The Influence of Selection Silviculture Biomass Harvesting on Soil Carbon, Nutrients, and Respiration in a Northern Mixed-Deciduous Forest

by

Jason Allen Shabaga

A thesis submitted in conformity with the requirements for the degree of Doctorate of Philosophy
Department of Geography
University of Toronto

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Abstract

Concerns have been raised about soil fertility following increased recovery of biomass in northern mixed deciduous forests. Several studies suggest that biomass extraction and enhanced decomposer activity can lead to losses of soil C and nutrients, increased nitrification, and reduced soil CO₂ efflux (FCO₂) from compaction and root senescence. However, results are inconsistent; differences may be linked to insufficient investigation and characterisation of variability in forest structure, silvicultural methods, and intensity and heterogeneity of disturbances. Without a comprehensive understanding of how soil biogeochemical processes respond to different types and intensities of harvesting disturbances, we cannot accurately predict losses and ecological sustainability of harvesting. My thesis tests this by evaluating changes to forest structure and various soil edaphic and physical properties following tree-length (TL) and more intensive biomass selection-harvests for 3 years and on primary and tertiary skid trails.

Several metrics of forest harvesting intensity were correlated to higher post-harvest FCO₂ rates and losses of soil and dissolved soil organic C (SOC/DOC), K⁺, and NH₄⁺. Increased canopy openness and soil temperatures accounted for 34-41% of elevated FCO₂. Woody debris inputs and SOC/DOC losses
correlated to higher autumn FCO₂ rates and NH₄⁺ losses, while harvested tree biomass correlated to lower summer rates and higher nitrate concentrations. Primary skid trails had low SOC/nutrient concentrations and FCO₂ from compaction and inhibited regrowth, potentially functioning as C sources. Biomass harvesting halved woody debris inputs relative to TL harvesting; otherwise, short-term treatment differences were nominal. However, estimated base cation losses through additional biomass recovery may produce net long-term soil depletion not observed in conventional harvesting.

These results support my hypotheses that harvesting increased decomposer and nitrification activity, losses of C and nutrients, and that harvesting and trail use intensity can potentially predict these changes. Ecosystem-scale projections of forest C and nutrient storage that do not distinguish between spatiotemporally variable source/sink components (e.g. skid trails, harvested forest) may not effectively estimate changes. Combined with a detailed mensuration of pre/post-harvest forest structure and environmental covariates, future studies that representatively sample these different areas may improve our ability to predict system responses to disturbances.
Acknowledgements

First and foremost I’d like to thank my supervisor, Nathan Basiliko. When I say that you’ve been a kind, generous, and patient supervisor, this is a terrible understatement. Thank you so much for everything you’ve given over the years, whether it be your generous financial and moral support, ceaseless enthusiasm, plethora of ingenious ideas, or boundless patience for a finished product well beyond my expected expiry date. You gave me plenty of much needed space to work out things for myself, yet always made yourself available on short notice for consultation whenever I needed it, even after you left for a different institution. In doing so, you provided great mentorship at the academic, professional, and even personal levels. Thank you.

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<th>Description</th>
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<td>BA</td>
<td>Basal area</td>
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<tr>
<td>CWD</td>
<td>Coarse woody debris</td>
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<tr>
<td>DWD</td>
<td>Downed woody debris</td>
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<td>FWD</td>
<td>Fine woody debris</td>
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Soil Respiration

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<td>FCO₂</td>
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<td>Rₛ</td>
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Soil Chemistry

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<tr>
<td>DOC</td>
<td>Dissolved organic carbon</td>
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<td>DOM</td>
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<td>DON</td>
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<td>SOC</td>
<td>Soil organic carbon</td>
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<td>SOM</td>
<td>Soil organic matter</td>
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Miscellaneous

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Description</th>
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<tr>
<td>LFH</td>
<td>Litter/fermented/humic horizon</td>
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<td>LMM</td>
<td>Linear mixed model</td>
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<td>ln</td>
<td>Natural log</td>
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<td>GPP/NPP</td>
<td>Gross/Net primary production</td>
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<td>PCA/PC</td>
<td>Principal component analysis/principal component</td>
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<td>TL/BIO</td>
<td>Tree-length/biomass harvesting treatment</td>
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Chapter 1
Introduction

1.1 Background and Justification for the Study

Forests cover one third of global land area and account for 55% of terrestrial net primary production (NPP), sequestering ≈34 Pg of C annually as biomass (Saugier et al., 2001). Wood and other forest products are integral to the commerce and culture of many societies, providing raw materials for construction and consumer goods, industry feedstocks, heat energy, and food supplies. Forests also provide ecosystem services such as habitat, filtration and storage of freshwater, biogeochemical cycling and storage of nutrients, and influencing regional climate patterns (Chapin, et al., 2002). Historically, intensive deforestation has resulted in substantial losses of aboveground biomass and soil organic matter (SOM), primarily as carbon dioxide (CO$_2$) emissions to the atmosphere. A 20% loss of global forest area since 1850 accounts for almost 90% of total estimated land-use C emissions, contributing half as much to atmospheric CO$_2$ inputs as fossil fuel use (Houghton, 1999, 2003). Patterns of land-use have changed in recent decades, and global forests now provide an average net annual sink of 1.11 Pg of C (Pan et al., 2011). Approximately 65% of this can be attributed to afforestation and improved management strategies in temperate forests of the northern hemisphere (Caspersen et al., 2000; Houghton, 2003; Pan et al., 2011).

The value of effective management strategies to maintain forest productivity, ecosystem health, soil C and nutrient storage, and sustainable harvesting cannot be understated, particularly in an era threatened by freshwater shortages, excess nitrogen deposition, and growing atmospheric CO$_2$ levels, contributing to climate change (Vitousek et al., 1997). Yet outcomes are highly variable, difficult to gauge, and subject to considerable disagreement amongst stakeholders and researchers (Johnson and Curtis, 2001; Luyssaert et al., 2010; Thiffault et al., 2011; Naudts et al., 2016). Approaches vary based on factors such as forest type, regional and local environmental conditions, management goals, economic cycles, and legislation and compliance. Furthermore, forest management is only beginning to consider the impact of use on soil C storage and nutrient retention capacity. Soils serve as the primary reservoir of nutrients and contain two-thirds of all carbon stored in temperate forests, underpinning the productivity of these ecosystems (Houghton et al., 2003). However, the relative contribution of accumulating soil C in afforested areas to ecosystem scale C storage has been much smaller than for
biomass, and the underlying dynamics less clear (Caspersen et al., 2000; Houghton, 2003). The availability of various nutrients and growth factors are in large part dependent on the condition of the soil and internal nutrient cycling processes. Disturbances such as removal of biomass and disruption to soil structure can fundamentally change these factors, potentially undermining the long-term sustainability of commercial forestry and forest ecosystem health.

Enhanced extraction of previously un-merchantable forest biomass for use in non-traditional markets has raised concerns about long-term ecological sustainability (OMNR, 2009; Richter et al., 2009; Janowiak and Webster, 2010; Zhang et al., 2010; Thiffault et al., 2011). Our current state of knowledge on the effects of harvesting intensity and biomass removal on soil health, structure, and fertility is under-developed (Vance, 2000; Laporte et al., 2003; Heckman et al., 2009). Contradictory results from several studies in varying temperate forest regions reveal a poor mechanistic understanding of factors contributing to SOM and nutrient accumulation and losses, which are likely linked to regional and localised differences in soil properties, forest ecosystem dynamics, and silvicultural methods. Without being able to connect these to biogeochemical processes, we are unable to predict the sustainability of intensified harvesting on long-term forest productivity and soil C storage. With a growing global interest in wood biomass utilisation for energy and other markets, and an emphasis on utilising C storage in ecosystems as a component in regional C emission budgets, more focus needs to be placed on assessing the current status of soil health and fertility and the impacts of disturbances on long-term health.

In this dissertation, I attempt to address several questions related to the impact of forestry operations on soil fertility and health by assessing changes to soil biogeochemistry following tree harvesting related disturbances to forest soils and ecosystems. I then define hypothetical disturbance-based mechanisms influencing known biogeochemical processes that may account for these effects. In chapters 2 and 3, I contrast the effects of two different partial-harvesting prescriptions with an unharvested control treatment on post-harvest changes to the rate of CO₂ efflux from the soil surface (FCO₂) and to pools of SOM and various nutrients key to plant growth. In chapter 4, I compare the same variables between trail areas utilised for forestry activities (i.e. skid trails) and adjacent harvested forest.

1.1.1 Forest Soil Biogeochemistry

1.1.1.1 Soil Properties and Forest Productivity

Forest productivity is driven and constrained by many factors, such as weather/climate, topography, structure of vegetative cover, management history, and edaphic conditions (Burger et al., 2002). Forest
soils are uniquely important amongst these, as they provide a physical substrate for growth, collect and retain precipitation, and function as the primary biogeochemical interface between terrestrial and atmospheric carbon and nutrient cycles. Soil taxonomic order, nutrient content, texture, depth, and acid-buffering capacity can vary significantly, and largely depend on regional bedrock parent materials, post-glacial history, and climate, all ultimately influencing forest productivity throughout the mixed-temperate forests (Burger et al., 2002).

In northern temperate forests, most available soil nutrients are tightly coupled to the recycling of detrital organic matter (Burger, 2002). The accumulation of this biomass is principally controlled by net primary productivity, whilst losses are associated with environmental constraints to degradation and the biological stability of the biomolecules present (Baldock, et al., 2004; Davidson and Janssen, 2006). Cold winters delay decomposition of accumulated plant materials on the forest floor, producing a horizon composed of forest litter, fibric, and humic materials. This LFH horizon serves as the interface for nutrients cycled between living biomass and mineral soils, regulated by comminution by invertebrates and mineralisation by fungi and microbiota to produce SOM and bio-available inorganic soil nutrients (Brady and Weil, 1998, Kögel-Knaber, 2002; Prescott, 2005; Bradford et al., 2009; Garten, 2009).

