Resources Canada, 2009) will be used to further test all above-recommended modifications to the CBM-CFS3. However, according to the NFI Ground Sampling Guidelines (Natural Resources Canada, 2009), BW is only measured if >10 cm, potentially leading to a systematic underestimate of the C stocks of ecosystems containing BW. Acknowledging that BW sampling is very time consuming, we would like to stress the importance of developing reliable sampling methods for BW estimation, possibly to be included in Canada's NFI and to parameterize the WD burial process in forest C models such as CBM-CFS3. The CBM-CFS3 predicted changes in forest biomass and DOM C stocks will thus become more accurate.

5. Conclusions

Measured live-tree, dead wood, and organic layer C stocks in high-boreal Labrador black spruce were in the lower range of those observed in other upland boreal forests. Although the CBM-CFS3 (version 1.0) represented measured live-tree C dynamics in harvested, burned, and old-growth high-boreal forests well, VBC parameters for calculating non-merchantable and branch C stocks in the Labrador black spruce sites had to be adjusted to accurately capture measured live-tree C stocks. Increases to the default CBM-CFS3 snag stem fall ($0.10\,\mathrm{yr}^{-1}$) and >10 cm WD ($0.06\,\mathrm{yr}^{-1}$) base decay rates improved agreement between measured and modelled DOM data, whereas the snag branch fall and ≤10 cm WD base decay rates did not need to be changed because modified VBC parameters decreased the non-merchantable and branch biomass C stocks and, therefore, modelled snag branch and ≤10 cm WD C stocks matched measured amounts. Both yield curves and VBC parameters must be considered when modelling forest C stocks using CBM-CFS3, as uncertainty of live-tree C estimates will affect all DOM C pools.

Mineral soil C stocks in high-boreal Labrador black spruce were high and comparable to those reported for forested Podzols and peatland sites. Higher than average organic layer and mineral soil C stocks can also be expected in other forests with cool wet climates such as coastal oceanic boreal forests (e.g., in Norway; Kjønass et al., 2000), or coniferous mountain forests (e.g., in the Tatra Mountains, Poland; Zielonka and Niklasson, 2001). The CBM-CFS3 was initially designed for well-drained upland forests; thus, the uncertainty of modelled organic layer and mineral soil C stocks increases with increasing bryophyte productivity and average soil moisture levels. In Labrador black spruce, organic layer and mineral soil DOM likely decays at lower rates than assumed by CBM-CFS3 default parameters. Modelled organic layer C stock estimates in Labrador black spruce were improved by reducing the aboveground slow base decay rate 50% of default (0.0075 yr^{-1}) reflecting the impact of bryophyte cover on organic layer decay rates. Mineral soil C stocks modelled using a preliminary belowground slow base decay rate (0.00207 yr^{-1}) optimized for Humo-Ferric Podzols were in better agreement with field-measured values than default estimates.

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4.6 Buried Deadwood

Buried deadwood stocks observed in the selected study sites ranged between 9.4–36.4 $Mg\ ha^{-1}$ (corresponding to 4.7–18.2 Mg C ha^{-1}), and considerably exceeded aboveground deadwood stocks in all but the recently harvested and middle-aged burned strata (Section 4.3). Moreover, BW volume exceeded live-tree volume in all strata by up to 93.5 $m^3\ ha^{-1}$; even the old-growth stratum contained more BW (179.3 $m^3\ ha^{-1}$) than live trees (88.1-164.2 $m^3\ ha^{-1}$). However, the data on BW abundance presented in (Hagemann et al. 2009) features large coefficients of variation (41–86%) and wide 95% confidence intervals ($\bar{x} - 72.8\%; \bar{x} + 92.2\%$), which is related to the sampling design associated with the acquisition of this data.

According to the NFI Ground Sampling Guidelines, BW is assessed based on point sampling along the two perpendicular 40-m line transects at each plot (Natural Resources Canada 2010a). This sampling scheme is optimized for sampling organic layer depth, a rather continuous variable which only gradually changes with distance. In contrast, the distribution of BW is likely similar to the distribution of aboveground WD, and thus spatially highly variable. The line intersect method of van Wagner and Olsen (1964) and its modifications are scientifically established methods for sampling the spatially discontinuous variable WD. It is therefore necessary to reassess BW abundance in the selected Labrador study sites using an appropriate sampling method, such as multiple triangular trenches employed in the following study to validate BW estimates provided by Hagemann et al. (2009).

In addition to improved BW abundance estimates, questions concerning the formation of BW need to be answered. Rates of WD burial likely depend on the balance between moss growth and WD decomposition rates. However, mosses are an omnipresent but little-studied component of boreal ecosystems (Bisbee et al. 2001, Turetsky 2003, O'Neill et al. 2006), and data on moss growth is limited (Turetsky et al. 2010). The effects of the moss layer on organic layer conditions and its role in the paludification process are increasingly investigated, but data on decay rates of WD debris after burial by moss are lacking. So far, knowledge on BW dynamics is based on inferences and – to some degree – speculation (Hagemann et al. 2009, 2010c). Field experiments analyses, like the ones presented in the following scientific articles, are thus needed to monitor WD conditions after burial associated changes in decay dynamics.

4.6.1 Hagemann U, Moroni M, Gleißner J, and Makeschin F. 2010. Accumulation and preservation of dead wood upon burial by bryophytes. Ecosystems 13(4): 600–611

Extended Abstract

Abundance of preserved deadwood buried by bryophytes in the organic layer of old-growth Labrador black spruce stands in this study exceeded estimates of a previous study on the same sites by >100% (389±39 vs. 179±46 $m^3\ ha^{-1}$) (Hagemann et al. 2009). Sampling errors of the data collected by trenching of triangular line transects in this study were considerably lower compared to the point sampling of the Hagemann et al. (2009) study. Alternative sampling methods are needed to facilitate accurate and efficient quantification of BW abundance and to allow for the inclusion of BW in deadwood and C inventories.

Stand-replacing wildfires consumed the organic layer and killed the previous stands, producing snags, which subsequently fell and became buried by moss, resulting in large amounts of wood buried in the lower half in the current organic layer. As new forest stands developed, self-thinning and senescence continuously produced minor amounts of WD for burial, most of which was located in the upper half of the organic layer. Accumulation of BW continues until the next stand-replacing fire kills most of the live trees and consumes part of the organic layer and wood buried within it. In regions with long FRI, such as humid Labrador, BW accumulation can thus proceed for much longer periods of time resulting in the vast amounts of BW observed in Labrador black spruce.

The experimental burial of standardized sample logs at various depths in the organic layer showed that burial significantly decreased WD temperature, increased WD moisture content, and tended to decrease WD respiration rates, indicative of reduced decomposition activity. Preservation of WD is likely initiated by a thin layer of fast-growing bryophytes overgrowing the WD surface before WD reaches advanced stages of decay, and before WD is entirely enveloped by organic layer material. This live bryophyte cover provides thermal insulation and moisture retention, and generates an environment unfavourable to decomposition. Two phases of the burial process may therefore be differentiated: i) the initialization phase, during which decomposition rates considerably decrease after the surface of WD located on top of the organic layer has been colonized by a thin layer of live moss, and ii) the burial phase, during which the WD is slowly enveloped in litter and dead moss as the organic layer accumulates.

As bryophytes are a vital component of many coniferous ecosystems throughout the circumpolar boreal and oroboreal forests, conditions conducive to WD burial are likely widespread. Buried wood may thus be more common than (Hagemann et al. 2009) suggested and may be of global relevance as habitat for bryophytes, fungi, or insects and a large mid- to long-term C store.

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ECOSYSTEMS

Accumulation and Preservation of Dead Wood upon Burial by Bryophytes

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ABSTRACT

Large amounts (389 ± 39 m^3 ha^{-1}) of preserved dead wood buried by bryophytes were found in the organic layer (OL) of overmature (146- to 204-year-old) black spruce (*Picea mariana* (Mill.) B.S.P.) forests in the high-boreal forest of eastern Canada. Stand-replacing wildfires consumed the organic layer and killed the previous stands, producing snags, which subsequently fell and became buried by moss, resulting in large amounts of wood buried deep in the current organic layer. As new forest stands developed, self-thinning and senescence continuously produced minor amounts of woody debris (WD) for burial, most of which was located in the upper half of the organic layer. The experimental burial of standardized sample logs at various depths in the organic layer showed that burial significantly decreased WD temperature, increased WD moisture content, and tended to decrease WD respiration rates, indicative of reduced decomposition activity. WD preservation may be initiated by a live bryophyte cover, providing thermal insulation and moisture retention, generating an environment unfavorable to decomposition. As bryophytes are a vital component of many coniferous ecosystems throughout the circumpolar boreal and mountain forests, conditions conducive to WD burial are likely widespread. Buried wood may thus be of global relevance as habitat and a large mid- to long-term carbon store.

Key words: woody debris; feathermoss; organic layer; *Pleurozium*; necromass; carbon cycling; buried dead wood.

INTRODUCTION

Dead wood and bryophytes are two important components of forest ecosystems (Harmon and others 2004; O'Neill and others 2006), but the ecological significance of bryophytes has received considerably less scientific attention than that of dead wood. Dead wood is integral to carbon (C) and nutrient cycles (Kurz and Apps 1993; Laiho and Prescott 2004), provides habitat for a range of species (Harmon and others 2004), and is an important component of forest structure (Debeljak 2006). Bryophytes are little studied components of forest ecosystems despite their widespread occurrence and functional importance in soil temperature, moisture, and nutrient regimes (Bisbee and

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Author Contributions: Ulrike Hagemann wrote paper, conceived and designed inventory, performed research and analysis; Martin T. Moroni conceived and designed study; Johanna Gleißner conceived and designed respiration study, performed research and analysis; Franz Makeschin conceived study.

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others 2001; O'Neill and others 2006), particularly in boreal and oroboreal forests where they form a continuous layer (Foster 1985; Simard and others 2009). In these ecosystems, bryophytes also play a key role in C cycling by (i) contributing considerably to net primary productivity and litter C input (O'Neill and others 2006), (ii) reducing organic layer (OL; O horizon; Soil Survey Staff 2006) temperature and nutrient availability while increasing organic layer moisture levels and acidity (Bisbee and others 2001), (iii) promoting paludification through the accumulation of a thick organic layer composed of poorly decomposable bryophyte and vascular plant substrates (Fenton and others 2005), and (iv) overgrowing and burying downed woody debris (WD; Hagemann and others 2009). Therefore, we expect WD that becomes buried in the organic layer to have lower temperatures, higher moisture content, and thus lower decay and respiration rates than unburied WD, resulting in the preservation and accumulation of buried dead wood (BW; Manies and others 2005; Hagemann and others 2009).

The incorporation of WD into the accumulating organic layer by vigorously growing bryophytes links the dead wood and bryophyte cycles, and results in the formation of a BW biomass and C pool (Boudreault and others 2002; Moroni 2006). Buried wood has received little research attention so far and has yet to be incorporated in forest models (Hagemann and others 2009). It was first observed in mountain forests dominated by yellow birch (*Betula alleghaniensis* Britton), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* L. (Mill.)), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (McFee and Stone 1966; Harvey and others 1981; Lang and others 1981). Recent studies have also found BW in various North American boreal forests (Brais and others 2005; Manies and others 2005; Moroni 2006), including overmature high-boreal black spruce (*Picea mariana* (Mill). B.S.P.) forests in Labrador, Canada (Hagemann and others 2009), where particularly large amounts of BW ($\leq 179\ \mathrm{m}^3\ \mathrm{ha}^{-1}$; exceeding unburied WD by up to 280%) were reported. However, all studies reported a high uncertainty of BW abundance, likely because study designs were not focused on assessing the abundance of BW.

Several factors indicate that a large proportion of the BW found in Labrador black spruce forests originates from the last stand-replacing wildfire, which predates the 146- to 204-year-old forests. Buried wood volume exceeded the live-tree volume of overmature stands; some of the deeply buried WD was charred, and pieces of it were up to about 250 years dead (515 years old; Hagemann and others 2009; Moroni and others 2010). A smaller proportion of BW likely originates from self-thinning and senescence, as both processes generate minor amounts of WD in slow-growing, low-density black spruce forests (Roberts and others 2006). With the organic layer slowly accumulating throughout stand development, WD generated from wildfires centuries before measurement is expected to occur as a deep cohort of BW pieces. Buried wood originating from self-thinning is expected to be distributed in low densities above the fire-generated cohort, and, being younger wood, is expected to be less decayed.

As the process of WD burial reduces aboveground WD stocks, it must be included with the three widely recognized WD volume reduction processes: decomposition, fragmentation, and leaching (Harmon and others 2004; Zhou and others 2007). However, unlike the above processes, WD burial is poorly documented with little to no data available on the abundance, characteristics, and dynamics of BW. The objectives of this study are to (i) accurately quantify the abundance of BW in old-growth high-boreal Labrador black spruce forests and confirm previously reported amounts, (ii) describe BW characteristics, that is, burial depth, size, decay and charring status, and test the assumption that a large proportion of BW volume originated from wildfire, and (iii) determine the impact of WD burial on BW temperature, moisture, and respiration rates, hypothesizing BW (a) to be cooler and wetter and (b) to have reduced respiration rates compared with unburied WD.

MATERIALS AND METHODS

Site Selection and Description

The study area is situated near Goose Bay, Labrador in the High-boreal Forest–Lake Melville Ecoregion (Ecoregions Working Group 1989), an extension of the Boreal into the Taiga Shield. Mean annual temperatures are −2.4 to −1.0°C (McKenney and others 2007), with approximately 1000 mm of precipitation evenly distributed throughout the year (Roberts and others 2006). The upland soils are mainly classified as Humo-Ferric Podzols (Soil Classification Working Group 1998) or as Typic Haplorthods (Soil Survey Staff 2006), and support the most productive forests of Labrador (Roberts and others 2006).

Three previously studied overmature forest sites (Table 2 in Hagemann and others 2009) were investigated in greater detail from July to August 2008. Sites are of medium productivity and support forests, likely of wildfire origin, dominated (>75%) by black spruce older than 140 years featuring an average height of 12–15 m and a crown closure of 50–75% (Government of Newfoundland and Labrador, unpublished report). Ground vegetation cover consisted of feathermoss (56–84%; mainly ***Pleurozium schreberi, Ptilium crista-castrensis***), foliose ground lichen (3–10%; mainly ***Peltigera aphtosa, Nephroma arcticum***), and peatmoss (0–7%; mainly ***Sphagnum russowii, S. capillifolium***). Detailed information on the study sites is presented in Hagemann and others (2009).

Field Measurements

Abundance

Three inventory plots were located randomly within each site, each comprising a 9-m equilateral triangle transect. Along each transect, a trench was dug exposing a vertical cross-section of the organic layer down to the mineral soil. All BW (WD buried >50% in the organic layer) intersecting the transect was measured using the line intersect method (Marshall and others 2000). The cross-sectional area of BW pieces was calculated as a circle for round, an ellipse for oval, and a rectangle for odd-shaped pieces. Odd-shaped pieces were not included in the size analysis due to unknown BW diameter, but were only found in small numbers. A decay class of 1 to 5 was assigned to each BW piece (Table 1; Natural Resources Canada 2010), and BW biomass was estimated by multiplying BW volume with wood density for the corresponding black spruce decay class (Table 1). Buried wood C stocks were calculated by multiplying BW biomass with 0.5 (Hagemann and others 2010). Presence of bark, charring, and ingrown roots, and organic layer thickness above (to live moss) and below (to mineral soil) each BW piece were recorded from the center of the BW piece.