The mineral soil horizons below the LFH comprises the largest reservoir of forest soil SOM, stored predominantly as mineral-bound humus with varying amounts of particulate organic matter (Schulze et al., 2009; Garten, 2009). This pool of SOM is considered recalcitrant to decomposition due to complex molecular structures and stabilisation with mineral surfaces (Lützow et al., 2006; Kalbitz and Kaiser, 2008). Inputs of SOM to the mineral soil are presumed to be sourced from the LFH and fine root turnover (Rasse et al., 2005). Some SOM is transferred by bioturbation, physical settling, and hydrologic fluxes of eluviated DOC and particulate SOC into the underlying mineral horizon (Solinger et al., 2001; Garten, 2009; Müller-Using and Bartsch, 2009). Yet the properties and dynamics of this SOM vary considerably from the LFH horizon, and the relative contribution of SOM from the LFH horizon to mineral horizons is unclear (Garten, 2009).

Most interactions between SOM, fungi and microorganisms, and plant roots take place in the rhizosphere, a thin layer of soil surrounding roots that is disproportionately biologically active relative to the bulk soil matrix (Hinsinger et al., 2009). The unique biogeochemistry of this zone allows the soil to provide many soil functions integral to forest productivity, including: enhanced access to soil nutrients and cation-exchange; reducing bulk density by increasing soil porosity, facilitating root growth and enhancing moisture retention capacity, and; providing soil aggregate stability to resist erosion (Brady
and Weil, 1998). To maximise interactions with the nutrient-rich LFH horizon trees produce dense fine root mats relative to the mineral soil beneath it. These often contain a considerable mass of mycorrhizal mycelium that facilitate rhizosphere exchanges (Lawrence et al., 1995; Högberg and Högberg, 2002; Paul, 2007).

1.1.1.2 Forest Floor Inputs

Annual leaf litter-fall is an important source of SOM and nutrient inputs for soil pools in northern temperate forests, providing labile low molecular weight organic matter compounds (e.g. sugars, amino acids, organic acids) that leach rapidly from freshly fallen leaves, recalcitrant C (e.g. lignin), and soluble labile nutrients (e.g. K, Na) that contribute to exchangeable pools (Chapin et al., 2002). Litter exclusion studies in temperate mixed forests have shown little change in LFH mass after 5-7 years, but substantial decreases in horizon thickness after 10 years fromm decomposition (Sayer, 2006). LFH horizon recovery after long-term depletion can take up to several decades, and the loss of forest productivity due to loss of vital nutrients remains evident decades later. Conversely, litter addition studies have shown rapid increases in mineral SOM, but overall, few studies have thoroughly examined the effect of leaf litter inputs to SOC storage (Sayer, 2006).

Downed woody debris (DWD) from tree branches and stems is another important source of organic matter to forest soils. Larger pieces are slow decaying, spatially clustered, and contain low concentrations of nutrients, but are considered valuable habitat for many invertebrates and vertebrates, serve as a source of energy and nutrients for fungi, and function as nurseries for seedling development (Harmon et al. 1986; Rudz, 2013). Leachates from DWD can contain relatively high concentrations of certain nutrients and dissolved organic carbon (DOC), potentially enriching the adjacent soil (Hafner et al., 2005; Shabaga et al., 2015). Finer pieces of DWD decay more rapidly and contain more nutrient dense tips, buds, and cambiums (Yanai, 1998; Müller-Using and Bartsch, 2009).

1.1.1.3 Soil Nitrogen Dynamics

Most northern temperate forests have been traditionally considered nitrogen-limited (Aber at al., 1989; Vitousek et al., 2010). Forest N pools consist primarily of organic N within living biomass, litter, and SOM. Inputs are primarily from dry and wet atmospheric deposition as NH$_4^+$ and NO$_3^-$ (Schlesinger, 1997), while losses occur via leaching of DON and inorganic N to groundwater and runoff, microbial reduction of NO$_3^-$ producing N$_2$O and N$_2$ via denitrification, and oxidation of NH$_4^+$ to NO$_3^-$ via nitrification, releasing N$_2$O as a by-product (Paul, 2007). As such, N-cycling within these systems is fairly contained;
most N is stored in SOM, losses are often seasonally influenced and minimal, and annual inputs from atmospheric deposition vary substantially by region, but typically meet or exceed loses.

1.1.1.4  Soil Respiration and CO$_2$ Efflux

Soils exchange gases with the atmosphere through diffusion gradients, absorbing atmospheric O$_2$ and emitting CO$_2$ produced by the collective biological activity of soil organisms. This process of soil respiration ($R_s$) comprises the largest source of global terrestrial CO$_2$ efflux (Heimann and Reichstein, 2008; Subke and Bahn, 2010), and is considered a robust indicator of soil biological activity, correlating to gross primary production (Brown et al., 1996; Chapin et al., 2002; Laporte et al., 2003). Soil respiration is the cumulative by-product of the decomposition of litter and SOM by heterotrophic soil organisms ($R_{hi}$), and the respiration of roots ($R_r$) from trees and other vegetation, measured by the rate of CO$_2$ efflux from the soil surface (FCO$_2$). The proportional contributions of $R_r$ to $R_s$ can range from 10 to 90% depending on forest type and season, but typically accounts for an average of 50% overall (Hanson et al., 2000; Subke et al., 2006; Peng et al., 2008). Seasonal patterns of $R_s$ are linked to changing soil temperatures, which are generally considered the best predictor of change in $R_s$ at any given location (Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Chapin et al., 2002). Soil moisture can also influence $R_s$, particularly where biological activity is constrained by drought or saturation (Peng et al., 2008; Webster et al., 2008).

The response of $R_s$ to temperature is commonly described by a Q$_{10}$ value, which represents the rate of change in respiration over a 10 °C range (Lloyd and Taylor, 1994). Generally measured over the course of a season, this “apparent” Q$_{10}$ also includes the influence of other edaphic and external environmental variables on $R_s$, such as: climate and weather events, the phenology of vegetation cover, hydrological regime, and nutrient and labile soil substrate availability (Raich and Schlesinger, 1992; Widén and Madji, 2001; Davidson et al., 2006). Consequently, the Q$_{10}$ of $R_s$ over a growing season reflects the sum of all environmental constraints and influences on both $R_r$ and $R_{hi}$ (Raich and Schlesinger, 1992; Boone et al., 1998; Peng and Thomas, 2006). This means that the proportional contributions of $R_r$ and $R_{hi}$ to $R_s$ may vary considerably by season; the contribution of $R_r$ to $R_s$ peaks during the growing season in mid-summer during peak photosynthetic activity, while the cessation of photosynthesis in the autumn reduces $R_r$ contributions, allowing $R_{hi}$ to become more influential to $R_s$. (Chapter 2; Shabaga et al., 2015).
1.1.2 Silvicultural Management of Mixed Forests

Silviculture practices in northern mixed-hardwoods vary by region, with intensities ranging from full-tree clear-cuts to minimally invasive partial-harvests (Laporte et al., 2003). In the province of Ontario, Canada, silvicultural guidelines developed by the Ontario Ministry of Natural Resources and Forestry (OMNR) define three types of silviculture practiced in the region: single tree/group selection, shelterwood, and clear-cut. Clear-cut silviculture is the most intensive method, removing up to 100% of all trees in cut-blocks, and is frequently used to manage for shade intolerant species, such as poplar and jack-pine, producing even-aged forest structures. Shelterwood silviculture involves removing most of the over-storey over two or three harvests to manage shade mid-tolerant or intolerant species such as yellow birch and red oak, resulting in an even-aged cohort.

In contrast, selection silviculture is the least intensive of these silviculture methods, and used to promote shade tolerant trees such as maple and beech through a mix of single-tree and group selection methods in repeated partial harvests (<30% of canopy trees, 15-25 year cycles). This method is meant to simulate allogenic forest disturbances (Webster and Jensen, 2007) by creating interspersed and variable-sized canopy gaps that promote regeneration of understorey species, maintaining a diverse and uneven-aged stand structure (OMNR, 1998). However, this does not precisely mimic natural disturbances, altering species composition by favouring shade-tolerant tree species (McClure and Lee, 1993) and producing soil disturbances from machinery, both of which ultimately can impact forest productivity, health, and carbon and nutrient pools (Burger, 2002).

1.1.3 Potential Soil Responses to Harvesting Disturbances

Forestry related activities produce many types of disturbances, altering the physical structure, microclimate, physiochemical properties, and biological activity of vegetation and soils, influencing functions necessary for tree growth and overall forest productivity (Burger, 2002; Laporte et al., 2003; Peng et al., 2008; Olajuyigbe et al., 2012). However, the specific mechanisms by which harvesting influences forest soil function and quality are poorly understood and characterised (Laporte et al., 2003). Most study has focused on intensive impacts of commercial thinning and silvicultural methods such as clear-cutting, sometimes using whole-tree harvesting, in boreal and mixed conifer stands. Under these circumstances, extensive harvesting disturbances, evenness of stand age, short-fire intervals, conifer dominated stands, and seasonal water-limitations may differently affect soil function than less intensive partial-harvest approaches (Johnson and Curtis, 2001; Laporte et al., 2003; Tang et al., 2005; Misson et al., 2005; Concilio et al., 2006).
Regardless, disturbances can be considerable even in partial-harvest systems. Removal of trees opens gaps in canopies, increasing soil insolation and reducing the interception of precipitation, which in turn alters spatial patterns of soil temperatures, moisture, and potential decomposer activity (Londo et al., 1999; Peng et al., 2008; Olajuyigbe et al., 2012). Fresh inputs of DWD and death of tree root systems and associated mycorrhizal associations provides a source of labile C necromass for decomposers within the soil matrix (Toland And Zak, 1994; Yanai, 1998; Högberg et al, 2001; Lee et al., 2003; Belleau et al., 2006; Thiffault et al., 2006; Sullivan et al., 2008; Olajuyigbe et al., 2012). Increased insolation may also stimulate growth of understorey vegetation (Beaudet et al., 2004; Jones et al., 2009), increasing fine root density and associated R (Yin et al., 1989; Claus and George, 2005; Peng and Thomas, 2006).