Burial Environment

Twelve decay class 2 sample logs with a middle diameter of 13.8 ± 0.1 cm were selected from the WD present within each site and cut to 30.7 ± 0.2 cm length. The ends were sealed with Water Stop polymer paint (MEM Bauchemie, Leer, Germany). Three burial plots were located along a 25-m transect placed randomly within each site. At each burial plot, four sample logs were placed at four different positions relative to the surface of the forest floor: P1—on top of the live moss layer, P2—half-buried in the organic layer but not moss-covered, P3—completely buried in the organic layer and covered by live moss, and

Table 1. (a) Description of Decay Classes Used to Classify Buried Dead Wood and (b) Dead Wood Density of Black Spruce in (kg m^{-3}) Used to Convert BW Volume to Biomass by Decay Class

	Decay class				
	1	2	3	4	5
(a) Decay class attributes[a]					
Wood texture	Intact, hard	Intact, hard to partly decaying	Hard, large pieces, partly decaying	Small, blocky pieces	Many small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging near ground, or broken	All of log on ground, sinking	All of log on ground, partly sunken
Twigs <3 cm (if originally present)	Twigs present	No twigs	No twigs	No twigs	No twigs
Bark	Bark intact	Intact or partly missing	Trace bark	No bark	No bark
Shape	Round	Round	Round	Round to oval	Oval
Invading roots	None	None	In sapwood	In heartwood	In heartwood
(b) Wood density by species (kg m^{-3})[a]					
Picea mariana (Mill.) BSP	410	341	272	203	134

[a] *Based on Canada's National Forest Inventory (Natural Resources Canada 2010).*

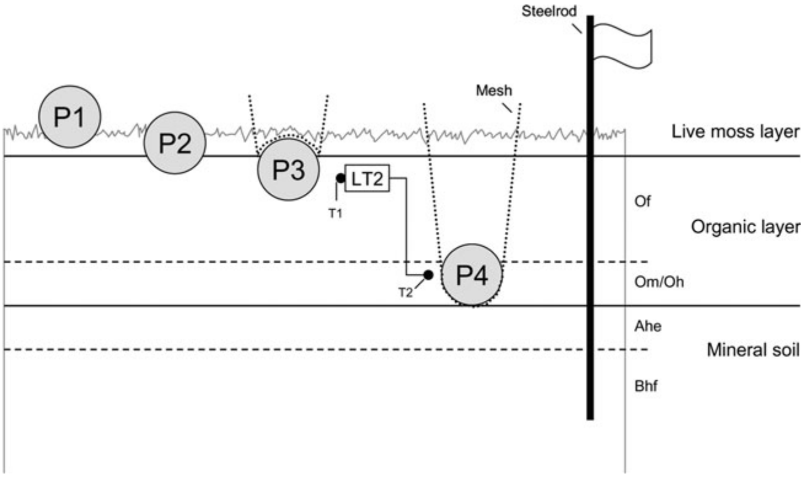

Figure 1. Burial positions of standardized sample logs. Organic layer and soil horizon terminology according to Soil Classification Working Group (1998).

P4—completely buried in the organic layer and in contact with the mineral soil (Figure 1). For plots P3 and P4, a plastic mesh (~10 cm) was inserted below the live moss layer or the sample piece, respectively, to facilitate handling and reduce the disturbance of the organic material covering the sample piece. In each site, a LogIT LT2 data logger (Supco Inc, Allenwood, New Jersey, USA) was installed at the center burial plot with two probes recording organic layer temperatures every 15 min at 2 and 20 cm depth (T1/2; Figure 1). At each plot, a corrodible steel rod (1.2 m) was implanted into the forest floor to assess oxygen availability (Fenton and others 2006).

Respiration, wood and air temperatures, and log mass were measured seven times from 13 July to 27 August 2008 every 7–10 days. After unearthing, logs were cleaned from attached organic material and handled carefully to avoid detachment of bark. Buried wood respiration was measured for 180 s using a clear acrylic closed chamber (19385 cm^3; Rubbermaid Inc.) connected to an EGM-4 infrared gas analyzer (PP Systems, Amesbury, Massachusetts, USA). Buried wood respiration (R_{BW}) was calculated as CO_2 concentration increment in the system volume per unit of emitting (lateral) wood surface and time. System volume was determined by deducting average log volume from the volume of the chamber and gas analyzer.

The temperature (T_{OL}) below each sample log was measured simultaneously with BW respiration using a temperature probe connected to the EGM-4. Organic layer moisture potential (Ψ_{OL}) was measured at the depth corresponding to the center log position using a 2900F1 Quick Draw Tensiometer (Soil Moisture Equipment Corp., Santa Barbara, California, USA). Wood temperatures were recorded in pre-drilled holes (Ø 4 mm) using waterproof digital type K thermocouple probes (DP8811WP, Mannix, New York, USA): T_{BWsap} at 2 cm (top sapwood) and $T_{BWheart}$ at 7 cm depth (heartwood). Between measurements, holes were sealed with wooden dowels to avoid equilibration. Ambient air temperature (T_{Air}) and relative humidity (RH%) were recorded 30 cm above the forest floor using a digital hygro-thermometer (SPER Scientific, Scottsdale, Arizona, USA). Log mass was taken using a digital hanging scale. Wood moisture content (u_{BW}) for each sampling date was calculated using date-specific field mass and absolute dry mass (105°C) determined on completion of the last measurement. Log density (D_{BW}) was calculated as dry mass (kg) to volume (m^2) ratio.

Statistical Analyses

Abundance

Associations between interval (for example, BW depth), ordinal (for example, decay class), and nominal (for example, charring) variables were determined using Spearman's ρ, the χ^2-test, and Kendall's τ, respectively.

Burial Environment

Differences in R_{BW}, T_{Air}, T_{BWsap}, $T_{BWheart}$, T_{OL}, u_{BW}, and Ψ_{OL} among burial positions were analyzed using univariate nested ANOVA with position ($k = 4$) and the respective variable as fixed factors, and stand nested within position as random factor ($n = 3$). Differences in T_{OL} at 2 and 20 cm depth were compared using the paired Wilcoxon signed-rank test. Correlations among R_{BW}, T_{Air}, T_{BWsap}, $T_{BWheart}$, T_{OL}, u_{BW}, Ψ_{OL}, D_{BW}, and OLT were calculated using Spearman's ρ. A factor analysis was employed to aggregate the environmental variables. The influence of all variables on BW respiration was determined using a hierarchical nested linear mixed model with position and environmental variables as fixed factors, and stand nested within position as random factor. Random variance components were calculated using Restricted Maximum Likelihood. Statistical analyses were conducted using SPSS 15.0.1 (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Buried Dead Wood Abundance

Volume of BW in the three stands amounted to 419.1 ± 92.1 (standard error of three triangle transects), 486.9 ± 46.7, and 261.1 ± 104.6 m^3 ha^{-1}, corresponding to C stocks of 40.7 ± 7.6, 46.7 ± 22.2, and 24.5 ± 10.5 Mg C ha^{-1}, respectively (Table 1). Variability in BW abundance was high both between and within stands.

Most BW was located in the lower half of the organic layer, which was largely less than 30 cm deep at all sites (Table 2). Distribution of BW volume by relative depth (burial depth as proportion of organic layer thickness) showed that 53–66% of the BW volume was located at relative depths of greater than 50% (Figure 2). Most BW pieces (73–78%) were also located in the lower half of the organic layer (Figure 2), with about 40% of all BW pieces in the lowest 25%. Large BW pieces (diameter ≥15 cm) were concentrated at 30–80% relative to organic layer thickness, equivalent to burial at 10–20 cm depth. Large WD pieces located higher within the organic layer were not counted as BW because they would not be buried greater than 50%.

Table 2. Buried Dead Wood Volume and Carbon Stocks, and Organic Layer Depth by Site

Variable	Site					
	OG-1		OG-2		OG-3	
	Mean	SE	Mean	SE	Mean	SE
Volume (m^3 ha^{-1})	419.1	92.1	486.9	214.5	261.2	104.6
Carbon stocks (Mg C ha^{-1})	40.7	7.6	46.7	22.2	24.5	10.5
Organic layer depth (cm)	24.3	0.6	22.3	0.8	18.4	0.8
	Min	Max	Min	Max	Min	Max
Volume (m^3 ha^{-1})	287.3	596.5	162.7	892.2	53.1	384.1
Carbon stocks (Mg C ha^{-1})	28.6	54.7	14.6	89.3	4.3	39.4
Organic layer depth (cm)	11.0	41.0	7.0	47.0	5.5	34.0

SE standard error; n = 3.

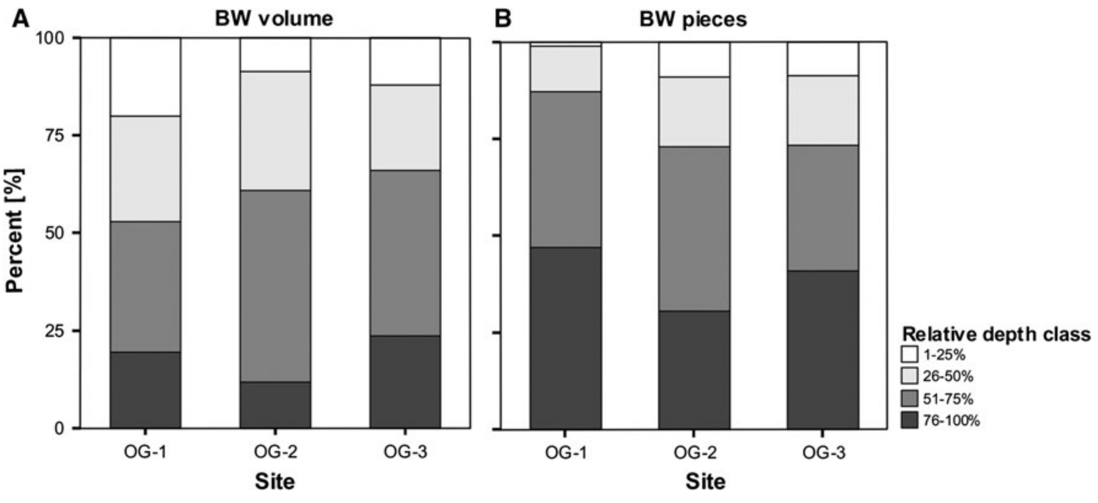

Figure 2. Buried dead wood volume by diameter class: **A** volume and **B** pieces.

The proportion of BW pieces in decay classes 1–5 was 0, 4, 21, 38, and 37%, respectively. The above proportions correspond to 0, 7, 15, 45, and 33% of BW volume. Decay status was more advanced for BW located lower in the soil profile, that is, at higher relative depths ($\chi^2 = 563.8$; $\tau = 0.294$; $P \leq 0.001$). Of the 16% of all BW pieces that showed charring, 74.5% were located in the lower half, and 43.1% in the lowest quarter of the organic layer. Most BW pieces had no bark (76%) and featured ingrown roots (72%).

Burial Environment

Soil and Dead Wood Temperature

Organic layer and wood temperatures and their variability decreased with depth as the impact of surface air temperatures declined. Average daily T_{OL} at 2 cm depth (5.3–19.9°C) were significantly higher and more variable than at 20 cm depth (4.1–12.1°C; $P \leq 0.05$). Although no trend with time was observed for T_{OL} at 2 cm depth, T_{OL} at 20 cm depth increased steadily over the measurement period. In contrast, there was typical diurnal temperature variability at 2 cm depth, which was not observed for 20 cm T_{OL}.

Buried sample log (P3 and P4) temperatures T_{BWsap} and $T_{BWheart}$ were generally significantly lower than recorded for unburied (P1) and half-buried (P2) sample logs ($P \leq 0.05$; Figure 3A, B). Moreover, sample logs at the mineral soil surface (P4) were significantly cooler than sample logs buried just below the organic layer surface (P3) on 2 days (13/07, 22/08; $P \leq 0.05$; Figure 3A, B). Buried log temperatures T_{BWsap} and $T_{BWheart}$ were highly correlated, but correlation strength decreased with burial depth (from P1 to P4; $r = 0.939$ to $r = 0.857$; $P \leq 0.01$). Correlation of T_{BWsap} and T_{Air} decreased with burial ($r = 0.922$ to $r = 0.299$; $P \leq 0.05$), whereas correlation of $T_{BWheart}$ and T_{OL} increased ($r = 0.294$ to $r = 0.739$; $P \leq 0.05$).

Dead Wood, Organic Layer Moisture, and Aeration

Buried sample log moisture content (u_{BW}) tended to increase with burial depth, but variability in individual sample log moisture levels was high within burial position (Figure 4). On more than half of the measurement dates, u_{BW} of sample logs touching the mineral soil (P4) were significantly higher than for those not in contact with the mineral soil (P1–P3; $P \leq 0.05$). Buried wood moisture content u_{BW} was correlated to wood density D_{BW} ($r = -0.644$; $P \leq 0.01$) and T_{OL} ($r = -0.228$; $P \leq 0.01$), but not to Ψ_{OL}, except for P3 ($r = -0.354$; $P \leq 0.01$). Steel rods featured black rust at depths 29 cm or greater, indicating limited oxygen availability (Fenton and others 2006).

Buried Dead Wood Respiration

Respiration R_{BW} of sample logs was highly variable with averages ranging from 0.11–0.22, 0.13–0.23, 0.11–0.16, and 0.09–0.15 g CO_2 m^{-2} h^{-1} for positions P1, P2, P3, and P4, respectively (Figure 5). On

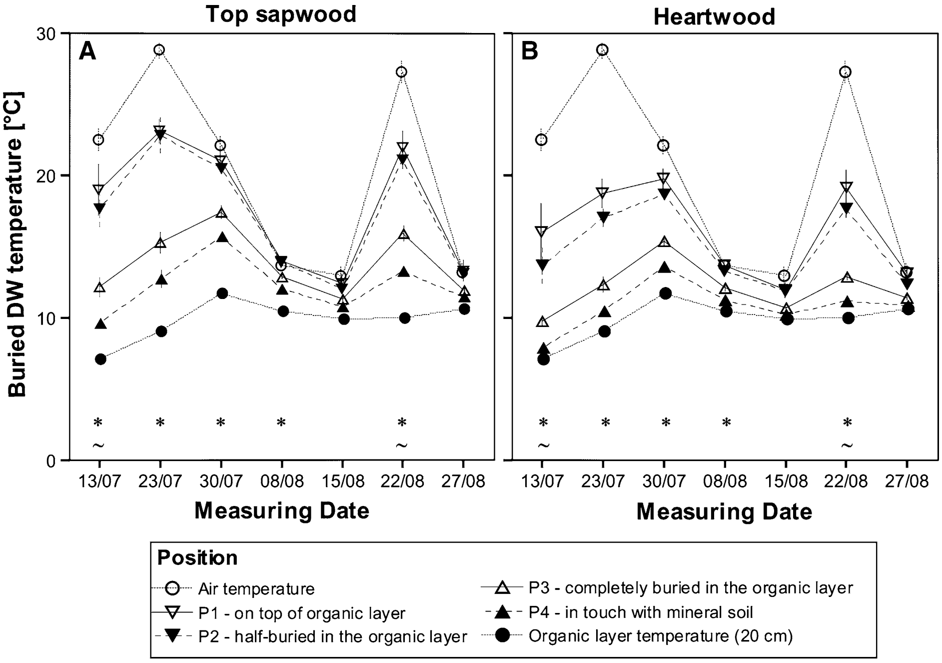

Figure 3. Buried dead wood **A** top sap, and **B** heart temperature by position and measurement date; ambient air and soil temperature (20 cm depth) at the time of measurement are shown for comparison.
* Significant differences between P1/2 and P3/4, ~ significant differences between P3 and P4; $P \leq 0.05$.

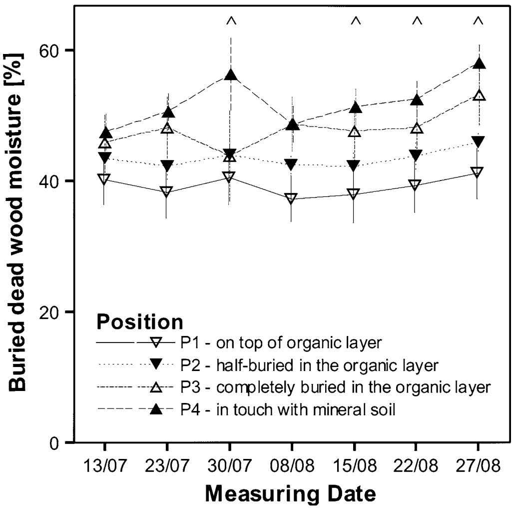

Figure 4. Buried dead wood gravimetric moisture content by position and measurement date. * Significant differences between P1/2 and P3/4. ^ Significant difference between P1 and P4; $P \leq 0.05$.

two measurement days (13/07, 22/08), R_{BW} of buried samples logs (P3/P4) was significantly lower than recorded for unburied and half-buried logs (P1/P2; $P \leq 0.05$). Correlation between R_{BW} and T_{Air}, T_{BWsap}, and T_{BWheart} decreased with burial depth from P1 ($r = 0.505$, 0.596, 0.631, respectively; $P \leq 0.01$) to P4 (r = n.s., 0.263, 0.279, respectively; $P \leq 0.05$), whereas the correlation with T_{OL} tended to increase (r = n.s. to $r = 0.288$; $P \leq 0.05$).

Aggregation of independent environmental factors yielded three components that explained 68.4% of total variable variance (Table 3a). The first, second, and third component accounted for 32.5, 22.7, and 13.2% of total variance, respectively. Components 1, 2, and 3 were dominated by the following factors: (1) T_{Air}, T_{BWsap}, and T_{BWheart}, (2) T_{OL} and RH%, and (3) u_{BW} and D_{BW}. The hierarchical nested Linear Mixed Model showed T_{BWsap} to be the main influential environmental variable in determining R_{BW}, followed by OLT, the interaction between u_{BW} and D_{BW}, whereas burial position was not an explanatory variable (Table 3b). Random variance was mainly attributed to within-site (that is, plot) variability.