Large areas of forest (up to 20%) are cleared to develop skid trail systems for site access. These areas can experience considerable compaction effects from machinery that persist for decades, decreasing pore space and gas exchanges for biological activity and root growth (McNabb, 1994; Laporte et al., 2003; Frey et al., 2009; Ezzati et al., 2014). Conversely, physical mixing of soils damages fine root systems, disrupting rhizosphere function and mycorrhizal associations, and introduces labile C from the surface into mineral soils, which may stimulate the decomposition of recalcitrant carbon through breakdown of aggregates and “priming” of microbial communities (Kuzyakov et al., 2000; Fontaine, et al., 2007; Blagodatskaya and Kuzyakov 2008; Heimann and Reichstein, 2008; Crow et al., 2009). This may create an environment that reduces microbial competition with tree roots and mycorrhizae for resources, favouring decomposer activity. Disturbed soils can increase leaching rates of DOC to deeper soils (Kreutzweiser et al., 2008), potentially priming the decomposition of these C stocks.

Some studies have highlighted concerns over potential reductions to forest productivity due to long-term soil nutrient depletion through biomass removal and a legacy of soil acidification causing enhanced leaching, (Yanai et al., 1999; Watmough and Dillon 2003; Thiffault, et al., 2011). Other studies focusing on post-harvest changes to SOM storage in soils, particularly soil organic C (SOC) and N, and C flux to the atmosphere, have shown a wide range of responses dependent on forest type, intensity of harvest, soil horizon, soil parent material and taxonomic classification (Johnson and Curtis, 2001; Yanai et al., 2003; Chatterjee et al., 2008; Nave et al., 2010).
1.1.4 Evidence of Harvesting Disturbance Impacts on Soils

1.1.4.1 SOM and Nutrient losses

Changes to SOM from harvesting disturbances are highly variable due to site and management factors (Vance, 2000). A meta-analysis by Johnson and Curtis (2001) found no overall or time based change to overall SOC and total soil N storage from harvesting, except where there was intense burning, mechanical disturbance, or soil tillage (Janowiak and Webster, 2010). When tree cover and harvest type were considered as factors, they found a 7-10% decline in SOC and total N following whole tree harvesting, a non-significant 7% decline in SOC and a 9% increase in total N in deciduous forest soils, and a 9% decline in total N in mixed forests. They also found a 25% increase in mineral SOC and total N following saw-log harvesting in conifer dominated forests, which they attributed to mixing of residues into the soil. Using similar methods, Nave et al. (2010) also found an increase in mineral soil SOC in conifer dominated stands (8%). Unlike Johnson and Curtis (2001), they specifically considered forest floor SOC content and soil types, and found large declines to SOC in the LFH (36%) of in deciduous forests, substantial declines in shallow mineral horizons (25%) of Brunisols/Inceptisols, and a significant overall SOC decline of 8% following a comparison of clear-cut and thinning harvests.

Reductions to litter inputs and increased stem and biomass removal may reduce post-harvest volumes of DWD, impacting the rate of SOM accumulation in long-term soil pools. In litter manipulation studies, Garten (2009) and Nadelhoffer et al. (2004) found no change in mineral soil carbon stocks from either additions or restrictions after 4-5 years. Other studies have shown changes. Ponge et al., (1993) note a two-fold increase in mineral soil C after 2-5 years of litter additions in a temperate deciduous forest, and considerable mineral soil C losses were reported 10 years after removal of litter in clear-cut sites distributed across North America as part of the long term soil project (LTSP) (Power et al., 2006). Soils experiencing long-term (multi-decade) litter removal in forests have shown substantial decreases to N, base cations, and P (30-70%). Pools of K and P decrease most rapidly (<4 years), but generally little change occurs within the first year or two (Sayer, 2006).

Janowiak and Webster (2010) suggest that removal of DWD, substantially shortening rotation periods, and harvesting of sub-merchantable trees and brush would be more likely to reduce SOM. Yet Power et al. (2005) found that removal of slash following a clear-cut produced little change in soil C (0-30 cm) after 10 years across. The presence of DWD as harvest residues may also influence N cycling. Harvesting has been shown to increase nitrification rates and leaching of NO$_3^-$ (Bormann and Likens, 1979; Yanai et al., 1999), and Vitousek and Matson (1985) linked lower N mineralisation rates and soil NO$_3^-$
concentrations to removal of post-harvest woody residues in whole tree harvests relative to stem-only harvesting, attributing this differences in labile C inputs.

1.1.4.2 Changes to Soil Respiration Rates

In general, study results have been conflicting, variedly reporting increases, decreases, or no changes at all (Hendrickson et al., 1989; Mattson and Swank, 1989; Londo et al., 1999; Laporte et al., 2003; Peng and Thomas, 2006; Peng et al., 2008; Stoffel et al., 2010, Kurth et al., 2014). This inconsistency reveals a large gap in our mechanistic understanding of the effects of harvesting disturbances on soil \( \text{FCO}_2 \). In part, this may be due to insufficient consideration for the heterogeneity of large scale or microsite differences such as residual forest structure, surface scarification, canopy openings, mixing of forest floor materials into mineral soil, and compaction (Johnson and Curtis, 2001; Laporte et al., 2003). If \( \text{FCO}_2 \) varies considerably due to these effects, research designs may require more extensive sampling networks to accommodate this heterogeneity (i.e. more replicates to improve statistical power), measurement of known covariates to adjust for differences (e.g. soil temperature and moisture), or blocking of replicates that meet the criteria for unique conditions (e.g. skid trails). Since the type, distribution, and extent of these disturbances may vary considerably based on the types harvesting operations (e.g. selection harvests, clear-cuts, thinning, and whole tree removal) and forest ecosystems (boreal, mixed-deciduous, mixed-conifer, etc) represented amongst these studies, we would anticipate considerable differences. These would affect \( \text{FCO}_2 \) in two main capacities:

1) Over-arching factors that influence overall \( \text{R}_s \):
   - A decrease in overall \( \text{R}_s \) from reduced gas exchanges following compaction and increases to soil moisture and water-filled pore space
   - An increase in overall \( \text{R}_s \) due to elevated soil temperatures

2) Factors that differently influence contributions of plant roots (\( \text{R}_n \)) and heterotrophic organisms (\( \text{R}_h \)):
   - A decrease in \( \text{R}_n \) from root senescence, followed by an increase with vegetation regrowth
   - Inhibition of root growth from compaction and associated \( \text{R}_n \) during recovery
   - An increase in \( \text{R}_h \) from stimulation of decomposition rates, followed by a decline as post-harvest supplies of labile C are depleted
   - Reductions to leaf litter inputs may reduce annual labile C inputs to soils until the canopy has recovered, reducing \( \text{R}_h \)
Increases to canopy openness following harvest will increase soil insolation rates and temperatures. This openness will also increase direct interception of precipitation with the soil surface. Combined with lower evapotranspiration rates in harvested plots this could alter patterns of soil moisture, likely increasing availability in some locations while decreasing in others. These openings are heterogeneously distributed, and depending on the soil conditions beneath them, may influence Rs. Increased moisture may contribute to higher Rs where limiting (Peng et al., 2008), while saturation of pore space can inhibit gas efflux. This is exacerbated by compaction, where reduced soil porosity facilitates saturation and minimises air-filled pore space for gas exchanges, reducing Rs (McNabb et al., 2001). The heterogeneity of these effects may contribute to the inability to detect specific changes to Rs when sampling is insufficient to accommodate this variance. However, most compaction from machinery is concentrated on skid trails in selection silviculture; these trail span large portions (up to 20%) of managed forest areas, and have been shown to substantially decrease Rs, particularly when soils are saturated (McNabb et al., 2001). This well-defined and substantial component of these systems can be readily integrated into research designs through representative and/or targeted sampling methods. Yet these areas remained largely uncharacterised with regard to their specific role in influencing post-harvest patterns of Rs at the site scale.

In contrast, other examples of heterogeneously distributed post-harvest impacts to forest sites tend to differently influence the main contributing components to Rs: Rr and Rh. Increases to decomposition rates in soils from root turnover and DWD leachates and subsequent loss of SOM would be expressed by an increase in Rh. Conversely, reduced litter inputs in harvested areas may also reduce labile C and nutrient pools over time, limiting Rh (Sayer, 2006). Similarly, reductions to live root biomass from cut trees would decrease Rs, while post-harvest regeneration of vegetation would increase root density and Rs. Since measuring total Rs may confound these signals, these would ideally be measured separately in studies. Unfortunately, accurate separation of Rh and Rs is challenging, and the main methods to distinguish between them are either expensive and impractical (e.g. isotope analysis), risk confounding disturbance signals between harvesting impacts and physical separation of roots from a body of soil (e.g. root exclusion collars, trenching, and ex-situ soil incubations), or kill the surrounding vegetation, making them unsuitable for a harvesting and recovery based study (e.g. cutting or girdling trees or herbicide application) (Hanson et al., 2000; Larionova et al., 2006; Lalonde and Prescott, 2007).

Isotope analysis involves the administration of a tracer such as 14C/13C labelled CO2 in pulses or continuously to plants contained in sealed chambers (Hanson et al., 2000). This creates a unique isotopic signature in FCO2 that can be used to determine the proportion of root contributions to Rs. However,
the challenge of containing entire trees and variability of $R_R$ over the course of seasons and years, imprecision in pulse-based applications, and the expense of isotopes and analysis makes this method highly impractical for use in stand-scale studies. More accessible methods include physical exclusion of roots, either by the use of root exclusion collars or trenching, to separate a volume of soil from the influence of root respiration. $FCO_2$ measured from this soil provides a $R_K$ only reference measurement, and is contrasted to $R_S$ measured from adjacent non-excluded soils. Collars have the advantage of being small enough to capture small-scale differences, allowing them to be well-dispersed across study sites and used in split plots and fully-crossed designs, while trenching requires somewhat larger areas for assessment.