DISCUSSION

Buried Dead Wood Abundance

Abundance of BW measured in overmature Labrador black spruce stands in this study exceeded estimates of a previous study on the same sites by more than 100% (389 ± 39 vs. 179±46 $m^3 ha^{-1}$; Hagemann and others 2009). Measured amounts of BW are thus similar to amounts observed in mountain Douglas-fir stands containing trees considerably larger than Labrador black spruce (370–430 $m^3 ha^{-1}$; Harvey and others 1981). Compared with this study, the point sampling of Hagemann and others (2009) underestimated BW abundance and produced higher sampling errors (coefficient of variation 77 vs. 30%). Unlike unburied WD, BW cannot be visually assessed, making its abundance difficult to quantify. Trenching allows for a more detailed inventory of BW, but is a very time-consuming technique. Moreover, trench location is crucial as BW is characterized by high spatial variability, due to the spatial variability of WD (Manies and others 2005) and organic layer consumption by

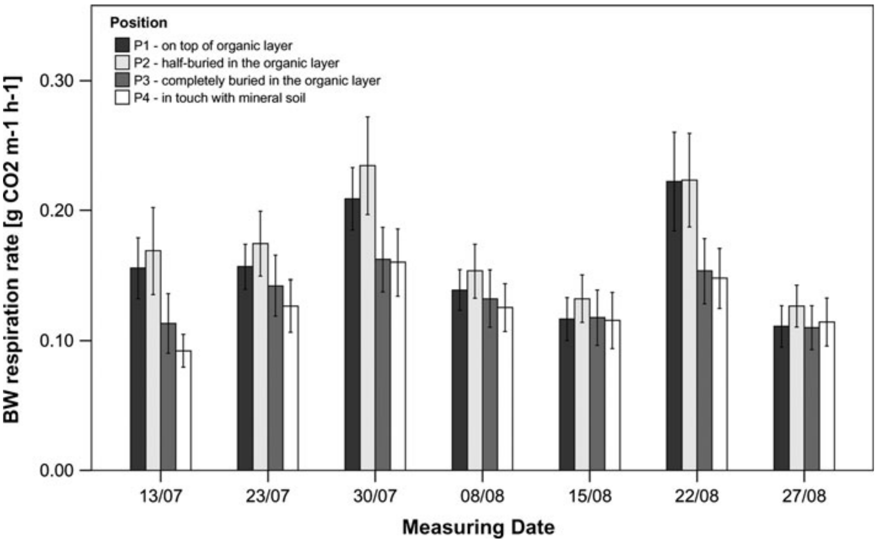

Figure 5. Buried dead wood respiration rates (in g $CO_2\ m^{-2}\ h^{-1}$) by position and measurement date.

Table 3. Summary Statistics for (a) Factor Analysis Showing Component Matrix and Explained Variance, and (b) Hierarchical Nested Linear Mixed Model (LMM) Analysis Describing the Influence of the Listed Variables on Buried Dead Wood Respiration

(a) Factor analysis	Variance		
Component	Total	%	Cumulative %
1	2.600	32.5	32.5
2	1.813	22.7	55.2
3	1.059	13.2	68.4

	Component			
Variable	1	2	3	Communalities extraction
T_{Air}	0.684	−0.543	−0.135	0.780
T_{BWsap}	0.982	0.047	0.107	0.979
T_{BWheart}	0.895	0.269	0.200	0.914
T_{OL}	0.359	0.747	0.288	0.769
Ψ_{OL}	−0.028	0.301	0.052	0.094
u_{BW}	−0.177	−0.453	0.620	0.621
D_{BW}	0.095	0.394	−0.667	0.609
RH%	−0.443	0.660	0.273	0.707

(b) LMM analysis

Variable	FT[a]	F	Wald Z	P	Variance (%)
Intercept		40.101	na†	≤ 0.001‡	
Burial position	F	0.137	na†	0.741	
Site(Burial position)	R	na†	1.003	0.316	2.8
Plot(site)	R	na†	1.841	0.066	73.1
Measuring day	F_{rep}	0.099	na†	0.754	
T_{BWsap}	F	52.510	na†	≤ 0.001‡	
u_{BW}	F	4.869	na†	0.030‡	
D_{BW}	F	4.595	na†	0.035‡	
$u_{\mathrm{BW}} \times D_{\mathrm{BW}}$	F	8.091	na†	0.006‡	
OLT	F	11.147	na†	0.001‡	
Error					24.1

Note for (b): Position, BW top sap temperature (T_{BWsap}), BW moisture content (u_{BW}), BW density (D_{BW}), and organic layer thickness (OLT) are a fixed factor; site nested within position and plot nested within site are random factors; measuring day accounted for repeated measurements.

[a] *FT factor type; fixed (F) and random (R) factors; F_{rep} = repeated.*

† *The statistic is not applicable to this factor type.*

‡ *Significant at $\alpha = 0.05$.*

fire (Shetler and others 2008). Thus, alternative sampling methods could greatly facilitate accurate and efficient quantification of BW abundance, as recommended earlier by Shaw and others (2008) for sampling forest soils. Buried wood could then be included in dead wood and C inventories as suggested previously by Hagemann and others (2009).

Abundance of BW, particularly of 15 cm or greater diameter logs in advanced decay stages, and percentage of charred BW pieces were highest in the lower half of the organic layer, indicating that most BW originated from the last or previous stand-replacing wildfires, and supporting earlier assertions of post-fire BW preservation (Hagemann and others 2009). Wildfires produce large numbers of snags that mostly fall within 25–33 years in the boreal forest (McRae and others 2001; Moroni 2006), thereby creating large amounts of 10 cm or greater WD around 20 years following fire (Moroni 2006). Although feathermoss is often completely consumed by wildfire (Smith and others 2000), it can recolonize burned sites within 30–70 years following fire (O'Neill and others 2006; Longton 2009), with recolonization occurring faster following low-intensity fires or under moist conditions

(Kershaw and others 1994), as are prevalent in the humid high-boreal forest. In Labrador, WD created by wildfire can persist up to 70 years after fire, thus being available for burial as feathermoss recovers (Hagemann and others 2009). Given the large volume of deeper, that is older, BW in Labrador, moss recolonization and subsequent burial of fire-derived WD appears to be fairly efficient up to five decades after fire at these sites.

The large amount of BW found at the interface of the organic layer and mineral soil indicates that preservation of WD is initiated by moss cover before a piece of WD is entirely enveloped in organic layer material. Any BW piece located at the interface of the organic layer and mineral soil (Figure 2) must have fallen on either bare soil or a sparse moss layer that had recently recolonized the site following the dead wood-generating disturbance. In either case, the rate of organic layer accumulation at this time would have been low (Fenton and others 2005; O'Neill and others 2006). If BW preservation depended on complete burial, enveloping of the mostly 15 cm or greater logs would have taken a long time, and a large portion of WD would thus have decayed before being entirely buried, which is in contrast with the large amount of BW located at the interface of the organic layer and mineral soil. More likely, preservation was initiated by a thin layer of fast-growing bryophytes overgrowing the WD surface before WD reached advanced stages of decay (Bisbee and others 2001; Manies et al. 2005), and before WD was entirely enveloped by organic layer material.

In addition to stand-replacing disturbances, self-thinning and senescence also contribute to BW accumulation. In general, little WD is created in the course of self-thinning in slow-growing, low-density Labrador black spruce (Government of Newfoundland and Labrador, unpublished growth curves), but tree mortality increases when these forests enter the gap dynamics phase at the age of about 185 years (Harper and others 2005). However, annual mortality in Labrador black spruce is likely less than in more dense balsam fir and black spruce stands in Newfoundland, where 2.1–2.4% of stems larger than 9 cm die and fall down per year (Moroni and Harris 2010). As a considerable amount of BW volume (~48%) was located in the upper half of the organic layer, the burial process in these gap-driven Labrador spruce stands is likely be very efficient, that is, most coarse WD generated by senescence must be buried rather than decayed to explain the large amounts of WD found in the upper half of the organic layer. All evidence suggests that the burial process encompasses two phases: (i) a considerable decrease in the decomposition rate after the surface WD located on top of the organic layer has been colonized by a thin layer of live moss (initialization phase), and (ii) the slow enveloping of the WD in dead moss as the organic layer accumulates (burial phase).

Senescence continuously produces WD for burial until the next stand-replacing fire kills most of the live trees and consumes part of the organic layer and the wood buried within it (McRae and others 2001; Fenton and others 2005). However, the fire-return interval for central Labrador is estimated at 300 to 500 years—longer than for other boreal forests (Foster 1985; McRae and others 2001)—and BW accumulation can, therefore, proceed for much longer periods of time resulting in the vast amounts of BW observed in Labrador black spruce.

Buried Dead Wood Environment

Burial significantly alters both the temperature and moisture regime of WD. As WD is buried deeper within the organic layer, its temperature and moisture regime are increasingly regulated by the organic layer, which is characterized by minimal diurnal temperature variability, low temperatures, and high moisture contents at a depth of only 20 cm. Even in the late summer, daytime BW temperatures can thus be up to 8°C lower than unburied WD temperatures (Figure 3A, B), due to the temperature buffering effect of the thick moss-derived organic layer (Fenton and others 2005; O'Neill and others 2006). High organic layer moisture contents not only increase the specific heat capacity of BW (Yu and others 2002) and BW moisture content compared with unburied WD (Figure 4), but also result in the formation of oxygen-depleted zones at 29 cm or greater depth, which corresponds to the mineral A horizon or to the lowest layers of the organic layer and wood buried within it (Table 1). In Labrador high-boreal black spruce, cool, wet, anaerobic, and antimicrobial conditions can, therefore, prevail in the organic layer throughout the summer, resulting in low BW decomposition rates.

Low BW respiration rates are indicative of minimal decomposition activity (Chambers and others 2001). Measured BW respiration rates (0.09–0.23 g CO_2 m^{-2} h^{-1}) in Labrador black spruce are similar to rates of WD respiration in Manitoba (Bond-Lamberty and others 2003), but considerably lower than soil surface efflux in Labrador (0.55–0.91 g CO_2 m^{-2} h^{-1}; *data not shown*) and Alaska (0.92 g CO_2 m^{-2} h^{-1}; O'Neill and others 2006). Buried wood respiration rates tended to be lowest for completely buried logs (P3/4; Figure 5). The expected significant reduction in respiration rates with burial depth may have been masked by measurement errors due to the unearthing of the sample logs. Removing sample logs from the CO_2-elevated organic layer environment changed the pressure and CO_2 concentration gradient and likely resulted in an initial CO_2 flush and an overestimate of the BW respiration rate (Bain and others 2005). Long-term mass loss and fragmentation studies may thus provide more accurate data of the BW decay and preservation than short-term respiration measurements.

Unlike Hagemann and others (2009), we suggest that BW preservation may be initiated by the colonization of the WD surface by live moss rather than the enveloping of WD in organic layer material (Figure 5). The largest decrease of WD temperature and increase of WD moisture content occurred between partially buried but not moss-covered (P2), and entirely buried and moss-covered BW pieces (P3; Figures 3, 4). Bryophytes feature high water absorption and retention capacities as well as low thermal conductivity under dry and high thermal capacity under wet conditions (Bisbee and others 2001; O'Neill and others 2006). An insulating, poikilohydric, and antimicrobial live bryophyte layer may therefore exert an influence on WD similar to that of the organic layer, thus initiating changes in WD temperature and moisture regime, and consequently facilitating BW preservation.

The live-tree biomass of the studied humid high-boreal black spruce forests in Labrador falls within the lower range of values for closed-canopy boreal forest (compare Hagemann and others 2010). Accordingly, abundance of aboveground WD was also in the lower range of values reported for old-growth boreal forests composed of similar-sized trees (compare Hagemann and others 2009), for example, in Manitoba (Bond-Lamberty and others 2003; Manies and others 2005), Quebec (Brais and others 2005), and Newfoundland (Moroni 2006). Although the studied forests were mostly older than old-growth or mature forests of other studies (81–155 years; Bond-Lamberty and others 2003; Brais and others 2005; Manies and others 2005) and their fire return interval is considerably longer than that of other boreal forests (Foster 1985; McRae and others 2001), organic layer stocks and depths were similar to those reported for other boreal forests (Smith and Heath 2002; Howard and others 2004; Martin and others 2005; compare Hagemann and others 2010). Buried wood stocks largely exceeded most values reported in the literature (Brais and others 2005; Manies and others 2005; Moroni 2006), but most studies reporting BW were not focused on assessing the abundance of BW resulting in high uncertainty of BW abundance.

Given the similarities of various boreal forest types with respect to climate, live tree, WD, and organic layer stocks, and bryophyte ground cover, we speculate that—depending on disturbance regime and stand age—BW can be found in differing amounts in cool coniferous ecosystems with sustained moss growth around the world, both throughout the circumpolar boreal forests (Ahti and others 1968; Hämet-Ahti and others 1974; Ecoregions Working Group 1989) and in elevated regions south of the boreal (Zielonka and Niklasson 2001). Burial of WD would thus be more common than Hagemann and others (2009) suggested and BW likely forms a globally important mid- to long-term C store (Moroni and others 2010). However, data on global BW abundance, the impact of disturbances on BW, and its ecological significance, for example, for bryophytes, fungi, or insects, is lacking. Further studies of BW stocks and the burial process will contribute to the understanding and modelling of dead wood and C cycles of coniferous forests and the possible habitat functions of BW.

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4.6.2 Moroni M, Hagemann U., and Beilman D W. 2010. Dead wood is buried and preserved in a Labrador boreal forest. Ecosystems 13(3): 452–458

Extended Abstract

Radiocarbon-derived ages of black spruce stems buried near the bottom of the organic soil horizon ranged between 54 and 515 years before 2008. Calibrated ^{14}C age uncertainties are large and range between 50–380 years before 2008 due to sharp increases and variable amounts of atmospheric $^{14}CO_2$. Constraining the minimum age of buried stems by the current stand age, buried stems had been dead for more than 250 years, with some well-preserved wood having been formed up to 450 years ago. Estimates are considered conservative due to potential contamination with younger C.

Charcoal was identified on buried wood at all sites, indicating that buried wood likely originated from intense stand replacing fires that consumed the organic layer allowing snags to fall to the mineral soil surface, where they were subsequently overgrown by moss. While most aboveground dead wood decays or becomes fragmented within 70 years of tree death in the studied forests, the presence of old yet well-preserved buried wood suggests that decay rates are greatly reduced when downed deadwood is quickly overgrown by moss. The clearly discernible wood structure in several samples (similar to Decay Class 4; NATURAL RESOURCES CANADA 2010a) indicates a surprising degree of preservation given the long time span since deadwood creation. The process of deadwood burial and its resultant addition to a large and long-enduring belowground C pool should be considered when estimating dead wood abundance for habitat or forest C accounting and cycling in coniferous forests with dominant bryophyte ground cover.

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ECOSYSTEMS

Dead Wood is Buried and Preserved in a Labrador Boreal Forest

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ABSTRACT

Large amounts (36.4 Mg ha^{-1} or 179 m^3 ha^{-1}) of buried dead wood were found in overmature (146–204-year-old) black spruce (*Picea mariana* (Mill.) B.S.P.) forests in the high boreal region of eastern Canada. Amounts of this size indicate that burial reduces rates of wood decay producing an important component of long-term carbon (C) storage. Radiocarbon-derived ages of black spruce stems buried near the bottom of the organic soil horizon at three old-growth sites were up to 515 years old. Together with information on current stand age, this suggests that the stems have been dead for more than 250 years. Most aboveground dead wood decays or becomes fragmented within about 70 years of tree death in these forests. The presence of old yet well-preserved buried wood suggests that decay rates are greatly reduced when downed dead wood is quickly overgrown by moss. Thus, the nature and type of ground-layer vegetation influences the accumulation of organic matter in these forests. This process of dead wood burial and the resultant addition to a large and long-enduring belowground C pool should be considered when estimating dead wood abundance for habitat or forest C accounting and cycling.

Key words: biomass; black spruce; carbon; necromass; *Picea mariana*; snags; woody debris.

INTRODUCTION

Dead wood (DW) is integral to a range of ecosystem functions, including provision of habitat for numerous species (for example, Harmon and others 2004; Simon and others 2002) and carbon (C) and nutrient cycling (for example, Kurz and Apps 1993; Laiho and Prescott 2004; Harmon and others 2004; Manies and others 2005). The few studies that report buried wood abundance show a wide range of buried downed DW biomass storage, 0.2–36.4 Mg ha^{-1}, amounts often equivalent to or greater than unburied downed DW (3–1674%; Brais and others 2005; Hagemann and others 2009; Lang and others 1981; Manies and others 2005; Moroni 2006), with the largest amounts (36.4 Mg ha^{-1} or 179 m^3 ha^{-1}; 23–725% unburied downed DW biomass; Figure 1) from boreal black spruce (*Picea mariana* (Mill.) B.S.P.) forests in Labrador, Canada (Hagemann and others 2009).

Large amounts of buried wood in Labrador black spruce forests is indicative of long-term storage where rates of decay appear suppressed (Hagemann and others 2009). Burial of woody debris in the organic layer is promoted by the vigorous growth of bryophytes in the groundcover layer (Hagemann

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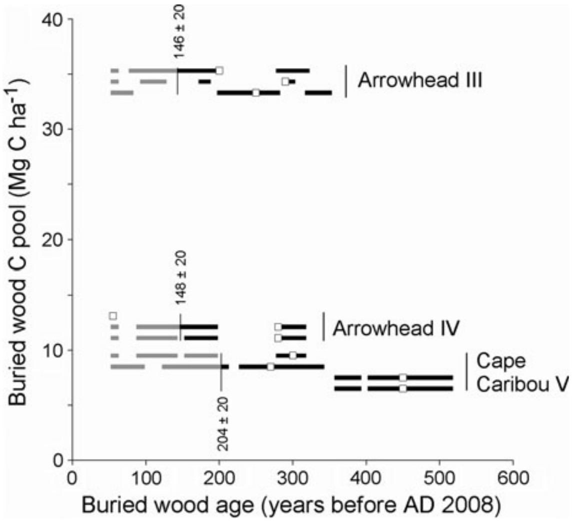

Figure 1. ^{14}C-derived age of buried tree stems compared to the buried wood C pool in three old-growth black spruce sites in central Labrador, Canada. *Horizontal bars* show 2σ age uncertainties (Stuiver and Reimer 1993) and open squares are the medians of each 2σ age distribution (Table 1). *Solid bars* show ages older than current mean stand age (indicated) and *filled bars* show ages younger than current mean stand age.

and others 2009), typical of many coniferous forests (Wilton 1964; Bisbee and others 2001). Labrador experiences a cold wet environment (Environment Canada 2010) producing a cold wet organic layer, conditions enhanced by the presence of a bryophyte layer (Foster 1985; Kasischke and Johnstone 2005), likely resulting in buried DW decay rates that are dramatically lower than decay rates of unburied DW as suggested by other authors (Foster 1985; Manies and others 2005). Calculating decay rates of woody debris based on aboveground measurements of woody debris abundance may, therefore, overestimate decay rates as the potentially large component of DW that is quickly buried would be missed.

In this study, we measure the radiocarbon (^{14}C) age of buried wood excavated from the organic layer at the boundary between mineral and organic soil horizons in old-growth Labrador black spruce forests. We hypothesize that suppressed decay rates allow for substantial necromass to accumulate belowground, which would be evident in well-preserved buried wood that is centuries old.

Materials and Methods

Site Selection and Description

The study area is near Goose Bay, Labrador, Canada in the ''High-boreal Forest–Lake Melville'' Ecoregion (Ecosdistrict 452, Ecoregion 6; Ecoregions Working Group 1989), which is the easternmost extent of the Boreal Shield Ecozone and a narrow extension of the boreal forest into the Taiga Shield Ecozone. Forests on well-drained sites in the region are the most productive local forests and are dominated by black spruce mixed with balsam fir (*Abies balsamea* (L.)) and white birch (*Betula papyrifera* Marsh.) (Rowe 1972).

Three old-growth forest sites of stand type bS842M (Government of Newfoundland and Labrador, unpublished), the most common productive forest type in the region, were selected for study (Table 1). This forest type is dominated by black spruce (>75%) older than 140 years with an average height of 12–15 m, crown closure of 50–75%, and of medium productivity (for merchantable yield). The bS842M stand type typically attains a maximum gross merchantable volume (GMV) of about 140 m^3 ha^{-1} at stand ages of around 110–150 years, before going into gap dynamics at an average GMV of about 113 m^3 ha^{-1} (Table 2). Site elevation ranges from 161 to 257 m, and mean annual temperature is between −2.2 and −1.8°C (McKenney and others 2007). Mean annual precipitation of approximately 1,000 mm is well distributed throughout the year and is among the highest amounts for boreal North America (Foster 1985; Environment Canada 2010). Stand age at our study sites was estimated to be 146–204 years based on tree-ring counts from increment bores (Hagemann and others 2009).

Field and Laboratory Measurements

Field measurements and sampling were conducted in August 2008. Within each of the three forest sites, a 27-m-long trench was excavated to the bottom of the organic horizon to expose a vertical cross section of the organic layer and buried DW. Organic layer depth was measured every 27 cm within each trench. From each excavation, three or four individual buried stems (for a total of 10 stems) located near the interface of the organic layer and mineral soil with minimum diameters of 10 cm were sampled (Figure 2). Samples of approximately 150 cm^3 were excavated from the approximate center of each stem. Care was taken to avoid the exterior of the stem to prevent contamination of samples with modern C, as stems were often mixed with organic or mineral soil material and penetrated by roots and fungal hyphae.

Excavated 150 cm^3 stem samples were returned to the laboratory and air dried. Charcoal was identified on the surface of some buried wood from

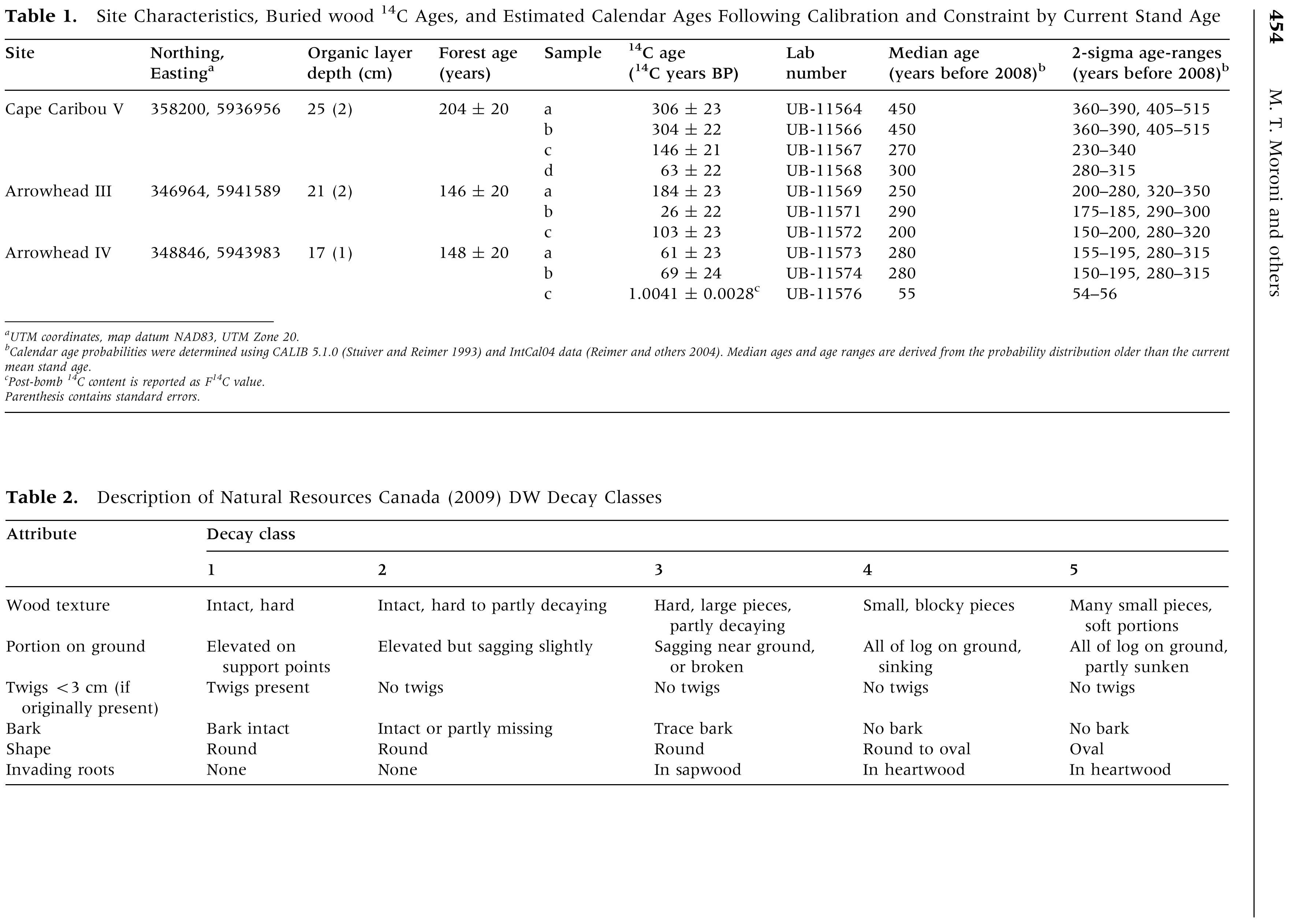

Table 1. Site Characteristics, Buried wood ^{14}C Ages, and Estimated Calendar Ages Following Calibration and Constraint by Current Stand Age

Site	Northing, Easting[a]	Organic layer depth (cm)	Forest age (years)	Sample	^{14}C age (^{14}C years BP)	Lab number	Median age (years before 2008)[b]	2-sigma age-ranges (years before 2008)[b]
Cape Caribou V	358200, 5936956	25 (2)	204 ± 20	a	306 ± 23	UB-11564	450	360–390, 405–515
				b	304 ± 22	UB-11566	450	360–390, 405–515
				c	146 ± 21	UB-11567	270	230–340
				d	63 ± 22	UB-11568	300	280–315
Arrowhead III	346964, 5941589	21 (2)	146 ± 20	a	184 ± 23	UB-11569	250	200–280, 320–350
				b	26 ± 22	UB-11571	290	175–185, 290–300
				c	103 ± 23	UB-11572	200	150–200, 280–320
Arrowhead IV	348846, 5943983	17 (1)	148 ± 20	a	61 ± 23	UB-11573	280	155–195, 280–315
				b	69 ± 24	UB-11574	280	150–195, 280–315
				c	1.0041 ± 0.0028[c]	UB-11576	55	54–56

[a] *UTM coordinates, map datum NAD83, UTM Zone 20.*

[b] *Calendar age probabilities were determined using CALIB 5.1.0 (Stuiver and Reimer 1993) and IntCal04 data (Reimer and others 2004). Median ages and age ranges are derived from the probability distribution older than the current mean stand age.*

[c] *Post-bomb ^{14}C content is reported as $F^{14}C$ value.*

Parenthesis contains standard errors.

Table 2. Description of Natural Resources Canada (2009) DW Decay Classes

Attribute	Decay class				
	1	2	3	4	5
Wood texture	Intact, hard	Intact, hard to partly decaying	Hard, large pieces, partly decaying	Small, blocky pieces	Many small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging near ground, or broken	All of log on ground, sinking	All of log on ground, partly sunken
Twigs <3 cm (if originally present)	Twigs present	No twigs	No twigs	No twigs	No twigs
Bark	Bark intact	Intact or partly missing	Trace bark	No bark	No bark
Shape	Round	Round	Round	Round to oval	Oval
Invading roots	None	None	In sapwood	In heartwood	In heartwood

Figure 2. Wood buried at Cape Caribou V showing (**A**) the sampled Cape Caribou Va buried stem laying on the mineral soil surface in a more than 20-cm-deep organic layer, (**B**) large amounts of wood buried in the organic layer, and (**C**) 450-year-old wood from Va and Vb; the three left most samples are charred. In all the samples, annual growth rings and blocky wood structure are clearly visible.

all sites and was visible on the Cape Caribou Va sample (Figure 2). Ingrown fungal mycelia and roots were removed by hand from buried wood under a stereo microscope before individual wood fragments were selected for ^{14}C measurement.

^{14}C Measurement

From each 150 cm^3 stem sample, three or four small, randomly selected fragments of wood (about 100–200 mg each) were composited. Potential carbonate and humic acid contamination was removed from the composited wood by standard acid–base–acid pretreatment (65°C, 0.5 N HCl for 1 h, 0.5 N NaOH for 1 h, 0.5 N HCl for 4 h) at the ^{14}CHRONO Centre, Queen's University, Belfast. Samples were combusted to CO_2 at 900°C for 6 h in the presence of CuO and Ag in evacuated quartz tubes. An aliquot of CO_2 was cryogenically purified, then converted to graphite by hydrogen reduction for analysis by AMS. ^{14}C ages were calibrated to calendar ages using the IntCal04 curve and CALIB 5.1 (Reimer and others 2004; Stuiver and Reimer 1993). We report buried stem ages as years before excavation and measurement (before 2008 AD) and rounded off to the nearest decade. The buried wood sample Arrowhead IVc had greater than modern ^{14}C content (bomb carbon), and the calendar age corresponding to this level of ^{14}C was determined using CaliBomb (http://intcal.qub.ac.uk/CALIBomb/frameset.html).

RESULTS

The depth of the organic layer ranged from 17 to 25 cm (Table 1). The deepest organic layer was encountered at Cape Caribou V, which supported the oldest trees (204 ± 20 years). Arrowhead III and Arrowhead IV organic layer depth ranged from 17 to 21 cm deep under forests of similar age (146–148 ± 20 years). Portions of wood sampled from Cape Caribou Va and b were composed of small blocky pieces with clearly discernable wood structure (for example, rings; Figure 2) consistent with the description of wood of Decay Class 4 (Table 2).

The probability distributions for the ^{14}C-derived age of buried stems spanned 54–515 years before 2008, but were typically older than 200 years before 2008 (Table 1; Figure 1). Calibrated ^{14}C age uncertainties are particulary large between 50 and 380 years before 2008 owing to sharp increases and variable amounts of atmospheric $^{14}CO_2$ (Reimer and others 2004). To constrain age estimates, we conservatively assumed that buried DW is older than the living trees at these sites, and assigned a minimum age for buried stems at the current stand age. The median age of the remaining probability distribution, the constrained age, for each stem was between 240 and 450 years before 2008 (Table 1). Buried wood at the Cape Caribou V site was clearly very old, with some wood having been formed about 450 years ago. In contrast, the

Arrowhead IVc sample was found to contain anthropogenic bomb C (Table 1) indicating C fixed since 1952. Because this stem was located at the bottom of a well-developed 22-cm-deep organic layer in a stand with 148-year-old living trees, this sample is suspected to have been buried more than 50 years ago and subsequently contaminated with recently formed tissues, such as ingrown roots. If other stem ages were similarly influenced by younger C, then our ^{14}C-derived ages of buried wood are conservative. Well-preserved buried stems at old-growth black spruce sites in Labrador were likely fixed from atmospheric CO_2 200–450 years before 2008.

Discussion

Radiocarbon measurements, tree demographics, and the presence of stems and charcoal near the interface of the organic and mineral soils provide evidence that wood buried has been dead for 250–500 years (Figure 1). Such buried DW longevity is far longer than aboveground DW is expected to persist. Following stand replacing natural disturbance of mature balsam fir or black spruce in Newfoundland and Labrador, dead trees fall to become woody debris that typically decays and fragments completely within 70 years (Moroni 2006; Hagemann and others 2009). Buried wood dead for 250–500 years is indicative of DW preservation upon burial.

The ^{14}C ages of buried DW reflect the time since wood C was photosynthetically fixed from atmospheric CO_2, which our results indicate was up to 515 years before sampling. The average maximum lifespan of black spruce trees is about 200 years, but trees as old as 280 years have been reported (Fowells 1965; Vincent 1965). The oldest buried stems at Cape Caribou V have been dead for at least 170 years (450 years median age (Table 1)—280 years maximum black spruce age; Table 2), but probably not less than 250 years (450 years median age—200 years average maximum black spruce age). However, only wood removed from the center of the base of a buried tree would have been part of the living tree for its entire lifetime. At our study sites, all samples were taken from 10–15-cm-diameter horizontal-lying stems (Figure 2), that is, wood fixed sometime after the tree began to grow. In addition, buried trees of this stem size are not likely to have achieved their maximum age. Thus, buried trees from the Cape Caribou Va and b forests are likely to have been dead for more than 250 years and potentially as long as 515 years (Table 1).