Several studies have shown effective results using root exclusion methods in non-harvest related studies, demonstrating seasonal partitioning of $R_R$ and $R_K$ contributions to overall soil respiration (Chapter 2; Shabaga et al., 2015). However, both these methods can either produce disturbance effects comparable to or more severe than those from harvesting disturbances, and/or prevent the detection of root damage from harvesting. The collar method requires either forced insertion of a plastic collar into the soil to the desired depth of exclusion, or excavation of an intact soil core that is packed within a collar and reinserted into the soil. In either case, even careful insertion or extraction and replacement of cores will likely involve mixing and/or compaction. Roots left in the soil collar will decompose, confounding $R_R$ losses by increased $R_K$; it may takes months or years before roots are sufficiently decomposed to inhibit this effect, varying by ecosystem (Boone et al., 1998; Hanson et al., 2000). If roots are removed prior to repacking, the soils become extensively mixed and unrepresentative of the local conditions. Furthermore, collars may substantially influence soil moisture retention by reducing drainage and gas exchanges, fundamentally altering an important covariates influencing spatial variability of $R_S$.

Trenching is less damaging to the soil structure of the sample area than collars, but suffers from a similar drawback: the influence of root decomposition. Some studies have removed smaller roots near the surface, but leave deeper larger roots. Regardless, root removal imposes the same problems of mixing as for root collars, potentially influencing microbial priming and gas exchanges due to changes in density. Additionally, trenching requires modification of a sufficiently large area, which may prove difficult where tree densities prohibit efficient trenching. Comparisons of $FCO_2$ from adjacent locations as $R_S$ may not provide a comparable balance of $R_R$ and $R_K$ that would have been represented in the trenched plot due to variations in moisture, SOM, proximity of roots and species of tree, etc.
In light of these insurmountable challenges, most studies assessing post-harvest changes to FCO\textsubscript{2} consider only total R\textsubscript{S}. Yet there may be other options to infer changes to decomposition rates and reductions to root respiration, such as evaluation of seasonal patterns of FCO\textsubscript{2}. Since R\textsubscript{S} contributes primarily to R\textsubscript{S} during summer and much less during the autumn, differences in the seasonal patterns of FCO\textsubscript{2} between harvested and unharvested areas may reveal changes to root contributions (e.g. lower summer values) and decomposition rates (e.g. higher autumn values). Additionally, changes in these seasonal patterns in the years following harvest (e.g. increasing summer values and declining autumn values) may also reveal if recovery is influencing outcomes. Few studies have regularly measured FCO\textsubscript{2} over the span of multiple post-harvest growing seasons, limiting their ability to isolate these effects.

1.1.5 Intensification of Biomass Harvesting

Traditional forest markets have changed considerably over the past decades while operational costs have risen, resulting in a decline in the Ontario forestry sector. Previous methods of ecologically sustainable silviculture established to meet market needs have since been reappraised to consider entrance in developing alternative markets, such as wood biomass for as bioenergy (OMNR, 2009; Richter et al., 2009; Zhang et al., 2010; Thiffault and Paré, 2016). Strict guidelines for selection silviculture of the tolerant hardwood forests leaves little room for large-scale changes without influencing outcomes that might compromise ecological stability and sustainability of harvests, and most conventionally harvested wood retains sufficient market value to make it inefficient for low value usage, despite market instability. As such, development of biomass intensive harvest methods in the tolerant hardwood region have focused largely on retrieval of previously un-merchantable biomass that requires minimal additional cost to retrieve (Wolf et al., 2014; Thiffault and Paré, 2016).

Small changes to selection silviculture prescription guidelines, such as a smaller topping diameter and minimal diameter at breast height (DBH), have been proposed to increase retrieval of materials traditionally retained as on-site harvest residuals that contribute to downed woody debris. These changes are relatively modest, aiming to maintain the same residual basal area as a traditional harvest and retain most harvest residuals on-site, particularly when contrasted to clear-cuts and biomass intensive harvest methods in other regions such as whole tree and stump/root extraction (Egnel, 2011; Thiffault et al., 2011). Regardless, concerns persist over the intensified removal of DWD materials that have poorly investigated roles in forest nutrient cycles (Janowiak and Webster, 2010), particularly since recent evidence suggests removal of tops and stumps may disproportionately induce SOM and soil nutrient losses in northern climates over several harvesting cycles (Egnel, 2011; Thiffault et al., 2011).
Since the northern temperate forest region of Ontario lies within the Canadian Shield region, an area typified by shallow and acidic post-glacial sandy loam soils, these area are considered vulnerable to nutrient losses from disturbance and biomass removal (Watmough and Dillon, 2003; Phillips and Watmough, 2012). Furthermore, patterns of mechanical activity during operations may also vary from selection harvests: a greater number of harvested stems and longer and/or larger load masses from skidding and hauling traffic may increase physical disturbance effects such as soil abrasion, mixing, compaction, and damage to understorey vegetation (e.g. sapling and seedlings). Increased harvesting of smaller diameter trees may influence patterns of post-harvest regrowth, while potential reductions to seedling density might impact regeneration rates.

1.1.6 Summary of Disturbance Effects and Research Gaps

Soil compaction, soil mixing and microbial priming, reduced root activity, restrictions to leaf litter inputs, and introduction of labile harvest residuals such as DWD and root necromass are all spatially constrained phenomena that may influence biogeochemical processes in forest soils. Reductions to DWD volumes from intensified retrieval of historically un-merchantable biomass through forest management may also play a role in post-harvest SOM and nutrient dynamics. I have summarised these factors in a conceptual model (Fig. 1.1) based on whether anticipated harvesting disturbances might stimulate or constrain factors regulating soil biogeochemical processes, and highlighted several measures of harvest intensity and recovery that may serve to predict changes to soil function.

Disparities amongst the results of studies examining post-harvest gains or losses of nutrients and changes to soil respiration indicate that differences in regional and localised factors such as forest type, silvicultural management, harvest intensity, and microsite conditions play a role in influencing biogeochemical processes. This indicates a need for a more focused approach to isolating these factors in studies to better determine over-arching post-harvest mechanisms of soil biogeochemistry. To accomplish this, designs must account for: a) the inherent high spatial variability of soil nutrient pools, SOM, and soil physical and edaphic properties; b) differentiate these between short-lived LFH pools and long-term mineral soil; c) the method and intensity of harvesting disturbances; and, d) separating the influence of spatial heterogeneous disturbances at smaller scales (e.g. individual tree) from broader-scale disturbances (e.g. skid trails) that may induce differing and confounding effects on each other, masking their individual contributions that might also account for variability amongst studies.
1.2 Research Objectives

The overall objectives of this thesis were to: 1) test if a modified selection silviculture method for increased biomass retrieval differently affected soil edaphic properties and function from a conventional selection harvest; 2) identify potential biogeochemical processes and disturbance mechanisms eliciting post-harvest changes by linking soil respiration and chemistry to post-harvest changes in environmental covariates such as forest structure and soil temperature and moisture, and; 3) identify easily mensurated measures of harvest intensity based on changes to forest and soil structure/cover that can be used to predict harvesting impacts on soil edaphic properties and function.

Defining disturbance mechanisms as they relate to forest and soil properties will improve our ability to predict changes to long-term soil fertility and the sustainability of different harvesting intensity and methods in different regions, such as biomass harvesting. However, the forests and soils of Central Ontario are heterogeneous, in part reflecting the variability in the topography and micro-climate of the landscape on which they rest. Similarly, disturbance related changes to a forested ecosystem are also varied and complex, often expressing variation on scales that are impractical to account for (e.g. individual tree roots or pieces of woody debris). As such, it is difficult to isolate and test for many specific disturbance effects when considering results over areas large enough to identify broader-scale patterns. One way in which to compensate for this effect is to treat this variation as random noise and
use sufficient random sampling to overcome this “error”. Alternatively, one can attempt to account for influential covariates at practical scales of mensuration that might account for this variance, both serving to improve the ability to detect underlying experimental effects and providing a metric for predictability of responses. Another method is to attempt to isolate major disturbance effects a priori and test for differences amongst these and comparatively undisturbed areas as part of the study design.

In this dissertation, I utilised all these methodologies within three different studies, considering overall effects in plots harvested using two different methods (conventional vs. biomass harvesting) and skid trails (primary vs. tertiary) relative to unharvested forest. Since there is little precedent in the literature to indicate if C and nutrient levels and respiration rates would consistently increase or decrease during the growing season or time since harvest, this necessitated specification of hypotheses that more broadly consider temporal patterns linked to known biogeochemical processes:

1. Increases to decomposition rates and decreases tree root activity from harvesting will decrease summer and increase autumnal soil respiration rates and produce losses of available soil C and exchangeable nutrients
2. These changes will be reflective of the type and level of harvesting disturbance; increasing biomass removal will decrease root activity but increase decomposition related effects, including nutrient and C losses
3. Depletion of labile C supplies and regrowth of vegetation in the years following harvesting will show a decline in elevated decomposition rates towards baseline and an increase root activity, changing the seasonal pattern of soil respiration and stabilising C and nutrient losses
4. Compaction of and damage to the structure of soils on skid trails will reduce soil-atmosphere gas exchanges and overall biological activity commensurate with the intensity of trail use, reducing FCO₂ and influencing patterns of soil C and nutrients

The basis for both these hypotheses is related to harvesting disturbance-based changes in both the physical structure of soils and forest and shifts in patterns of biological activity. This will produce exaggerated temporary imbalances in soil environmental conditions and autotrophic and heterotrophic physiological activities relative to a steady-state condition based on “natural” gap-dynamic variations. These are outlined in section 1.3 “Potential Impacts of Harvesting Disturbances on Soils”. Further consideration of potential mechanisms linking soil properties and disturbance mechanisms elicits several specific objectives throughout the following chapters based on study in a managed mixed deciduous forest of Ontario:
**Chapter 2:** i) Determine the effect of two intensities of partial harvesting on rates of FCO$_2$ relative to unharvested controls; ii) Examine the seasonal patterns and post-harvest recovery of FCO$_2$ for three years; and iii) Model the differences in FCO$_2$ rates between harvested and unharvested forests accounting for temperature and moisture, and test for harvesting effects independent of these variables.

**Chapter 3:** Assess if biomass harvesting reduced soil C and nutrients relative to conventional single-tree selection harvesting methods and unharvested controls based on reduced harvesting residue biomass inputs.

**Chapter 4:** i) Compare the effect of two different skid trail intensities on rates of FCO$_2$ and pools of soil C and base cations relative to adjacent forest harvested using single-tree selection; and ii) Compare changes to SOC and base cations before and at the end of the post-harvest growing season.