Charcoal was identified on buried DW at all three sites, and was found on the surface of Cape Caribou V samples (Figure 2). Charred wood that is buried for centuries is indicative of significant original charring that likely resulted from intense stand-replacing fires that consumed the organic layer and allowed snags to fall to the mineral soil surface. These snags likely form much of the enormous abundance of buried wood encountered in the study sites (Table 1; Figure 1). The timing before present of the last stand-replacing fire at Cape Caribou V is clearly older than the age of the current forest (204 years). In addition, regeneration delays of decades are not unusual following intense fires in Labrador (compare Hagemann and others 2009). These forest dynamics support the ^{14}C-age evidence that buried wood has been dead for more than 250 years.

A surprising degree of preservation is required for wood that has been dead more than 250 years to remain at Decay Class 4 (Table 2). Further to this, rates of buried wood decay are likely slower than those indicated by this decay class and time since death, because DW probably decayed before it fell to the ground and became buried.

Snag longevity for black spruce is about 25 years in Labrador (Hagemann and others 2009) where a snag is likely to stand until it begins to lose structural integrity at approximately Decay Class 3 (Table 2). Once DW falls, burial appears to result from bryophyte groundcover overgrowth in Labrador (Hagemann and others 2009), a process requiring woody debris to make ground contact. Initially, fallen woody debris is often elevated from the forest floor and does not sag to the ground until it has significantly decomposed (Decay Class 3 or greater, Natural Resources Canada (2009); Table 2). Thus, even if DW fell relatively undecayed, it likely progressed to a higher Decay Class before burial. Cape Caribou Va and b samples likely progressed from Decay Class 1 to 3 in the first few decades following tree death as unburied DW, and from decay class 3 to 4 or higher in the following 2–5 centuries as buried wood.

In humid boreal forests, a combination of factors appears to favor enhanced preservation of buried wood including a cool growing season, high annual precipitation, microtopography that enhances moist conditions, a long fire-return interval, and vigorous bryophyte growth in the ground layer (Hagemann and others 2009). Bryophytes form a dense mat of groundcover in many boreal forests (Larsen 1980), which has been long recognized to decrease temperatures, increase moisture content, and reduce nutrient availability in soils (Tamm

1953; Oechel and van Cleve 1986). Vigorous moss growth is required to overgrow downed DW, which is further optimized in cool wet climates (Wilton 1964; Bisbee and others 2001). Microbial activity is slowed in cool conditions and wet bryophyte groundcover can further promote soil heat loss (Oechel and van Cleve 1986; Prescott and others 2000; Hermann and Prescott 2008). In addition, a wet organic layer can act as a fire retardant (Kasischke and Johnstone 2005; Manies and others 2005), increasing fire-return intervals and promoting DW preservation between fire events. Humid coniferous forests are common throughout the circumpolar boreal forests (Ahti and others 1968; Hämet-Ahti and others 1974; Ecoregions Working Group 1989) and at higher elevations south of the boreal biome (Clark and others 1998; Zielonka and Niklasson 2001). Thus, DW burial and long-term belowground persistence may be more common than previously considered. The presence or absence of a bryophyte ground layer and its associated characteristics may be overlooked as an important soil C stabilization factor (Swift and others 1979; Moore and others 1998; Prescott 2000).

In coniferous forests with small-diameter trees, DW is commonly reported to be a short-term C pool (for example, Moroni 2006). However, in cool humid coniferous ecosystems downed DW may become an important C store following burial. This mechanism and C pool have received little attention to date and the transfer of unburied woody debris stocks to buried DW has been previously attributed to decay and atmospheric flux. It may be important to consider the loss of aboveground DW habitat to burial in habitat availability studies (for example, for small birds in Labrador; Simon and others 2002), and to examine the role of buried wood as habitat for soil fauna or burrowing organisms, which to the authors' knowledge is yet to be described. We suggest that accounting for DW burial in black spruce forests and similar forest ecosystems would be a step toward accurate accounting and modeling of forest C cycles (Kurz and others 2009) in forests where buried wood is a potentially large and long-lived C pool.

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5 Synthesis and Discussion

5.1 Critical Review of Study Methodology

5.1.1 Site Selection

All selected sites are located within independent forest polygons distributed throughout Ecozone 6, Ecodistrict 452, with a maximum distance between sites of $<$50 km, and were selected based on a number of criteria: forest type, disturbance history, level of maturity at disturbance, and productivity range, thus decreasing between site variability. The relative proximity of the sites adds strength to comparisons between sites of different disturbance history, especially when compared with the geographical distribution of sites in other studies. For example, Sturtevant et al. (1997) examined WD in NL balsam fir-dominated forests following harvesting, sampling sites from western to central NL, and crossing recognized ecozones and climate gradients, and Krankina and Harmon (1995) examined dynamics of deadwood in Russian boreal forests by combining data collected from closed forests of medium to high productivity. The range in site conditions and subsequently the climatic and geological variability of this study is thus comparable to or lower than that of similar studies, aiming to minimize unavoidable but undesired site effects. Nevertheless, to ensure independence of observations, effects of clustering of the selected study sites were analyzed by introducing a clustering variable ('Forest Area') into the hierarchical nested linear mixed model analysis of deadwood stocks along the harvesting chronosequence (Hagemann et al. 2009). 'Forest Area' was not a significant explanatory variable, indicating that site clustering did not introduce artefacts.

One of the selected study sites featured a spatial mix of medium and poor site productivity classes (Echo Lake I; Table 3.2), possibly associated with lower live tree biomass prior to harvesting than at the other recently harvested sites. In consequence, deadwood, organic layer, and mineral soil C stocks were expected to be lower compared to the other sites of this stratum, because of lower input rates of dead organic matter. Collected C data of the Echo Lake I site reflected the expected differences, particularly with respect to organic layer, mineral soil, and total ecosystem C stocks (Hagemann et al. 2010c). This illustrates the long-term effect of site productivity on net primary productivity and biomass input into the DOM C pools (Kane et al. 2005), and subsequently the need to select study sites with more or less identical site productivity levels for studying the forest C cycle.

5.1.2 Chronosequence Approach

Chronosequences, i.e. series of similar sites differing in time since disturbance, are often used in ecological studies when investigating long-term temporal dynamics that are difficult to identify through short-term experiments at individual sites (Pickett 1989, Yanai et al. 2000, Fukami and Wardle 2005). Chronosequences created by direct space-for-time substitution are built on the assumption of site similarity with respect to all factors (Yanai et al. 2000, 2003; e.g., in this study, slope, climate, geology, soil type, and stand structure) but the factor being examined, i.e. time since disturbance (Diochon et al. 2009). The most serious limitation and source of error of this particular chronosequence approach is thus the effect of unknown variation in any of the above-mentioned factors on the temporal dynamics of interest (Yanai et al. 2000, Fukami and Wardle 2005). The weaknesses of direct space-for-time substitution may be counteracted by (i) site replication (spatial replication),(ii) resampling (temporal replication) or long-term observation, (iii) multi-region or multi-species comparison, and (iv) sampling design accounting for within-site spatial variability (Yanai et al. 2003, Diochon et al. 2009).

Chronosequences of forest stands are often not replicated due to a lack of comparable sites (e.g., Wang et al. 2003, Bond-Lamberty et al. 2004b, Howard et al. 2004, Bond-Lamberty et al. 2006, Boulanger and Sirois 2006, Czimczik et al. 2006); particularly sites supporting mature or old-growth stands unaffected by recent disturbances used as reference (Diochon et al. 2009). Benefiting from the remote location of central Labrador, this study was based on a threefold-replicated chronosequence of harvested stands and three replicates of old-growth reference stands. Three accessible and comparable burned sites corresponding to the recently and older harvested sites could not be identified, therefore limiting the originally planned post-fire chronosequence to three middle-aged burned sites. The site replication captured the spatial variability at the landscape level, thus reducing possible erroneous inferences from the chronosequence due to between-site differences. Within-site variability was captured by multiple replicates of all plots and transects.

Temporal replication, i.e. resampling of the chronosequence, or long-term observation of the study sites may be the most powerful tool to minimize errors related to the chronosequence approach (Fukami and Wardle 2005), but cannot be implemented within a 4-year project. In anticipation of follow-up studies, precise GPS coordinates of all sites have been recorded and selected study sites have been permanently marked to allow for resampling. An extension of the chronosequence to other ecoregions would also have exceeded the scope and resources of this study. However, the current study was developed as a counterpart to a similar chronosequence study of deadwood and C stocks in insular Newfoundland (Moroni 2006). Another study was recently completed in Nova Scotia (Moroni and Ryan 2010). Selected results of this study can thus be directly compared to more southerly ecoregions and to other species (e.g., balsam fir, sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.).

5.1.3 Buried Wood Sampling

The triangular-trench sampling design employed to assess buried wood abundance in the Hagemann et al. (2010a) study was based on the line intersect method originally developed by Warren and Olsen (1964), which is considered a reliable method for assessing downed linear structures such as woody debris (van Wagner and Olsen 1964, Affleck 2010). Various modifications of the original method have been tested, particularly with respect to the number, length, and layout of the transects (Marshall et al. 2000, Oehmichen 2007, Affleck 2010). It cannot be assumed that all woody debris orientation angles are equally present within a site, because windfall or logging may result in an orientation bias, i.e. a predominant direction of alignment (Marshall et al. 2003). van Wagner (1982) emphasizes that equilateral triangle transects with a random starting point and initial direction significantly reduce maximum errors due to orientation bias while minimizing walking distance during sampling. The application of a sampling methodology chosen in consideration of the characteristics of the studied ecosystem component (buried wood) rather than the NFI point-sampling method resulted in a significant reduction of the coefficient of variation from 77% (Hagemann et al. 2009) to 30% (Hagemann et al. 2010a), and thus reliable estimates of buried wood abundance.

5.1.4 Deadwood Respiration Measurements

Representative measurements of woody and buried wood respiration in the selected sites would ideally have included samples from all decay and size classes, which would have resulted in reduced replications or measurements spread over several days. Therefore, standardized sample pieces were used to minimize between-log variability and allowed for the detection of disturbance-induced differences in respiration. Although prior to sampling, all logs were classified as black spruce decay class 2 logs, wood densities calculated based on absolute dry weight (307–517 $kg\ m^{-3}$; data from Gleissner 2009) after measurements had terminated considerably exceeded the average density of NFI decay class 2 black spruce wood (340 $kg\ m^{-3}$; Natural Resources Canada 2010a). The range of wood densities determined for logs visually classified by several professionals as having the same decay status raises questions regarding the accuracy of visual decay classifications and their assessment attributes with respect to the representation of ther actual deadwood decay status (Brown 2002). Previously, Campbell and Laroque (2007) reported that the visually assessed decay status is not related to time since tree death, likely due to large variability in live wood density and/or the considerable heterogeneity of within-log decay progress observed by Pyle and Brown (1999). The use of *ex situ* standardized samples (e.g., non-decayed wood stakes or cellulose sticks) in future deadwood respiration studies may minimize between- and within-log variability of wood density and decay status, but will require long, possibly multi-year incubation times to allow for the colonization of sample logs by site-specific decomposer communities.

Woody debris respiration measurements themselves were an additional source of variability. First, the unearthing of buried wood sample logs was associated with changes in the CO_2 concentration gradient, because the air entrapped in organic layer pores (580–780 $\mu mol\ mol^{-1}$) features considerably higher CO_2 concentrations than ambient air (385 $\mu mol\ mol^{-1}$; PUMPANEN ET AL. 2003). A sudden increase in the CO_2 concentration gradient may result in short flushes of CO_2, i.e. high initial respiration rates (DAVIDSON ET AL. 2002). At the same time, buried wood sample logs are subjected to drastically warmer temperature regimes during measurement, which may artificially enhance respiration rates; an effect which becomes more pronounced with increasing measurement duration. As initially high respiration rates and subsequent tapering off were not observed in 5-minute test measurements, measurement duration was set to 3 minutes and logs were replaced in their original position as quickly as possible ('just-in-time') to minimize changes in log temperature and associated respiration artefacts.

Measurements of woody debris and buried wood respiration could not be conducted synchronously at all sites due to logistic constraints. Although the woody debris or buried wood plots of all strata were measured within one day, respectively, time of measurement introduced a measurement bias due to diurnal temperature dynamics. Sampling order of the three strata and the sites within the strata was therefore changed for each measurement date, aiming to ensure that each stratum was measured similar times in the morning (9:00–12:00 *h*), noon (12:00–15:00 *h*), or afternoon (15:00–18:00 *h*; GLEISSNER 2009). Bias due to sampling order was thus minimized, and a maximum range of environmental parameters (e.g., temperatures) was captured throughout the measurement season. Between-strata differences were likely enhanced on some dates while being masked on others. Significant differences between the strata are considered reliable and conservative, because the remaining time-of-measurement bias increased data variability, thus decreasing the likelihood of stochastic differences to be statistically significant. In order to clearly separate effects of disturbance history from sampling biases, 'Time of measurement' was included as an independent factor in the linear mixed model analysis, thus separating impacts of disturbance history and environmental variables from confounding impacts of measurement time.

5.2 Humid Boreal Forests - A Rare Ecosystem Group?

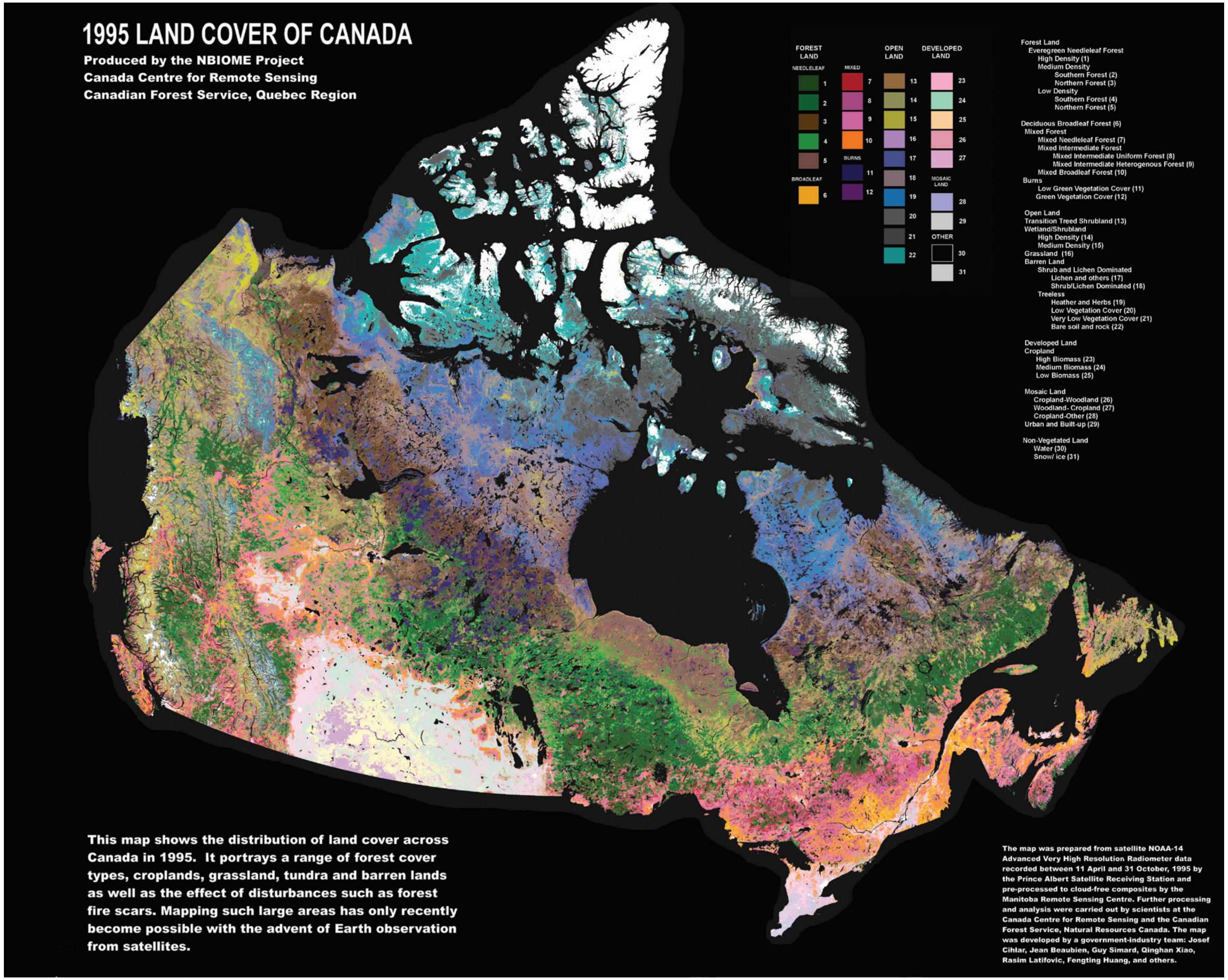
Results of this study show that more or less poorly drained humid black spruce forests in Labrador feature certain ecological processes, such as the bryophyte-driven burial of woody debris, which distinguish this forest type from other boreal and non-boreal forests. Certain moss species have been recognized as "ecosystem engineers" due to their controls on soil climate and decomposition processes (Shetler et al. 2008, Lindo and Gonzalez 2010) and receive increasing scientific attention (Vitt et al. 2001, Turetsky 2003, Harden et al. 2009, O'Donnell et al. 2009b). However, few studies in boreal forests have reported on buried wood (Brais et al. 2005, Manies et al. 2005, Moroni 2006), which was first observed in mountain forests dominated by yellow birch, red spruce (*Picea rubens* Sarg.), balsam fir, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; McFee and Stone 1966, Harvey et al. 1981, Lang et al. 1981). However, studies linking the presence of buried wood to the presence of vital bryophytes, climate, soil characteristics, or ecosystem type in general are lacking. The question thus arises as to how far the results of this study are applicable to other ecosystems within (e.g., forests dominated by balsam fir or jack pine) and outside (e.g., mountain forests) the boreal biome, and as to how far they can be extrapolated to a larger scale.

Independent of latitude, species composition, or soil type, some boreal forest types exhibit common features, such as an extensive ground cover of bryophytes, elevated organic layer and soil moisture contents. These are indicative of the occurrence of processes such as woody debris burial and/or paludification, thus justifying the classification of these boreal forests as a functional ecosystem group, i.e. a group of ecosystems from various ecoprovinces, ecoregions, or ecodistricts exhibiting similar dynamics (Environment Canada 2010b). The control of bryophytes on soil climate and decomposition dynamics takes effect mostly via elevated moisture levels (Turetsky 2003, Lindo and Gonzalez 2010). Hence, this functional ecosystem group could be termed "humid boreal forests", similar to the terminology used to describe the climate of the Labrador study sites as a perhumid, i.e. very humid, high-boreal ecoclimate (Environment Canada 2010b). A national Canadian forest ecosystem classification scheme is still under development (Natural Resources Canada 2010b). However, various provincial forest ecosystem classification systems exist (e.g., for Newfoundland and Labrador by Wilton 1964 and Meades and Roberts 1992), classifying the Canadian boreal forest into specific forest types based on vegetation and soil characteristics. Similarly, Russian spruce forests have been classified into five main spruce communities, of which the three most common ones feature continuous carpets of bryophytes as relevant ecological components (Sukachev 1928). However, to the author's knowledge, humid boreal forests are not a separately defined entity in any of these provincial, national, or international classification schemes, and potentially encompass various coniferous forest types across moist, wet, and very wet ecosystem series (e.g., Sukachev 1928, Meades and Roberts 1992).

Based on the results from Labrador and a comprehensive literature review, humid boreal forests may be tentatively defined as "**boreal forest ecosystems featuring a bryophyte-dominated ground vegetation layer associated with low soil temperatures, high moisture levels, low dead organic matter decomposition rates, and subsequently – in the absence of stand-replacing disturbances – an accumulation of buried wood embedded in a thick organic layer**". The following ecosystem characteristics could be possible parameters for refining this definition in the course of future research by means of quantitative classification thresholds:

- ▹ Ground vegetation: The ground vegetation layer of humid boreal forests is dominated by vital bryophytes, which alter the moisture and temperature regime of the organic layer and mineral soil, contribute considerably to ecosystem productivity, nutrient and C cycling, and decrease organic matter decomposition rates (HARDEN ET AL. 1997, TURETSKY 2003, LINDO and GONZALEZ 2010). Bryophytes are also components of less humid systems (LINDO and GONZALEZ 2010), possibly resulting in the occurence of bryophyte-driven processes outside of the boreal biome.
- ▹ Moisture regime: Humid boreal forests feature high organic layer and soil moisture levels resulting from (a) high annual precipitation, as typical of oceanous climates (e.g., Atlantic Coast of Canada and Norway), (b) poor soil drainage due to soil type or topography (e.g., podzols or Canadian Clay Belt), or (c) a combination of these, as found in Newfoundland and Labrador.
- ▹ Temperature regime: Humid boreal forests feature low mean annual temperatures resulting in short growing seasons, possibly discontinuous permafrost, moderate forest productivity, and dead organic matter accumulation (SWANSON ET AL. 2000, TURETSKY ET AL. 2005).
- ▹ Organic layer: As a result of the moisture and temperature regime and the presence of bryophytes, humid boreal forests feature a thick organic layer which, in the absence of large-scale disturbances, continuously accumulates, thus driving the paludification process and decreasing site productivity (SIMARD ET AL. 2007, 2009).

The studied black spruce sites in Labrador can thus be considered a typical example of the above-defined humid boreal forest ecosystem group, featuring high annual precipitation, low mean annual temperature, moderately well-drained podzols, bryophyte-dominated ground vegetation, and thick organic layers. It must be noted that certain mountain, i.e. oroboreal, forests may also feature the characteristics listed above (LANG ET AL. 1981, ZIELONKA 2006), and could therefore be considered humid boreal forests. Following an accepted definition of humid boreal forests as a functional ecosystem group, its distribution can be mapped and its national and global relevance evaluated in the context of land cover or C cycling. The parametrization of forest C models may be thus improved, and the implementation of management recommendations developed in consideration of the characteristics of this new ecosystem group can be initiated (e.g., HAGEMANN ET AL. 2010b).



This map shows the distribution of land cover across Canada in 1995. It portrays a range of forest cover types, croplands, grassland, tundra and barren lands as well as the effect of disturbances such as forest fire scars. Mapping such large areas has only recently become possible with the advent of Earth observation from satellites.

The map was prepared from satellite NOAA-14 Advanced Very High Resolution Radiometer data recorded between 11 April and 31 October, 1995 by the Prince Albert Satellite Receiving Station and pre-processed to cloud-free composites by the Manitoba Remote Sensing Centre. Further processing and analysis were carried out by scientists at the Canada Centre for Remote Sensing and the Canadian Forest Service, Natural Resources Canada. The map was developed by a government-industry team: Josef Cihlar, Jean Beaubien, Guy Simard, Qinghan Xiao, Rasim Latifovic, Fengting Huang, and others.

Figure 5.1: AVHRR Land Cover Map of Canada. *AVHRR Carte de la Couverture Terrestre du Canada* (Cihlar et al. 1995).

Humid boreal forests could be mapped based on a combination of climate and bryophyte distribution maps identifying ecosystems where bryophytes contribute considerably to ecosystem primary productivity (Peckham et al. 2009). However, bryophyte cover is not continuously estimated in most forest inventories, e.g., the Canadian NFI (Natural Resources Canada 2010a). Although differences in spectral properties between feathermosses and *Sphagnum* have been reported (Bubier et al. 1997), bryophyte mapping based on airborne sensors is still under development (Rapalee et al. 2001, Peckham et al. 2009). In Canada, the distribution of humid boreal forests can be approximated using the Advanced Very High Resolution Radiometer (AVHRR) Land Cover Map of Canada (Rapalee et al. 2001; Figure 5.1). Based on the descriptions of the AVHRR land cover classes (Steyaert et al. 1997), classes featuring a ground cover dominated by mosses can be identified and mapped, as previously done for the BOREAS Southern Study Area (Rapalee et al. 2001). For example, in Figure 5.1, bryophyte ground cover is associated with AVHRR classes 1–5, 7–9, and 13–15. Although insufficient spectral and spatial data resolution limits the applicability of the derived bryophyte distribution data at smaller scales, maps with a 1-km to 10-km resolution will provide crucial information for forest ecosystem modelling at regional and national scales (Rapalee et al. 2001, Peckham et al. 2009). The bryophyte distribution map could be further refined by incorporating digital elevation models and soil type or drainage maps, which add spatially explicit information on topography, wetland cover, permafrost distribution, and hydrological controls on vegetation (Bisbee et al. 2001, Turetsky et al. 2005). Despite limited fine-scale resolution, it is obvious that bryophytes cover large parts of the boreal landscape, e.g., more than 60% of the 11,298-km^2 BOREAS Southern Study Area (Rapalee et al. 2001), thus influencing C cycling at large scales (Lindo and Gonzalez 2010). A similar extent of bryophyte occurrence can be expected for Scandinavia and Russia, because the boreal biome is a mosaic of variably drained forests, upland forests, and true wetlands (Apps et al. 1993, Bhatti et al. 2006). Therefore, humid boreal forests are potentially an ecosystem group of global relevance with respect to land cover and C cycling (Bond-Lamberty et al. 2007a).

5.3 The Fate of Deadwood in Humid Boreal Forests

Deadwood dynamics are linked to the most important processes operating in forest ecosystems. Amounts and characteristics of deadwood depend on tree net primary productivity, mortality, and breakage due to self-thinning, senescence, and disturbances, while deadwood residence time is mainly influenced by deadwood characteristics such as species or dimensions, by climate, and by decomposer abundance and activity (Harmon et al. 2004, Laiho and Prescott 2004). A potential classification of humid boreal forests as a separate ecosystem group thus ought to be justified by deadwood dynamics that differ from those of other boreal forests, e.g., the accumulation of large amounts of buried wood.

5.3.1 Deadwood Creation

Forest diameter structure is likely more important in determining aboveground deadwood abundance than climate (Harmon et al. 2004, Hagemann et al. 2009). Small-treed old-growth and mature boreal forests throughout North America featured similar amounts of aboveground deadwood (Bond-Lamberty et al. 2003, Moroni 2006), while larger-treed old-growth forests in Scandinavia composed of Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*) contained considerably larger amounts of woody debris and snags (Linder et al. 1997, Siitonen et al. 2000, Karjalainen and Kuuluvainen 2002, Rouvinen et al. 2002). Abundance of aboveground deadwood in Labrador was in the lower range of values reported for old-growth boreal forests composed of similar-sized trees (Bond-Lamberty et al. 2003, Manies et al. 2005, Brais et al. 2005, Moroni 2006, Hagemann et al. 2009), because of the relatively low live tree biomass (Bhatti et al. 2003, Wang et al. 2003, Hagemann et al. 2010c) and the low stand density typical of Labrador black spruce, which is associated with the creation of very small amounts of deadwood in the course of self-thinning (Roberts et al. 2006).

Similar to other boreal forests, stand-replacing disturbances are the main drivers of deadwood creation in humid boreal forests, creating large amounts of deadwood in single events. Clearcut harvesting, for example, generally produces large amounts of <10 cm woody debris in small-treed boreal forests (Mattson et al. 1987, McRae et al. 2001, Moroni 2006, Hagemann et al. 2009). Contrarily, wildfire typically generates large amounts of snags which subsequently collapse, thus contributing to a peak of fire-generated woody debris 20–30 years after fire (McRae et al. 2001, Pedlar et al. 2002). Harvest-generated woody debris is generally smaller and shorter than woody debris originating from fire-generated snags (Densmore et al. 2004, Stevenson et al. 2006), which often retains little bark and features charred surfaces (Mackensen and Bauhus 2003, Manies et al. 2005). Differences in deadwood creation and its characteristics are thus more pronounced between disturbance types than between humid and other boreal forests.

5.3.2 Deadwood Reduction

In contrast, processes of deadwood reduction such as fragmentation, leaching, decomposition, and burial are influenced by disturbance and ecosystem type, i.e. by climate. Decomposition is a microbially-driven process that intensifies with increasing temperature (Boddy 1983a, Liu et al. 2006, Peng et al. 2008), resulting in generally lower deadwood decomposition rates in colder regions (Coûteaux et al. 1995, Kirschbaum 1995). Moisture has been identified as the second main driver of the decomposition process, inhibiting it at low and high moisture levels (Boddy 1983b, Progar et al. 2000, Jomura et al. 2008). Given similar temperature regimes and tree species, deadwood decomposition rates are therefore reduced where deadwood moisture content is either too low or too high to sustain the biological activity of a vital decomposer community (Griffin 1977, Boddy 1983b, Sollins et al. 1987, Chambers et al. 2001). For example, snags generally feature low moisture contents and thus low decomposition rates (Wei et al. 1997, Naesset 1999, Boulanger and Sirois 2006). Median snag falldown rates vary between 16 and 40 years regardless of ecosystem type (Lee 1998, Storaunet and Rolstad 2004, Aakala et al. 2008), but with a tendency towards lower falldown rates in dry post-fire conditions (Boulanger and Sirois 2006). At the other end of the moisture scale, respiration rates of moist to wet woody debris in old-growth Labrador humid boreal forests were lower than reported for similar but drier woody material in field and laboratory analyses at various temperatures (Wang et al. 2002, Bond-Lamberty et al. 2003, Hagemann et al. 2010b). In the absence of stand-replacing disturbances, humid boreal forests therefore likely feature lower deadwood decomposition rates than warmer and drier boreal forests.

Disturbances such as clearcut harvesting and wildfire alter ecosystem temperature and moisture regimes and thus the decomposition environment. Organic layer temperatures generally increase post-disturbance due to canopy removal, while moisture levels can increase due to lower plant transpiration (Elliot et al. 1998) or decrease due to higher evaporation (Londo et al. 1999), depending on factors such as forest type, aspect, or slope (McRae et al. 2001). Despite generally high ecosystem moisture levels, summer respiration of woody debris in burned Labrador black spruce forests was limited by high woody debris temperatures and moisture contents below the fibre saturation point (Hagemann et al. 2010b), reflecting increased forest floor temperatures and evaporation rates following canopy removal by wildfire (McRae et al. 2001, Jomura and Dannoura 2006). In drier boreal forest types, such as found in Alaska, this moisture-induced limitation of woody debris respiration is likely even more pronounced (Jomura and Dannoura 2006). Fire also changes the wood decomposability by charring the wood surface, which is subsequently transformed into a decay-resistant shell, i.e. “case-hardened”, due to below-fibre saturation moisture levels and excessively high air temperatures following fire (Marra and Edmonds 1996, Mackensen and Bauhus 2003, Manies et al. 2005). Although charcoal is very resistant to decomposition (Zackrisson et al. 1996, Kane et al. 2007), evidence of the effect of charring on the decomposition of woody debris is ambiguous (Shorohova et al. 2008). While decomposers that penetrated the charred wood surface through cracks may be favoured by increased wood temperatures (Mackensen and Bauhus 1999), wood desiccation due to increased evaporation limits decomposer activity, resulting in low decomposition rates of burned wood and/or bark (Shorohova et al. 2008). Woody debris decomposition rates in burned boreal forests may therefore be considerably lower than in comparable old-growth forests.

Clearcut harvesting also removes the forest canopy, resulting in higher forest floor and woody debris temperatures (McRae et al. 2001, Progar et al. 2000, Hagemann et al. 2010b). However, individual mature trees, tree regeneration, and vascular plants remaining on site provide shading and decrease wind movement (Keenan and Kimmins 1993), thus reducing the heating and drying of woody debris and the organic layer (Prescott et al. 2004, Devine and Harrington 2007, Moroni et al. 2009). The higher degree of preservation of the bryophyte layer during harvesting and its rapid recovery following harvesting also counteract the desiccation of woody debris by means of moisture retention, vertical and lateral water transfer, and moisture-induced cooling (Devine and Harrington 2007, Jomura et al. 2008, Hagemann et al. 2010a). In clearcut humid Labrador black spruce, post-harvest woody debris respiration rates were therefore significantly higher than in old-growth stands (Hagemann et al. 2010b). This effect will be less pronounced in drier boreal forests where woody debris is more likely to dry out due to lower ecosystem moisture levels. The impacts of disturbances on deadwood decomposition thus mainly depend on the disturbance type, but the magnitude of these effects differs between different ecosystem types depending on the prevalent temperature and moisture regime.

5.3.3 Bryophyte-driven Burial of Woody Debris

Aboveground woody debris stocks in humid Labrador black spruce stands not only decrease by the commonly acknowledged pathways of decomposition, fragmentation, and leaching (Mackensen and Bauhus 1999, Zhou et al. 2007), but also by bryophyte-driven burial (Hagemann et al. 2009, 2010a). Although woody debris burial is a poorly documented process (Section 4.6) that has been observed in boreal and oroboreal forests globally (McFee and Stone 1966, Harvey et al. 1981, Lang et al. 1981, Brais et al. 2005, Manies et al. 2005, Moroni 2006), evidence suggest that the burial process encompasses two phases: I) a considerable decrease in the woody debris decomposition rate and thus the initiation of preservation after its surface has been colonized by a thin layer of live moss (initialization phase), and II) the slow enveloping of woody debris in dead moss and tree litter as the organic layer accumulates (burial phase; Figure 5.2; Hagemann et al. 2010a).