**All Chapters:** Identify potential harvesting disturbance mechanisms based on biogeochemical processes to account for observed differences and changes to patterns of FCO$_2$ and soil chemistry between treatments.

### 1.3 Organisation of Chapters

This dissertation is organised into five chapters. Three of these chapters have been written in the format of scientific manuscripts. The first two of these, Chapters 2 and 3, are based in the same field sites, Chapter 2 examines post-harvest changes to soil respiration, measured as efflux of CO$_2$ from the soil surface (FCO$_2$), temperature, and moisture between two differing intensities of single tree selection harvesting relative to an unharvested control. In Chapter 3, I compare pre, one, and three-year post-harvest SOC and nutrient data between the same harvesting treatments. In chapter 4 I compare differences in FCO$_2$, SOC, and nutrients between primary and tertiary skid trails and adjacent harvested forest in the beginning and the end of the post-harvesting growing season. Lastly, a synthesis of these findings to broader conclusions is described in the Chapter 5.
Chapter 2
Seasonal controls on patterns of soil respiration and temperature sensitivity in a northern mixed deciduous forest following partial-harvesting

2.1 Abstract

Disturbances can alter CO$_2$ efflux from soils (FCO$_2$) by altering the microclimate, structure, and biogeochemical properties of forest ecosystems. Results of prior studies are unclear if and how partial harvesting of northern deciduous forests affects FCO$_2$. These mixed responses may be due to differences in harvesting levels, time since harvest, and the spatial and seasonal heterogeneity of treatment effects and soil properties. To account for this spatio-temporal dependence, subject-level regression models were produced from regular measurements of FCO$_2$ and soil temperatures during the 2010 to 2012 growing seasons following tree-length (TL) and more intensive biomass (BIO) harvests. In this paper, I compare seasonal and inter-annual post-harvest recovery trends for measured and temperature-corrected soil respiration rates and the sensitivity of soil respiration to temperature (as Q$_{10}$).

FCO$_2$ values from TL/BIO treatments exceeded unharvested controls, recurrently peaking in the autumn (average for TL/BIO: 28%/17%, p≤0.05) and waning in the summer (14%/10%, not significant). A comparison of measured FCO$_2$ vs. modelled respiration values corrected for temperature differences indicated that higher soil temperatures following canopy thinning accounted for 34 to 41% of these differences in 2010 but <15% by 2012. Initially lower in 2010, Q$_{10}$ and summer respiration values for harvested treatments exceeded those of controls by 2012, and despite waning temperature differences, average annual effect sizes corrected for temperature differences did not decline. Autumn and basal respiration rates were correlated with post-harvest fine woody debris volumes in 2010 (r$^2$=0.58/0.57, p≤0.01), summer rates in all years decreased with harvested tree basal area (r$^2$=0.42-0.58, p≤0.05), and the post-harvest basal area of understorey vegetation predicted increasing Q$_{10}$ effect sizes from 2010-2012 (r$^2$=0.81, p≤0.01). With consideration to studies demonstrating that the contribution of root respiration (R$_r$) to FCO$_2$ is highest in summer, I propose that partial harvesting initially restricts R$_r$ and peak summer respiration rates, but compensates for this decline by increasing basal respiration rates and FCO$_2$ through elevated temperatures and decomposition rates from canopy thinning and harvest residue substrate inputs (i.e., woody debris and root necromass). During post-harvest recovery, forest
understorey regrowth reduces soil temperatures but influences patterns of FCO$_2$ by increasing summer respiration and Q$_{10}$ values in harvested treatments, likely by increasing R$_R$.

2.2 Introduction

Forest management and other land-use changes such as conversion of forest to agriculture contribute half as much to the accumulation of atmospheric carbon dioxide (CO$_2$) as fossil fuel consumption (Houghton, 1999, 2003; Shevliakova et al., 2009). A substantial portion of these losses are from changes to soil respiration dynamics following disturbance (Chapin et al., 2002). Soil respiration (R$_S$) comprises the largest source of global terrestrial CO$_2$ efflux (FCO$_2$) (Heimann and Reichstein, 2008; Subke and Bahn, 2010), and is a product of respiration from the decomposition of litter and soil organic matter (SOM) by heterotrophic soil organisms (R$_H$), and the respiration of roots (R$_R$) from trees and other vegetation. In forests, the proportional contributions of R$_R$ to R$_S$ can vary substantially, ranging from 10 to 90% depending on the method of measurement, forest type, and season (Hanson et al., 2000; Subke et al., 2006; Peng et al., 2008). Undisturbed forests typically fix more CO$_2$ as biomass than they respire (Chapin et al., 2002), but harvesting can temporarily decrease net primary production (NPP), potentially turning a forest into a net source of atmospheric CO$_2$ (Janisch and Harmon, 2002; Peng et al., 2008). Conversely, forest regrowth can increase NPP, restoring positive carbon balance (Brown et al., 1996; Chapin et al., 2002).

Temperature is widely considered the best predictor of R$_S$ in a single geographic location (Raich and Schlesinger, 1992); rising temperatures increase gross primary production (GPP) and soil decomposition rates, producing a commensurate increase in FCO$_2$ (Lloyd and Taylor, 1994; Chapin et al., 2002). Between 10 and 30 °C this is commonly empirically modelled as an exponential relationship, though outside this temperature range other models are more appropriate (Lloyd and Taylor, 1994; Davidson et al., 2006; Tuomi et al., 2008). Seasonal patterns of FCO$_2$ are linked to changing soil temperatures; however, the response of R$_S$ to temperature can vary between and within ecosystems depending on many factors, including: climate/weather events, vegetation cover, hydrological regime, etc (Raich and Schlesinger, 1992; Davidson et al., 2006). This seasonal response is often described by a Q$_{10}$ value, which represents the rate of change in respiration (i.e., model slope) over a 10 °C range (Lloyd and Taylor, 1994). Seasonal “apparent” Q$_{10}$ differs from “true” Q$_{10}$ by including the influence of phenology on the temperature sensitivity of respiration, but remains a useful measure of the relative temperature sensitivity of R$_S$ in an ecosystem (Widén and Madji, 2001; Davidson et al., 2006). Apparent Q$_{10}$ (henceforth referred to as simply Q$_{10}$) can be used to predictively model FCO$_2$ at specific temperatures,
including reference temperatures (e.g., 10 °C - \( R_{10} \)) that are often calculated to represent “basal” respiration rates (i.e., rates minimally influenced by temperature).

Other soil properties can play a role in regulating \( R_s \), such as soil moisture and substrate availability, but often express more complex relationships. Substrate availability, as root photosynthates and labile organic inputs, is differently regulated by phenology (Davidson et al., 2006; Sampson et al., 2007). \( R_h \) is constrained by seasonal variations in root activity and environmental triggers on physiology (e.g., day length, minimum temperatures), particularly in deciduous species, while \( R_l \) is affected by seasonal variations in labile substrate availability such as leaf litter drop in autumn (Janssens et al., 2001; Chapin et al., 2002). Consequently, contributions of \( R_h \) to \( R_s \) differ relative to \( R_l \) between mid-summer and winter dormancy (Högberg et al., 2001; Janssens et al., 2001; Jarvi and Burton, 2013), producing different \( Q_{10} \) values for \( R_h \) and \( R_l \) (Boone et al., 1998). The cumulative FCO\(_2\) response of both to changes in temperature over a growing season reflects the overall \( Q_{10} \) of \( R_s \) (Raich and Schlesinger, 1992; Boone et al., 1998; Peng and Thomas, 2006).

Soil respiration can increase with soil moisture availability but is often constrained by drought or saturation, producing parabolic relationships over broader ranges (Peng et al., 2008; Webster et al., 2008). Soil moisture values can vary considerably with microtopography and SOM, and contributions to \( R_s \) may be confounded by other ecosystem and edaphic properties (e.g., vegetation cover, root density, soil texture, soil substrates) (Janssens et al., 2001; Davidson et al., 2006). The localised confluence of these variables may disproportionately enhance or inhibit \( R_s \), contributing more to the spatial heterogeneity of FCO\(_2\) than small differences in soil temperatures (Janssens et al., 2001; Widén and Madji, 2001). Therefore, variations in \( Q_{10} \) and \( R_{10} \) values indirectly represent the product of spatio-temporally regulated soil and forest ecosystem properties (e.g., soil moisture, substrates) that contribute to the heterogeneity of \( R_s \) (Davidson et al., 2006).

Ecosystem disturbances such as harvesting and subsequent recovery can produce considerable changes to these properties, potentially affecting \( R_s \). North American eastern mixed forests are often managed using single-tree and group selection methods in repeated partial harvests (<30% of canopy trees, 15-25 year rotations). These mimic natural disturbance regimes and create numerous interspersed canopy gaps of variable size that promote regeneration and succession of understorey species, maintaining a diverse and uneven-aged stand structure (OMNR, 1998). Nevertheless, harvesting operations produce disturbances that alter the physical structure, micro-climate, physiochemical properties, and biological activity of forest soils and vegetation (Laporte et al., 2003 Laporte et al., 2003; Peng et al., 2008;
Olajuyigbe et al., 2012), disrupting natural biogeochemical cycles that determine the proportional contributions of \( R_R \) and \( R_H \) to \( R_S \). This may yield different FCO\(_2\) rates for the same temperature in soils of harvested and unharvested forests, reflected in altered \( Q_{10} \) and \( R_{10} \) values.