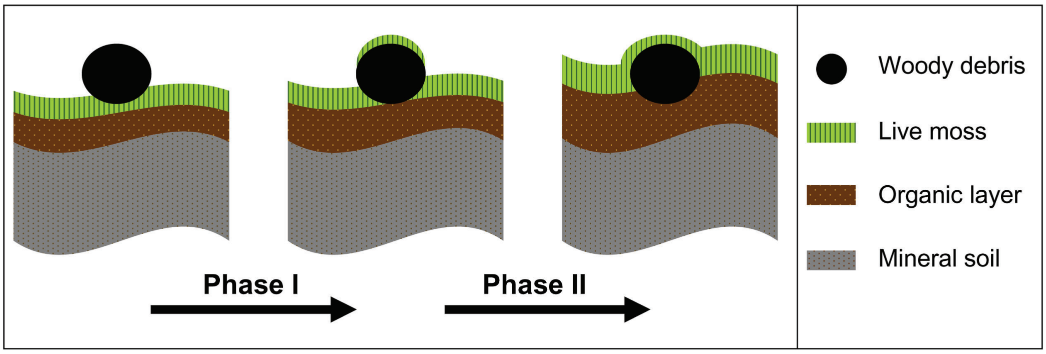


Figure 5.2: Simplified graph of the two phases of the woody debris burial process. *Illustration simplifiée des deux stages du processus de l'enterrement de bois mort.*

The occurrence of buried wood principally requires the presence of a vital bryophyte layer which can overgrow woody debris before it has completely decomposed (Hagemann et al. 2010a). Woody debris burial can thus occur only under temperature and moisture conditions that increase bryophyte growth and decrease woody debris decomposition rates to the point where bryophyte colonization and growth rates exceed woody debris decomposition rates. These conditions are typical of humid boreal forest ecosystems featuring expansive bryophyte ground cover, low decomposition rates, and paludification dynamics (PRESTON ET AL. 2006, SIMARD ET AL. 2009, LINDO and GONZALEZ 2010). However, they may also occur in other less cool and humid forest ecosystems outside of the boreal biome, resulting in different degrees of burial efficiency and buried wood preservation.

The efficiency of the burial process likely increases with increasing bryophyte productivity, decreasing decomposition rates, and increasing abundance of woody debris available for burial (HAGEMANN ET AL. 2010a, MORONI ET AL. 2010). The amounts of buried wood observed in Labrador humid boreal black spruce forests may thus be among the highest possible, due to the combination of low annual temperature, high moisture levels, low decomposition rates, high bryophyte productivity, and abundance of woody debris (HAGEMANN ET AL. 2010a). Ecosystems which are drier, warmer, or significantly colder will likely have less buried wood due to lower bryophyte productivity, higher decomposition rates and vascular plant dominance, or less abundant woody debris, respectively. Future studies should therefore investigate sites located along gradients of the most important factors determining occurrence and efficiency of woody debris burial, e.g., from humid to dry. In the absence of recent disturbances, the presence of large amounts of buried wood may thus help in defining humid boreal forests as a functional ecosystem group by means of quantitative temperature and moisture-related variables, because the presence of buried wood is indicative of bryophyte-regulated deadwood, organic layer and soil C cycles (BOTTING and FREDEEN 2006, SIMARD ET AL. 2007, TURETSKY ET AL. 2010).

The duration of buried wood preservation will likely also differ between ecosystems along temperature or moisture gradients. While buried wood preservation appears to be initiated by a live moss cover, the degree of preservation is expected to not only depend on temperature and moisture regimes, but also on disturbance frequency (HAGEMANN ET AL. 2010a, MORONI ET AL. 2010). Cool and moist organic layer conditions result in low buried wood respiration and decomposition rates (HAGEMANN ET AL. 2010a), and subsequently long-term accumulation and preservation of buried wood over several centuries (MORONI ET AL. 2010). Disturbances, however, may interrupt the process of buried wood accumulation, thus integrating the process of woody debris burial into the post-disturbance forest succession cycle (Figure 5.3). Stand-replacing fires, for example, can combust most of the live moss layer – particularly feathermosses – and a large portion of the organic layer and wood buried within it (SMITH ET AL. 2000, FENTON ET AL. 2005, HAGEMANN ET AL. 2010a).

Apart from regulating woody debris burial and preservation, bryophytes can also play a critical role in forest succession. For example, by lowering organic layer temperatures, bryophytes initiate the self-reinforcing paludification process leading from decreased decomposition rates to organic matter accumulation, elevated organic layer moisture contents, increased bryophyte productivity, and thus to lower organic layer temperatures; consequently resulting in lower tree density and a decline of forest productivity (FENTON ET AL. 2005,

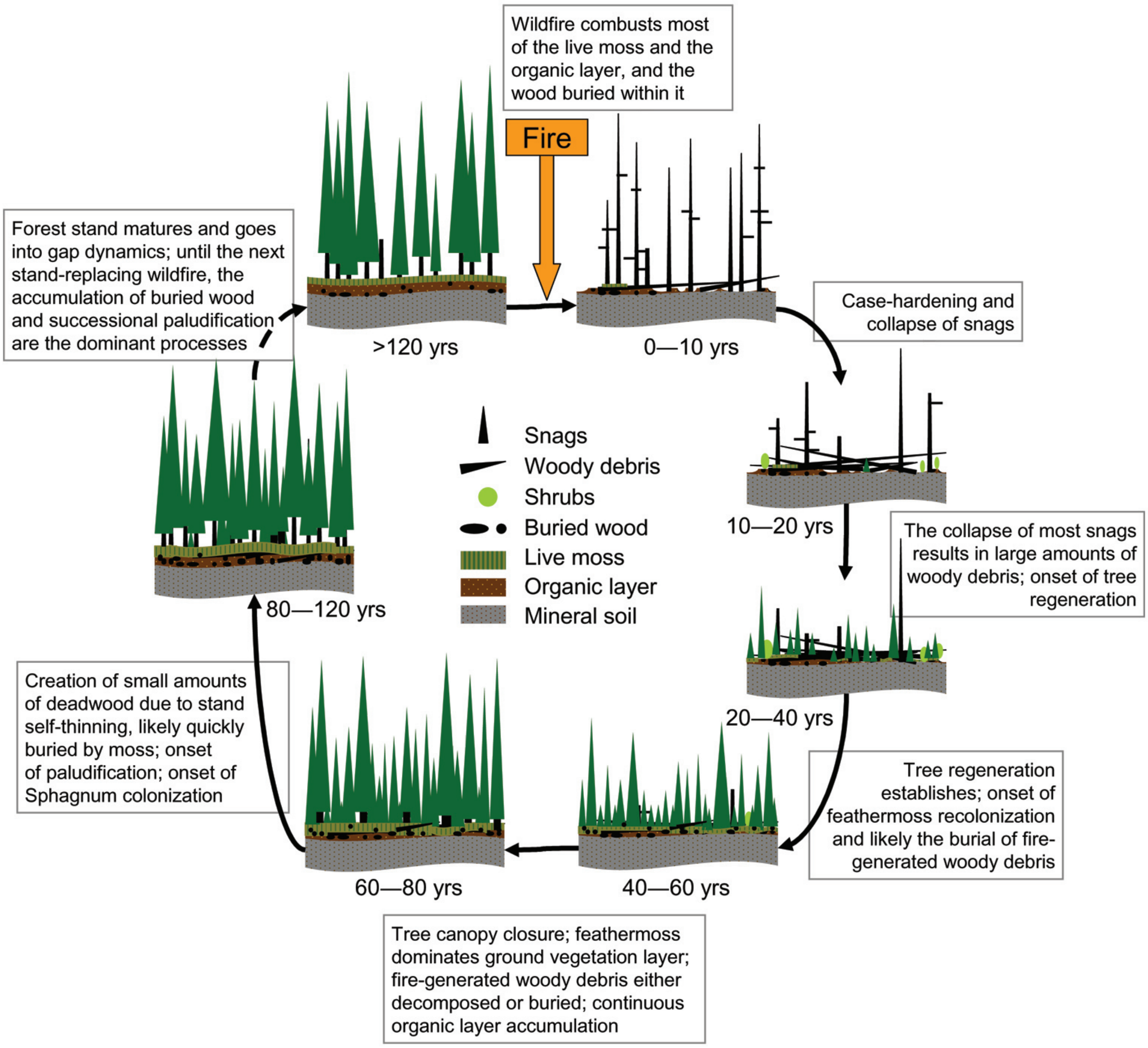


Figure 5.3: Simplified post-fire forest succession cycle and the accumulation of buried wood in humid boreal forests. *Cycle simplifié de la succession de forêt après feu et l'accumulation du bois enterré dans les forêts boréales humides.*

Simard et al. 2007, 2009). Moreover, bryophytes reduce organic layer consumption during wildfire by increasing organic layer moisture content, thus influencing seedbed conditions for post-fire tree reestablishment (Greene et al. 2007, Shetler et al. 2008). Potentially enhanced by charcoal (Wardle et al. 1998), feathermosses recolonize burned sites within 30–70 years following fire (O'Neill et al. 2006, Longton 2009), by trend faster under moist conditions (Kershaw et al. 1994). Fire-created woody debris can persist up to 70 years (Bond-Lamberty et al. 2003, Moroni 2006, Hagemann et al. 2009). Hence, large amounts of case-hardened woody debris are available for burial several decades following fire (Figure 5.3).

Following clearcut harvesting, moss cover and growth potentially recover within 5 years following harvest (Nguyen-Xuan et al. 2000, Fenton et al. 2003, Palviainen et al. 2005a). In Labrador, where post-harvesting woody debris moisture levels were sufficient for woody debris to support decay fungi, woody debris respiration rates were higher under warmer post-harvest than under pre-harvest old-growth conditions (HAGEMANN ET AL. 2010b). Higher woody debris decomposition rates post-harvest (PROGAR ET AL. 2000, HAGEMANN ET AL. 2010b) are thus balanced by a faster recovery of the bryophyte layer (PALVIAINEN ET AL. 2005a). Therefore, burial likely considerably contributes to the disappearance of harvest-generated woody debris in less than 50 years following harvest in humid Labrador black spruce (HAGEMANN ET AL. 2009). In humid boreal forests, the two dominant disturbance types therefore produce large amounts of woody debris available for burial, accumulation, and preservation over several fire return intervals (HAGEMANN ET AL. 2010a, MORONI ET AL. 2010).

5.4 Attributes of the Humid Boreal Forest Carbon Cycle

5.4.1 Bryophyte-regulated Carbon Dynamics

In addition to altering the deadwood cycle, bryophytes also significantly influence forest ecosystem C cycling by contributing to net primary productivity, sequestering C in highly recalcitrant litter, regulating soil climate, and influencing disturbance severity (TURETSKY 2003, MANIES ET AL. 2005, SHETLER ET AL. 2008, LINDO and GONZALEZ 2010, TURETSKY ET AL. 2010). Live bryophyte C stocks are generally small compared to total ecosystem C stocks (VOGEL and GOWER 1998, O'CONNELL ET AL. 2003). E.g., humid Labrador black spruce contained live moss C stocks of ∼0.7 Mg C ha^{-1} (Figure 4.2) vs. total C stocks of 186–280 Mg C ha^{-1} (HAGEMANN ET AL. 2010c).

Despite being a relatively small-sized C pool, the live bryophyte layer contributes considerably to the forest–atmosphere CO_2 exchange (GOULDEN and CRILL 1997, MORÉN and LINDROTH 2000, BOTTING and FREDEEN 2006, KOLARI ET AL. 2006), and has a disproportional effect on organic layer, buried wood, and mineral soil C stocks. By increasing moisture levels, decreasing temperature, and adding recalcitrant litter, bryophytes reduce organic layer and mineral soil decomposition rates (HOBBIE ET AL. 2000, O'DONNELL ET AL. 2009a, TURETSKY ET AL. 2010), thus determining patterns of soil C storage at landscape and regional scales (TURETSKY ET AL. 2005) and driving the accumulation of organic matter C in a “globally significant magnitude” (SIMARD ET AL. 2007, LINDO and GONZALEZ 2010). Consequently, organic layer C stocks in humid Labrador black spruce stands were in the upper range of values reported for drier and warmer boreal forests, and mineral soil C stocks of moderately well-drained black spruce forests in Labrador largely exceeded values observed in drier upland boreal forests (HOWARD ET AL. 2004, MARTIN ET AL. 2005). The effects of bryophytes on organic layer and mineral soil C stocks become more pronounced with deteriorating soil drainage, eventually resulting in the conversion of humid boreal forests to peatlands by progressing successional paludification (HARDEN ET AL. 2000, FENTON ET AL. 2005, SIMARD ET AL. 2009).

Apart from altering organic layer and mineral soil C stocks, bryophytes also initiate the formation of the buried wood C pool, which to date has been considered in few forest ecosystem C studies (Moroni 2006, Hagemann et al. 2009, 2010c). Buried wood C stocks may amount to more than half of organic layer C stocks (Hagemann et al. 2009, 2010c), thus likely contributing significantly to the humid boreal forest C budget at a larger scale. The aboveground deadwood C pool is commonly reported to be a short-term C pool in small-treed coniferous forests (Bond-Lamberty et al. 2003, Moroni 2006). In contrast, buried wood is a mid- to long-term C pool, because radiocarbon-derived ages of up to 515 years and lower respiration rates following bryophyte colonization of the wood surface indicate significantly slowed decomposition rates compared to unburied woody debris. Moreover, the moisture-retaining bryophyte layer acts as a fire retardant (Kasischke and Johnstone 2005, Shetler et al. 2008), thus promoting the accumulation of buried wood C over the course of several forest generations (Hagemann et al. 2010a, Moroni et al. 2010). Accounting for woody debris burial will likely improve the accuracy of C accounting in ecosystems featuring low mean annual temperatures, high ecosystem moisture levels, a long fire-return interval, and vigorous bryophyte growth, i.e. in humid boreal forests.

5.4.2 Carbon Modelling of Humid Boreal Forests

The particularities of the humid boreal forest C cycle, i.e. the bryophyte-regulated accumulation of buried wood, organic layer, and mineral soil C, are not adequately captured in current forest ecosystem C models (Section 2.2.3; Bond-Lamberty et al. 2007a, Simard et al. 2007). Default CBM-CFS3 estimates, for example, attributed the reduction of woody debris C stocks to decomposition and atmospheric flux instead of transfer to buried wood C and considerably underestimated organic layer and mineral soil C stocks in humid Labrador black spruce (Hagemann et al. 2010c). Similarly, the dynamic soil model YASSO largely underestimated soil C stocks in Norway, because differential decomposition rates due to high soil moisture levels in the subsoil were not accounted for (de Wit et al. 2006). Given the ecological evidence provided in the previous sections, the interactive effects of bryophytes, temperature, and moisture on forest ecosystem C pools must be considered to more accurately model humid boreal forest C dynamics.

Water table, flow, and drainage could be introduced into forest C models from traditional wetland models such as the Peatland Carbon Simulator (PCARS; Frolking et al. 2002). However, these models require large sets of spatially explicit parameters that are often not available for forest ecosystems (Bond-Lamberty et al. 2007a). Instead of modelling water table depth and its effects on organic layer and mineral soil DOM decomposition, soil type-specific dead organic matter decomposition rates may considerably improve model estimates of soil C stocks (Shaw et al. 2008) while balancing the typical modelling tradeoff between accurate complexity and uncertain simplicity (Bond-Lamberty et al. 2007a, Kimmins et al. 2008).

Similarly, forest C models may not need to include the small-sized bryophyte C pool as a separate pool, which would be difficult to parameterize due to extensive uncertainties with respect to the growth rates of various functional bryophyte groups under various moisture and light regimes (Turetsky et al. 2010). Rather, for the CBM-CFS3 and other models, the presence of a vital bryophyte layer in a given forest ecosystem could be captured by adding a bryophyte module, which regulates the transfer of woody debris C to a newly introduced buried wood C pool, reduces organic layer and mineral soil decomposition rates, and potentially decreases tree growth rates and the likelihood of wildfire occurrence with simulated time since disturbance (Simard et al. 2007, 2009, Hagemann et al. 2010c).

The suggested alterations of existing forest C models such as the CBM-CFS3 can only be implemented based on adequate field data and sufficient understanding of the ecological processes. As woody debris burial is a poorly-documented process, knowledge about the underlying mechanisms, the chemical properties of buried wood, and the dynamics of the buried wood C pool is limited (Harvey et al. 1981, Klinka et al. 1995, Hagemann et al. 2010a, Moroni et al. 2010). The impacts of climate change and the associated changes in natural and anthropogenic disturbance regimes (Section 2.1) on the long-lived buried wood C pool and on the bryophyte layer that regulates buried wood dynamics are of particular interest. As temperatures rise, the recovery of bryophytes following harvesting may take longer due to increasing desiccation (Preston et al. 2006), thus possibly resulting in higher CO_2 emissions from decomposing harvest residues (Chertov et al. 2009). At the same time, fire frequency and intensity are predicted to rise (Burton et al. 2003, Flannigan et al. 2005, Bond-Lamberty et al. 2007b), potentially combusting a larger portion of the C stored in the organic layer and wood buried within it. Based on adequate data, forest C models may be used to simulate the effects of climate change and altered disturbance regimes on buried wood and and other forest C pools, thus offering the opportunity to develop forest management strategies aimed at minimizing C losses from and maximizing C sequestration in humid boreal forests.