For example, tree removal reduces live root density and leaf litter inputs, decreasing \( R_R \) and \( R_{H} \) (Bowden et al., 1993; Janssens et al., 2001; Sullivan et al., 2008). Machine activity can sever roots and mix soils; this may potentially stimulate SOM decomposition through microbial “priming” (Kuzyakov et al., 2000; Zummo and Friedland, 2011), but may also reduce gas exchanges through compaction, inhibiting both decomposition and root re-establishment (Frey et al., 2009, Peng et al., 2008). Root necromass and harvest residues such as fine woody debris (FWD) from tree tops provide labile substrates and nutrients, potentially increasing decomposition rates and \( R_{H} \) (Toland And Zak, 1994; Lee et al., 2003; Yanai, 1998; Belleau et al., 2006; Thiffault et al., 2006; Sullivan et al., 2008; Olajuyigbe et al., 2012). Canopy thinning and gap creation increases soil insolation and reduces interception of precipitation, altering spatial patterns of soil temperatures, moisture, and \( R_S \) (Londo et al., 1999; Peng et al., 2008; Olajuyigbe et al., 2012). Canopy gaps may also stimulate growth of understorey vegetation (Beaudet et al., 2004; Jones et al., 2009), increasing fine root density and associated \( R_R \) (Yin et al., 1989; Claus and George, 2005; Peng and Thomas, 2006).

Different levels of harvesting and residual forest structural properties may influence the intensity and duration of disturbance effects on \( R_S \). Intensified biomass removal can amplify harvesting disturbances by further reducing soil inputs of woody debris and leaf litter (Page-Dumroese et al., 2010; Janowiak and Webster, 2010) and increasing physical disturbances through additional mechanical activities (Page-Dumroese et al., 2010; Peng et al., 2008). Changing energy and wood-product markets have increased extraction of forest biomass (e.g., tops/branches and un-mERCHANTABLE stems) for use in non-traditional markets, including wood bioenergy to reduce fossil fuel CO\(_2\) emissions (OMNR, 2009; Richter et al., 2009; Janowick and Webster, 2010; Zhang et al., 2010). Yet the literature on the effects of partial harvesting and relative amounts of biomass removed on FCO\(_2\) rates in uneven-aged mixed deciduous forests remains under-developed; results may differ considerably with those from other management approaches (e.g., clear-felling, commercial thinning) or ecosystems (e.g., boreal, mixed conifer, sub-alpine) where \( R_S \) may be differently impacted by extensive harvesting disturbances, evenness of stand age, short-fire intervals, conifer dominated stands, and seasonal water-limitations (Laporte et al., 2003; Tang et al., 2005; Misson et al., 2005; Concilio et al., 2006).
Overall, we have a poor mechanistic understanding of harvesting-related disturbances on R₅ in partial-harvesting systems (Raich and Schlesinger, 1992; Laporte et al., 2003; Peng et al., 2008), with studies reporting increases, decreases, or no changes at all (Hendrickson et al., 1989; Mattson and Swank, 1989; Londo et al., 1999; Laporte et al., 2003; Peng and Thomas, 2006; Peng et al., 2008; Stoffel et al., 2010, Kurth et al., 2014). Despite acknowledgement of the potential importance of spatio-temporal dynamics to R₅ (Davidson et al., 2006), few studies specifically account for seasonality and post-harvest recovery patterns when assessing changes to FCO₂ following partial harvesting (Peng et al., 2008). Fewer still attempt to directly account for the role of post-harvesting soil temperatures differences on changes to FCO₂ by using subject-level Q₁₀ values in temperature-based FCO₂ models (Simmons et al., 1996; Widén and Madji, 2001; Sampson et al., 2007). Models that apply a single fixed (global) Q₁₀ value to all subjects when accounting for the effects of temperature on R₅ attribute spatial dependence to model error, limiting the ability of the model to distinguish between harvesting effects on FCO₂ and Q₁₀ and the variability inherent to forest ecosystems (Raich and Schlesinger, 1992; Davidson et al., 2006). Deriving unique Q₁₀ and R₁₀ values for each sampling location, using a wide range of seasonal temperature and FCO₂ measurements, accounts for this subject-level spatio-temporal dependence, potentially improving model accuracy and conserving harvesting-related effects on Q₁₀.

The objectives of this study were to (i) determine the effect of two intensities of partial harvesting (single-tree selection) on rates of FCO₂ relative to unharvested controls in a managed mixed deciduous forest in Central Ontario; (ii) examine the seasonal patterns and recovery of FCO₂ for three years; and (iii) model the differences in FCO₂ rates between harvested and unharvested forests accounting for temperature and moisture, and test for harvesting effects independent of these variables. Based on these objectives, I hypothesise that: (i) harvesting will increase FCO₂ rates relative to unharvested controls due to increased soil temperatures and access to labile C and nutrients for decomposers; (ii) effect sizes for FCO₂ rates will be higher in the autumn and lower in summer, and decline during recovery over 3 years; and (iii) increased biomass retrieval will not substantially influence FCO₂ rates relative to conventional harvest, but increases to FCO₂ will be related to the amount of cut forest.

2.3 Methods

2.3.1 Study Sites

The study was conducted within the Haliburton Forest and Wildlife Reserve (44°55′N, 78°50′W), a privately owned and commercially managed forest within the Great-Lakes St. Lawrence (GLSL) forest region of Central Ontario. The humid continental climate has a mean annual temperature of ≈5 °C and
1074 mm of precipitation with low monthly variation and ≈280 mm as snow (Environment Canada, 2015). Upland vegetation is dominated by sugar maple (*Acer saccharum* Marsh), American beech (*Fagus grandifolia* L.), yellow birch (*Betula alleghaniensis* Britt.), and eastern hemlock (*Tsuga canadensis* Britt.). The area has been managed for 50+ years using various intensities of partial harvest, most recently single-tree selection in 15 to 25 year harvest cycles. Soils overlie granite-gneiss Precambrian Shield bedrock and are shallow (0.5 – 2 m deep) and acidic (pH 4.2 – 6.2) Dystric Brunisols with organic-rich surface horizons and textures ranging from sandy loam to loamy sand. The topography comprises undulating hills and partially exposed bedrock, interspersed with numerous small wetlands. This study focused only on well-drained upland areas where commercial harvesting would typically occur.

Fifteen 2500 m² circular permanent sample plots centred in 1 ha blocks (Fig. 2.1) were randomly selected from a grid of blocks covering 279 ha of forest that was previously ground-validated for harvest suitability using regional Ontario silviculture guidelines (OMNR, 1998). Each plot contained 5 respiration subplots (1 m²) equi-radially distributed 20 m from the centre (total n=75).

Figure 2.1 Map of the mixed deciduous Haliburton Forest study site in Central Ontario, showing the distribution of plots, subplots, and harvesting treatments.

Treatments (Table 1 and 2) were randomly assigned to blocks and included an unharvested control (i.e., 20 years since previous partial harvest) and two selection-harvest treatments. One was a tree-length (TL) partial harvest applied according to Ontario Ministry of Natural Resources (OMNR, 1998) tree marking guidelines, removing ≈28% of tree basal area, mixed sizes, boles only, all stems >17 cm diameter at breast-height (DBH) with a target top diameter of 18 cm. The other was an intensified
biomass (BIO) harvest, similar to the TL treatment (=28% tree basal area removal) but with a reduced minimum stem DBH (>10 cm) and topping diameter (10 cm), and included removal of large branches, reducing downed woody debris residue relative to the TL treatment. Harvesting occurred in January and February of 2010, immediately before the first monitoring season.

2.3.2 Forest Mensuration

All trees >8 cm DBH within sample plots were tagged and diameter recorded to 0.1 cm prior to harvest in 2009; trees were reassessed after harvesting during the summer of 2010. Five equi-radially distributed transects running 30 m from the plot centre were used to assess fine woody debris (FWD). The diameter of all pieces of downed woody between 1-10 cm in diameter crossing each transect were measured and used to estimate FWD volumes. All pieces of downed woody debris in the plots >2 m long and >10 cm diameter at the centre were measured and mapped, then used to estimate coarse woody debris (CWD) volumes. Total saplings counts (2-8 cm DBH) were evaluated in five 50 m² sapling subplots equi-radially distributed 20 m from the plot centre and staggered between respiration subplots.

2.3.3 Soil Respiration

To capture both heterotrophic and root respiration (Rₗ), PVC soil flux collars (diameter = 10.2 cm) were installed in respiration subplots immediately post-harvesting in spring of 2010 to a depth of 2 to 3 cm and left to equilibrate with the environment. Collars were offset to avoid direct placement over woody debris and regenerating plants, but were often immediately adjacent to these areas or under suspended piles of woody debris. Disturbed soils were not specifically avoided or targeted. To measure FCO₂, collars were enclosed with a 1.5 litre PVC chamber containing a relief valve to equalise atmospheric and chamber pressures and connected via Tygon® tubing to a customised Infrared Gas Analyzer (IRGA) field kit (S151 CO₂ Analyzer; Qubit Systems). The chamber atmosphere was circulated and allowed to equilibrate at a flow rate of 150 ml min⁻¹ for several minutes until CO₂ concentrations readings stabilised in the chamber. Changes in headspace concentration measurements were recorded for 3 to 5 minutes and repeated when rates appeared unstable. The short measurement period aimed to minimise differences between ambient and chamber CO₂ concentrations, avoiding “chamber effects” where high CO₂ concentrations in chambers alter diffusion rates of CO₂ from soils (Davidson et al., 2002).

FCO₂ was measured every three weeks beginning early August 2010 until October 2010, and between late June and October in 2011 and 2012. Just before these measurements, air temperatures in the chambers were documented. To minimise daytime soil temperature differences, FCO₂ was measured
between 10 am and 4 pm on consecutive days. The number of sampling points (n=75) and distribution over a large area necessitated a 2 to 3 day collection period. To avoid FCO$_2$ “flushing” effects, measurements were not taken within 24 hours of significant rain events (Laporte et al., 2003). To calculate changes in the mass of CO$_2$ produced by area over time, FCO$_2$ rates were determined by using chamber CO$_2$ headspace concentrations and expressed as µmol CO$_2$ m$^{-2}$ s$^{-1}$. Soil temperatures were monitored using a probe inserted to a 5 cm depth beside the soil collar. During each FCO$_2$ measurement, soil core samples (5 cm depth) were collected adjacent to collars and oven-dried to determine gravimetric moisture content. Software analysis of hemispherical canopy photos was used to determine post-harvesting canopy openness and light diffusion (Regent Instruments WinScanopy version 2014a). Data from two subplots were discarded due to persistent flooding, which substantially inhibited FCO$_2$ rates relative to other subplots (adjusted total n=73).

2.3.4 Q$_{10}$ and Modelling Temperature-Adjusted Respiration Rates

To account for spatial heterogeneity in respiration rates, Q$_{10}$ was calculated for each subplot based on the van’t Hoff equation method used by Linder and Troeng (1981). A regression equation was defined from the natural logarithm of soil FCO$_2$ and temperature (°C) measurements between mid-summer and autumn values for each year (n=4-5):

\[
\ln(R_S) = \beta_0 + \beta_1 \times \text{Temperature \ °C} 
\]  

(1)

The $\beta_1$ coefficient was used to calculate Q$_{10}$:

\[
Q_{10} = e^{(\beta_1 \times 10)} 
\]  

(2)

Q$_{10}$ can be used to model FCO$_2$ rates at various temperatures. This approach was used to standardise measured FCO$_2$ values to 10 °C ($R_{10}$), producing “basal” respiration rates (Davidson et al., 2006; Acosta et al., 2008):

\[
R_{10} = R_S \times Q_{10}^{[(10-7)/10]} 
\]  

(3)

Basal respiration rates for each subject can differ substantially from those at higher temperatures due to differences in Q$_{10}$ values. To account for this effect, “peak” respiration rates at 20 °C ($R_{20}$) were calculated as the product of $R_{10}$ and Q$_{10}$:

\[
R_{20} = R_{10} \times Q_{10}^{[(20-10)/10]} 
\]  

(4)
R10 and R20 values were used to compare the theoretical upper and lower limits of FCO2 between treatments and to demonstrate seasonal patterns independent of temperature. However, to evaluate both seasonal and temperature dependent patterns of Rs that corrected for temperature differences between treatments and sampling locations, R10 and Q10 values were used to predictively model FCO2 rates (R_{Smean}) standardised to the mean control treatment temperature value from each measurement date.

\[ R_{Smean} = R_{10} \times Q_{10}^{\left[\frac{\left(T_{mean}-10\right)}{10}\right]} \]  

(5)

To compare changes to respiration associated with harvesting, the difference between mean TL and BIO treatment values and unharvested control values for each measurement date were used to determine the effect size of harvesting treatments. The magnitude of effect sizes were calculated as a proportion of the mean control value (except where otherwise indicated). For example:

\[ \frac{(R_S(TL \ or \ BIO) - R_S(control))}{R_S(control)} \times 100 = \% \ effeect \ size \]  

(6)

2.3.5 Hypothesis Testing and Statistical Methods

A linear mixed model (LMM; SPSS v.21) was used to test the hypothesis that harvesting affected Rs, R10, R20, R_{Smean}, and Q10 and to determine if temporal trends were associated with this effect (i.e., seasonal trends and differences across years). Each subplot was measured multiple times during each of three successive growing seasons (e.g., sampled in September for three consecutive years). This subject-based dependence was accounted for by including two nested within-subject factors (date within year) as repeated measures in the LMM, except for Q10 values which only used year since they were derived annually. Subplots were considered the first level in the model (subject). A variance component analysis using restricted maximum likelihood tests indicated no significant random effect (i.e., dependence) for subplots nested in plots/blocks, and Akaike’s Information Criteria (AIC) score values favoured a parsimonious marginal model using an unstructured covariance structure. Univariate (ANOVA) multiple comparison tests and pairwise post-hoc tests were used to interpret simple effects associated with significant interactions between year, date, and treatment effects. Significance tests used Fisher’s unrestricted least significant difference (LSD) method rather than more conservative corrections due to the low number of treatment groups and to better understand complex interaction effects without unnecessary loss of power (Saville, 2003).
All FCO₂ (R₅, R₁₀, R₂₀, and R₅mean) and Q₁₀ data were log-transformed prior to analysis to better fit the LMM assumptions of normal distribution, accounting for considerable skew and kurtosis and some heteroscedasticity in residuals (Peng et al., 2008; Herbst et al., 2009). Results were back-transformed and represented in units of µmol m⁻² s⁻¹. Mean annual respiration values and standard errors for each treatment group were calculated from the average of measurement date values for each subject within each year. Back-transformation produced uneven sized standard errors due to log transformations.

2.4 Results

2.4.1 Changes to Forest Structure Following Harvest

The basal area of trees for both harvesting treatments decreased significantly following harvest (TL: -27.1%, BIO: -27.8%; p≤0.001) and the residual basal area was significantly lower than in the control treatment (p≤0.001) (Table 2.1). Most of the removed basal area was in the >25 cm DBH size class (canopy trees), and the residual basal area and density of trees <25 cm DBH size class (understorey trees) did not differ significantly between treatments. Residual forest cover remained predominantly deciduous in all treatments (CTRL: 86.7%, TL: 73.9%, BIO: 76.0%), of which sugar maple was the main component (44.5%, 33.1%, 36.0%). There was no evidence of re-sprouting from cut trees.

Harvesting significantly increased FWD volumes in both harvesting treatments (Table 2.2; TL: +113.5, BIO: +41.9%, p≤0.01), producing residual volumes twice those of the control treatment (TL/BIO: 230.0%/+208.2%; p≤0.01). The TL treatment accrued nearly twice the volume of new FWD as the BIO treatment (+92%, p≤0.10), where the retrieval of tops and branches for biomass were a function of treatment design. The number of pieces of coarse woody debris (CWD) also increased significantly in TL and BIO treatments (TL: +37.0%, BIO: +18.4%, p≤0.05), and was higher than in the control treatment (TL: +58.9%, p≤0.05; BIO +39.5%, p≤0.10). In spite of this, CWD volumes did not change following harvest and remained insignificantly higher for harvested treatments; this was likely due to physical damage to existing CWD from machinery at rates similar to accrual.

Sapling basal area (includes all woody stems 2-8 cm DBH) declined in all treatments following harvest in 2010. This decline was more substantial in the TL and BIO treatments (-20.1%, p≤0.05 and -17.3%, p≤0.10) than in the control (-4.4%, p=>0.10), but values did not differ significantly amongst treatments before or after harvest, either by species or total basal area. Sapling basal area increased significantly in the following two years (Control: +21.8%, TL: +18.3, p=>0.10; BIO: +29.6%, p≤0.10) indicating initial
losses in harvested treatments had regrown to pre-harvest levels by 2012, but values in the control
treatment had increased similarly.

Table 2.1 Pre and post-harvest mixed deciduous forest tree properties in Central Ontario, Canada (control – unharvested, TL – tree-length harvest, BIO – biomass harvest, QMD – quadratic mean diameter), ± = standard error of the mean.

<table>
<thead>
<tr>
<th>Tree</th>
<th>Basal Area (m²/ha)</th>
<th>Density (#/ha)</th>
<th>QMD (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Timing</td>
<td>Treatment</td>
<td>Total</td>
</tr>
<tr>
<td>Pre: 2009</td>
<td>Control</td>
<td>28.29±1.37</td>
<td>4.32±0.60</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>28.19±1.64</td>
<td>4.71±0.52</td>
</tr>
<tr>
<td></td>
<td>BIO</td>
<td>28.89±2.58</td>
<td>6.04±0.75</td>
</tr>
<tr>
<td>Post: 2010</td>
<td>Control</td>
<td>28.27±1.37</td>
<td>4.31±0.60</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>20.35±1.63</td>
<td>3.87±0.46</td>
</tr>
<tr>
<td></td>
<td>BIO</td>
<td>21.05±1.97</td>
<td>5.15±0.79</td>
</tr>
</tbody>
</table>

Table 2.2 Pre and post-harvest mixed deciduous forest sapling basal area (woody stems 2-8 cm DBH) and downed woody debris volume in Central Ontario, Canada (control – unharvested, TL – tree-length harvest, BIO – biomass harvest, CWD – coarse woody debris, FWD – fine woody debris), ± = standard error of the mean.

<table>
<thead>
<tr>
<th>Sapling</th>
<th>Basal Area (m²/ha)</th>
<th>CWD (m³/ha)</th>
<th>CWD (m³/ha)</th>
<th>FWD (m³/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Timing</td>
<td>Treatment</td>
<td>&lt;25 cm</td>
<td>&gt;25 cm</td>
</tr>
<tr>
<td>Pre: 2009</td>
<td>Control</td>
<td>1.28±0.36</td>
<td>222±18</td>
<td>51.77±6.51</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>1.60±0.30</td>
<td>244±29</td>
<td>68.68±9.11</td>
</tr>
<tr>
<td></td>
<td>BIO</td>
<td>1.56±0.56</td>
<td>248±29</td>
<td>69.67±15.41</td>
</tr>
<tr>
<td>Post: 2010</td>
<td>Control</td>
<td>1.22±0.18</td>
<td>210±14</td>
<td>48.26±5.60</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>1.28±0.28</td>
<td>334±49</td>
<td>72.26±10.69</td>
</tr>
<tr>
<td></td>
<td>BIO</td>
<td>1.29±0.48</td>
<td>294±25</td>
<td>67.01±12.86</td>
</tr>
<tr>
<td>Post 2012</td>
<td>Control</td>
<td>1.49±0.32</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>TL</td>
<td>1.51±0.60</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>BIO</td>
<td>1.67±0.24</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>
2.4.2 Post-Harvesting Temporal Variations Amongst Measured R\textsubscript{S} Effect Sizes

Overall mean R\textsubscript{S} rates for the study period were higher for the TL and BIO treatments than unharvested controls (+18.6% and +15.2%), but the main effect of harvesting on R\textsubscript{S} was not significant (p=0.101; Table 2.3). However, a highly significant three-way interaction effect between treatment, date, and year (p=0.001; Table 2.3; Fig. 2.2) indicated that R\textsubscript{S} in harvesting treatments differed significantly from controls during specific measurement periods. Harvesting treatment values measured in early August 2010 were roughly the same or lower than those of the controls (TL: −5.9%, BIO: +0.7%; p=>0.10). This trend began to reverse in late August, when R\textsubscript{S} rates for both harvesting treatments exceeded those of controls (TL: +4.6%, BIO: +20.3%; p=>0.10). By September 2010, effect sizes became the highest recorded for the entire study period (TL: +43.2%, BIO: +39.2%; p≤0.01). A recurring pattern of larger effect sizes in the autumn (average of September and October: +17.4 to +27.8%, p≤0.05) and smaller effect sizes in mid-summer (average of July and August: +10.1 to +14.4%, p=>0.10) was found. Soil respiration rates remained higher in harvesting treatments than the control treatment until October 2012, when the rate in the BIO treatment declined to the lowest level measured during the study (−9.5%; p ≥ 0.10).