5.5 Conclusions

The estimation of the global forest C balance for purposes of policy development relies on accurately modelled estimates of C fluxes and pools, which in turn must be based on field-measured data from various forest ecosystem types (Chen et al. 2000, Smith and Heath 2001). This study has investigated all major forest C pools in old-growth and disturbed high-latitude boreal forest ecosystems that have rarely been the focus of scientific research despite being considered highly sensitive to climate change (Davidson and Janssens 2006). The comprehensive C stock data set of the studied forest stands was used to evaluate the CBM-CFS3, a national-scale C budget model, with respect to its applicability to Labrador black spruce forests and other forest types of the (yet to be defined) functional ecosystem group of humid boreal forests. While tree and aboveground deadwood C dynamics of Labrador black spruce were similar to those of drier or warmer boreal forests, processes related to the C cycle of the bryophyte-dominated ground vegetation, the organic layer, and the mineral soil differentiate these humid boreal forests from other forest ecosystems. In particular, the large amounts of buried wood observed in the studied stands were not captured by the CBM-CFS3, an indication of the existence of little-studied ecological processes, e.g., woody debris burial, which are not incorporated in current forest C models.

In terms of C modelling, the burial of woody debris by vigorously growing bryophytes corresponds to a transfer of C from the relatively short-lived aboveground woody debris C pool to a potentially very long-lived C pool, which is embedded in the organic layer C pool and currently not assessed by most forest C inventories. Buried wood is thus also not included in current forest C models, despite its potentially high abundance throughout large parts of the boreal biome. The site-specific combination of factors that favour vigorous bryophyte growth while limiting decomposition rates (e.g., low mean annual temperatures, short growing seasons, high ecosystem moisture levels due to high precipitation and/or insufficient drainage, and long fire return intervals) determines the degree to which the woody debris burial process operates in forest ecosystems. Basically, the burial of woody debris is conditional upon the presence of a vital bryophyte layer that can overgrow downed woody debris before it has entirely decomposed. Similar to the paludification process (Simard et al. 2009), bryophytes are therefore the key driver of the woody debris burial process.

Bryophytes are not only the most common ground cover type in boreal forests, but are an integral component of many coniferous forest systems outside the boreal biome (Lindo and Gonzalez 2010), having formed partial interdependencies with individual coniferous tree species (Carleton and Read 1991, Kershaw et al. 1994). Many carpet-forming bryophytes feature a high photosynthetic light-use efficiency (Whitehead and Gower 2001), thus thriving in well-shaded conditions below year-round foliated coniferous canopies (Kershaw et al. 1994, Vogel and Gower 1998, Bisbee et al. 2001). Buried wood may thus not only be common in the circumpolar boreal forest and at higher elevations south of the boreal biome where bryophytes dominate the ground vegetation layer, but potentially also occurs in micro-habitats of mixed forests where micro-climatic conditions are favourable for bryophyte growth and limit deadwood decomposition, e.g., on leaf-litter free hummocks, logs, and around tree bases (Kershaw et al. 1994). The bryophyte-driven burial of woody debris and the associated sequestration of C in a long-lived buried wood C pool thus likely occur over a wider range of environmental conditions than previously expected (Figure 5.4) and potentially are significant to the global C cycle.

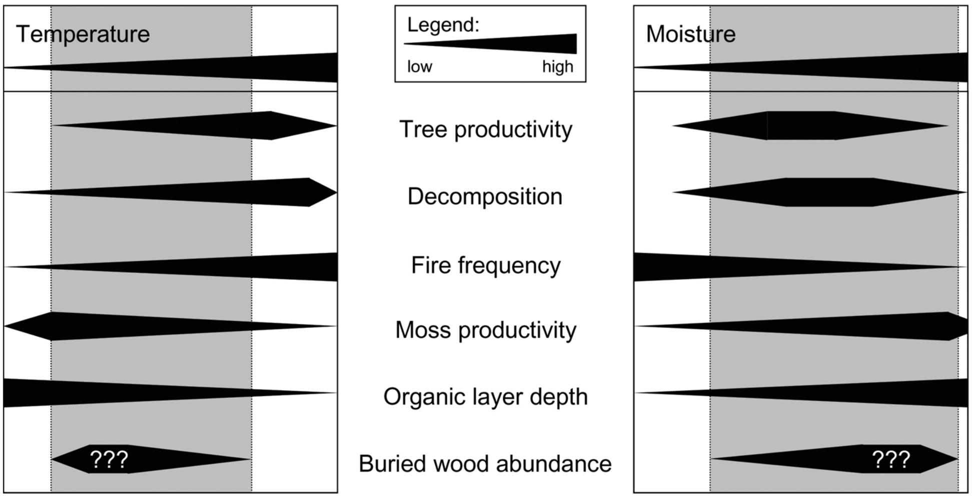


Figure 5.4: Potential occurrence of buried wood (shaded) with respect to temperature, moisture, and selected variables (schematic). *Occurrence potentielle du bois enterré (ombré) au niveau de la température, l'humidité et d'autres variables selectionnés (schématisé).*

The contribution of the buried wood C pool to the global forest C budget can be assessed once the distribution of forests with bryophyte-regulated deadwood, organic layer, and mineral soil C dynamics has been determined. However, in light of changing climate and disturbances regimes, the dynamics of the buried wood C pool and the bryophyte layer regulating its magnitude will be more important than their static magnitude. The balance between bryophyte growth and wood decomposition required for buried wood formation and preservation to occur is closely associated with forest temperature, moisture, and disturbance regimes, which are affected by climate change, particularly at higher latitudes (Malhi et al. 1999, IPCC 2007, Kurz et al. 2008a). As a result of increased mean annual temperatures, the transition zone between boreal conifer and deciduous forests is expected to shift north (men hapin III et al. 2000, Soja et al. 2007, Bonan 2008), likely reducing bryophyte ground cover due to the increased input of moss-smothering leaf litter and unfavourable light conditions during winter (Kershaw et al. 1994). Also, organic layer and buried wood decomposition rates may be enhanced (Davidson and Janssens 2006), potentially releasing large amounts of CO_2 to the atmosphere. Small changes of the forest micro-climate may thus result in significant changes of bryophyte growth and dead organic matter decomposition, and thus possibly altered forest CO_2 emissions. At the same time, however, the northern limit of the boreal forest zone is also expected to shift north due to altered temperature and moisture regimes (Soja et al. 2007, Bonan 2008), potentially expanding the area of bryophyte-dominated forest ecosystems.

The likelihood and magnitude of changes in forest CO_2 emissions from bryophyte-regulated forest ecosystems due to changing climate and disturbance regimes may be determined using C budget models. However, the uncertainties of these models with respect to the so-called secondary effects of climate change (e.g., increased growing season length, CO_2 fertilization, or shifting water table) are very large. The insufficiently quantified contribution of ground vegetation to the global C budget has also been identified as a major limitation to accurate forest C modeling (SELLERS ET AL. 1997). As the C balance (sink or source) is calculated as the relatively small difference between several large C fluxes, its value may be considerably exceeded by these uncertainties (CHEN ET AL. 2000). In addition, existing models are of limited use for modelling forests with bryophyte-regulated buried wood, organic layer, and mineral soil dynamics, because the impacts of bryophytes are currently not accounted for in most C budget models (BOND-LAMBERTY ET AL. 2007a). The adaptation of forest C models to more accurately reflect C dynamics of bryophyte-regulated forests is thus a major challenge.

Future research therefore needs to investigate the interaction between climate, bryophytes, and the forest C cycle. Based on current scientific knowledge, Figure 5.4 schematically illustrates relationships between selected variables and temperature or moisture, respectively. However, numerous other factors such as topography, light regime, or tree species composition interact with the shown variables in a highly complex biophysical system. In addition, the relationships between these environmental variables are not overlapping in two dimensions, but their interactions are spatially explicit and three dimensional, thus further contributing to uncertainty in forest C stock estimates (SMITH and HEATH 2001). Investigating individual processes such as woody debris burial by studying the interaction between climate, moss productivity, and buried wood abundance by means of temperature and moisture gradients will likely provide important impulses to improve the accuracy of forest C models. In light of climate change, it should particularly be a research priority to understand how bryophyte productivity and decomposition constraints will change with increasing temperature and varying moisture regimes. This understanding will allow for the identification of ecosystems such as humid boreal forests with the risk of potentially high C losses to the atmosphere, and the subsequent development of counteractive management strategies.

5.6 Condensed Research Perspectives

While the research objectives of this study formulated in Section 2.5 have been fully addressed, study results have led to numerous other research questions. The following presents an overview of issues that are insufficiently investigated and need to be addressed by future research (Figure 5.5).

▷ Buried wood

- Sampling: Inventory methods such as point sampling or trenching are unsatisfactory with respect to either data accuracy or sampling time and effort, respectively (Hagemann et al. 2010a). Alternative, possibly non-destructive sampling techniques are required and could greatly facilitate accurate and efficient quantification of buried wood, particularly for purposes of C modelling.
- Ecology: The loss of aboveground woody debris to burial may reduce habitat availability for certain species (e.g., Simon et al. 2002). At the same time, buried wood may serve as habitat for a wide range of soil fauna and fungi, a yet uninvestigated function of buried wood (Hagemann et al. 2010a, Moroni et al. 2010).
- Mechanisms of creation: The physical and chemical processes occurring that are initiated when the wood surface is colonized by mosses need to be investigated in more detail to better understand the associated decrease in woody debris decomposition rates (Phase I; Hagemann et al. 2010a). The accumulation rate of the organic layer, i.e. the balance of dead moss and tree litter input and decomposition rates, may help to determine woody debris burial rates (Phase II).
- Preservation: Radiocarbon-dating of selected buried wood samples from various depths can provide further information about the origin, the stratification, and the preservation of buried wood (Moroni et al. 2010).
- Disturbances: The impacts of disturbances such as wildfire and clearcut harvesting on amounts, characteristics, and dynamics of buried wood are largely unknown (Hagemann et al. 2010a).
- Climate change: Rising temperatures will increase forest floor temperatures and decrease bryophyte vitality and forest floor moisture content (Preston et al. 2006, O'Donnell et al. 2009b), thus potentially increasing buried wood decomposition rates and subsequently forest CO_2 emissions while decreasing the input of new buried wood due to decreasing bryophyte productivity.

▷ Bryophytes

- Sampling: Numerous methodologies exist for sampling bryophyte growth, e.g., cranked wire (Clymo 1970), mesh screen ingrowth (Gower et al. 1997, Vogel and Gower 1998), innate growth markers (Russell 1988, Oakland 1995), nylon thread markers (Asada et al. 2003), oil paint markers (Pouliot et al. 2010), fluorescent dye (Russell 1988, Harden et al. 2009), or gas exchange measurements (Russell 1988, Botting and Fredeen 2006), but not all of these methods have been compared exhaustingly. Advantages and disadvantages and the applicability of these methods to various functional moss groups or individual moss species need to be investigated further.

- Distribution: The distribution of forests with ecologically-relevant bryophyte layers needs to be determined by a) appropriate inventories, b) estimation based on factors such as forest type or drainage, or c) remote sensing methods (Rapalee et al. 2001, Preston et al. 2006, Peckham et al. 2009).
- Productivity: Although the available dataset on moss growth is currently increasing (Harden et al. 2009, Turetsky et al. 2010), information on the relationship between moss growth and various factors such as soil type, climate, or stand density is insufficient to adequately model moss productivity at large scales.
- Decomposition: While mass loss rates of certain bryophyte species or groups have been studied in different boreal ecosystems (Hobbie 1996, Moroni et al. 2005, Turetsky et al. 2010), reasons for the generally low decomposability of bryophytes still remain partially unclear (Preston et al. 2006). Potential causes include low nitrogen content and high content of phenolic compounds and structural carbohydrates (Lindo and Gonzalez 2010).
- Disturbances: The effects of disturbances such as wildfire or harvesting on the composition of the bryophyte layer have been studied (e.g., Fenton et al. 2003, Palviainen et al. 2005b). Little is known, however, about the impact of disturbances on the regulatory ecosystem functions of the bryophyte layer.

▷ Carbon modelling

- Bryophytes: The interactive effects of bryophytes, temperature, and moisture on forest ecosystem C pools must be introduced into forest C models to more accurately model humid boreal forest C dynamics (Bond-Lamberty et al. 2007a, Hagemann et al. 2010c).
- Buried wood: This mid- to long-term C pools needs to be accounted for in forest C models, e.g., by (a) developing a bryophyte module regulating the decomposition rates of woody debris, organic layer and mineral soil, (b) calibrating a woody debris to organic layer C pool transfer rate based on field-measured rates of moss growth and woody debris burial and modifying organic layer decomposition rates in humid boreal forests based on field-measured decomposition rates of buried wood, or (c) introducing a buried wood C pool (Hagemann et al. 2010c).

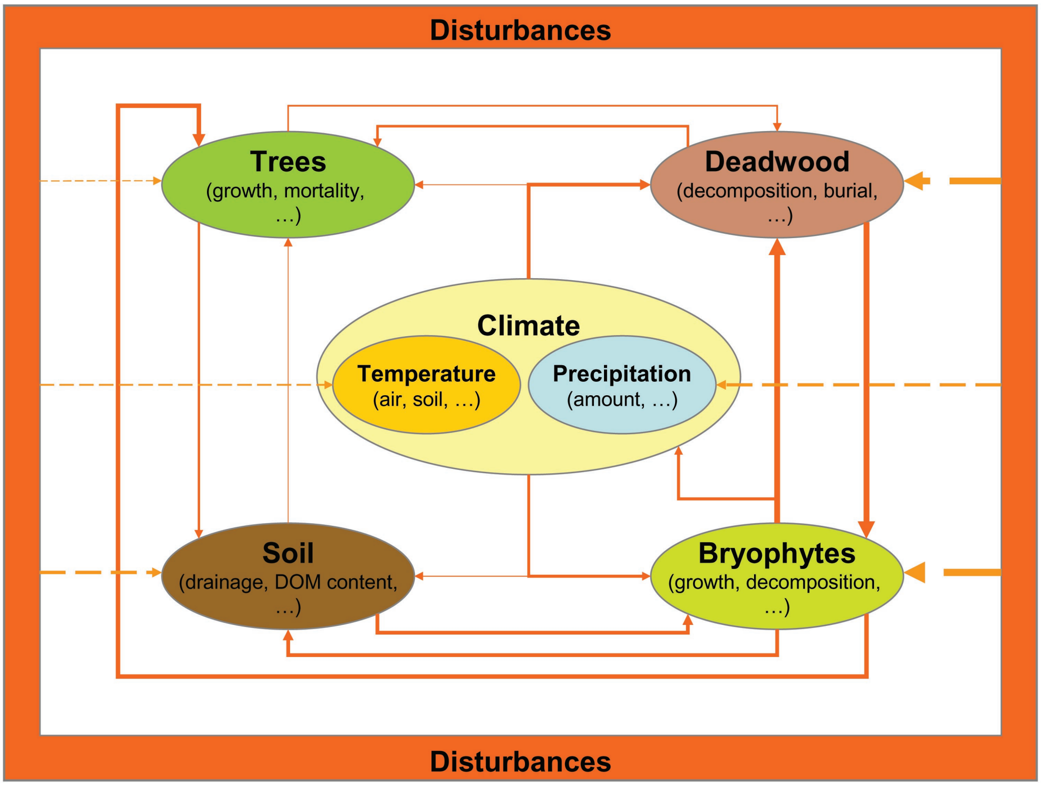


Figure 5.5: Knowledge gaps in humid boreal forest ecosystems. Wider arrows indicate larger lack of knowledge. *Les lacunes des forêts boréales humides. Des flèches plus larges démontrent des lacunes plus grandes.*

- Soil: In light of climate change, research is needed regarding the interaction between bryophyte-dominated organic layers, the temperature, and the moisture regime of the soil profile (Chertov et al. 2009), which determines the degree of C sequestration in boreal forest soils (Carrasco et al. 2006).

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Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskriptes habe ich Unterstützungsleistungen von folgenden Personen erhalten:

> Cindy Henderson; Analytical Services Laboratory, Canadian Forest Service (Laboranalysen)
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Weitere Personen waren an der geistigen Herstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater(s) in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

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