Table 2.3 Linear mixed model significance test results of main and interaction effects for soil carbon dioxide efflux (FCO\textsubscript{2}) from measured soil respiration (R\textsubscript{S}), soil respiration modelled at mean control treatment temperature values (R\textsubscript{Smean}), 10 °C (R\textsubscript{10}), and 20 °C (R\textsubscript{20}), the response of R\textsubscript{S} to temperature over a 10 °C range (Q\textsubscript{10}), and soil temperatures (Temp) for a mixed deciduous forest in Central Ontario. Also test results for the number of pieces of coarse woody debris (CWD\#) and volume of fine woody debris (FWD). Significant results in bold.

<table>
<thead>
<tr>
<th>Independent Factor</th>
<th>DF</th>
<th>Significance (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source</td>
<td>R\textsubscript{S}</td>
<td>R\textsubscript{Smean}</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Harvest (treatment effect)</td>
<td>2</td>
<td>0.101</td>
</tr>
<tr>
<td>Date (measurement date)</td>
<td>5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Year (year post-harvest)</td>
<td>2</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Harvest*Date</td>
<td>10</td>
<td><strong>0.003</strong></td>
</tr>
<tr>
<td>Harvest *Year</td>
<td>4</td>
<td>0.782</td>
</tr>
<tr>
<td>Date*Year</td>
<td>7</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Harvest<em>Date</em>Year</td>
<td>14</td>
<td><strong>0.001</strong></td>
</tr>
</tbody>
</table>
2.4.3 Influence of Insolation, Temperature, and Moisture on Respiration

Canopy openness and light diffusivity measurements collected during mid-summer 2010 were significantly higher in TL and BIO treatments than in controls (openness: +36.3% and +18.5%; diffusivity: +35.3% and +14.7%; p≤0.001), and were strongly correlated with soil temperature values averaged by plot (r²=0.41 and 0.33, p≤0.05). Mean annual soil temperatures (Table 2.4) were also significantly higher for both TL and BIO treatments in 2010 (+0.53 °C and +0.69 °C, p≤0.001) and 2011 (+0.83 °C and +0.43 °C, p≤0.001); values declined significantly by 2012, but remained higher than controls (+0.55 °C and +0.31 °C, p≤0.001). Mean annual soil temperatures had small coefficients of variation (CV) (2010: 3.5%; 2011: 4.7%; 2012: 4.8%) that varied little amongst treatments, indicating low spatial variability.

Moderately strong relationships were found between soil temperature and log-transformed \( R_S \) data pooled by year (2010, 2011, 2012: \( r^2 = 0.46, 0.43, 0.27; p≤0.001 \)), comparable with that found by Raich and Schlesinger (1992) for temperate deciduous forests (\( r^2 = 0.31 \)), but relationships within specific dates were generally insubstantial. Fitting individual regression lines for each subplot within every year produced stronger relationships (median annual \( r^2 \) for 2010/11/12 = 0.91/0.85/0.75, n=4-5), and results were generally significant at p≤0.10, making temperature a better predictor of \( R_S \) within years at the subject level.
Relative to temperature, mean annual gravimetric soil moisture values to a 5 cm depth had a high spatial variability (CVs for 2010, 2011, 2012: 48.7%, 55.4%, 47.0%), and values did not differ significantly amongst treatments. Soil moisture was generally lowest in summer with higher CVs (2010: 62.3%; 2011: 65.9%; 2012: 53.5%) and declined significantly from 2010-12 across all treatments with changes to precipitation (Table 2.4). Mean soil moisture values by measurement date were strongly correlated with total regional precipitation within the last 20 days ($r^2=0.50$, n=13, $p\leq0.01$); this relationship did not vary by treatment, and was stronger when the wetter 2010 year was excluded ($r^2=0.85$, n=9, $p\leq0.01$).

Several studies have found weak but significant relationships between soil moisture and FCO$_2$ (Laporte et al., 2003; Peng and Thomas, 2006; Webster et al., 2008) using linear, quadratic, or logarithmic functions. In my study, soil moisture values pooled by year were best correlated with log-transformed $R_s$ (2010: $r^2=0.02$, n=292, $p\leq0.05$; 2011/12: $r^2=0.06/0.05$, n=438/364, $p\leq0.001$); effects were strongest in the summer of 2012 ($r^2=0.09$, $p\leq0.001$) but disappeared by autumn. Results for data pooled within specific dates and treatments and subplot-level comparisons were inconsistent, and differences generally insubstantial. When soil moisture was used as a covariate in the LMM analyses, a significant interaction effect between FCO$_2$ and year had minimal impact on model adjusted means, slightly increasing TL treatment effect sizes (=1%) in 2012 but not affecting patterns or significance values. Therefore, since soil moisture did not substantially contribute to treatment differences it was excluded from the final models.

2.4.4 Temporal Changes to $R_{\text{Smean}}$ Effect Sizes and the Influence of Temperature on $R_s$

Temporal effect size patterns remained intact after correcting for temperature differences as $R_{\text{Smean}}$, but were lower than for $R_s$ values, and the main effect of treatment on $R_{\text{Smean}}$ was insignificant (Table 2.3). Annual $R_s$ effect sizes peaked by 2010-2011 and had either plateaued (TL) or declined (BIO) by 2012 (Fig. 2.3a). In comparison, annual $R_{\text{Smean}}$ effect sizes increased modestly between 2010-12 for the TL treatment and remained stable in the BIO treatment (Fig. 2.3a). The difference between $R_s$ and $R_{\text{Smean}}$ effect sizes represents the estimated proportion of the $R_s$ effect size explained by differences in soil temperature between harvested and control treatments (Fig. 2.3b). In 2010, temperature differences accounted for 34.0 to 40.7% of $R_s$ effect sizes for the TL and BIO treatments; by 2012, these declined to 15.6% and 10.6%.
Figure 2.3 a) Mean annual soil carbon dioxide efflux ($\text{FCO}_2$) effect sizes (%) for $R_s^1$ and $R_{\text{mean}}^2$ comparing harvested treatments (tree-length harvesting – TL; biomass harvesting – BIO) to unharvested controls for a mixed deciduous forest in Central Ontario. Asterisks denote significant post-hoc pairwise test differences between harvested treatments and control values within each year (*$p$≤0.10, **$p$≤0.05). Error bars = standard error for differences of means; b) Modelled proportion of annual $R_s$ effect sizes accounted for by temperature differences between harvested (TL and BIO) and control treatments represented by the difference between annual $R_s$ and $R_{\text{mean}}$ values. Error bars = standard error for differences between $R_s$ and $R_{\text{mean}}$ values. $^1R_s =$ Measured soil respiration; $^2R_{\text{mean}} =$ soil respiration modelled to mean control treatment values.

The interaction effect between treatment, date, and year remained highly significant ($p$=0.002) for $R_{\text{mean}}$, and seasonal effect size patterns for closely resembled those of $R_s$. $R_{\text{mean}}$ effect sizes for August 2010 were even lower than $R_s$ values (TL: $-8.8\%$, BIO: $-3.8\%$; $p$=>0.10), suggesting that post-harvest $\text{FCO}_2$ rates may have been initially depressed relative to controls in spring/early summer 2010. Seasonal effect sizes in autumn (averaged September and October values) were lower than for $R_s$ values but remained substantial; these declined from 2010-2012, though more modestly for the higher TL treatment values (+26.7% to +20.2% $p$≤0.05) than the lower BIO treatment values (+19.2 to +1.7%; $p$=>0.10) (Fig. 2.4). In contrast, summer $R_{\text{mean}}$ effect sizes (averaged July and August) were more substantial for the BIO treatment, but both treatments increased similarly from 2010-2012 (TL: $-4.5\%$ to $+10.7\%$; BIO: $+4.2\%$ to $16.7\%$; $p$=>0.10).
Figure 2.4 Mean annual autumn (September/October) and summer (July/August) soil carbon dioxide efflux (FCO$_2$) effect sizes (%) for R$_{\text{mean}}$ comparing harvested treatments (tree-length harvesting – TL, biomass harvesting – BIO) to unharvested controls for a mixed deciduous forest in Central Ontario. Asterisks denote significant post-hoc pairwise test differences between treatment and control values within each year (*p≤0.10, **p≤0.05). Error bars = standard error for differences of means. $^1$R$_{\text{mean}}$ = soil respiration modelled to mean control treatment values.

2.4.5 Post-Harvesting Changes to Basal and Peak Respiration Rates and Q$_{10}$

Mean annual Q$_{10}$, R$_{20}$, and summer R$_{\text{mean}}$ values declined from 2010 to 2012 across all treatments despite no significant changes to annual peak temperatures for the same periods. This decline was more substantial in the control treatment (Table AI-I), accounting for increasing summer and peak respiration effect sizes. During 2010, harvested treatments had higher basal respiration rates (R$_{10}$ = TL/BIO: +26.1%/+15.0%, p=>0.10) and lower peak respiration rates (R$_{20}$ = TL/BIO: −13.8%/-1.8%, p=>0.10) than the control treatment (Fig. 2.5), decreasing the seasonal range of R$_S$ relative to temperature and producing significantly lower Q$_{10}$ values (TL/BIO: −31.7%/-17.8%, p=0.001) (Fig. 2.6). Within 2 years this trend had reversed: harvested treatment R$_{20}$ values substantially exceeded those of the control treatment (TL: +18.2%, p=>0.10; BIO: +34.8%, p<0.05), while R$_{10}$ values remained elevated in the TL treatment and declined substantially in the BIO treatment (+15.0% and -0.6%, p=>0.10). This shift was reflected in the 2012 Q$_{10}$ values, with the TL treatment reaching parity (+2.7%, p=>0.10) and the BIO treatment surpassing the control treatment (+35.6%, p<0.05). Model interaction effects between treatment and year indicate these shifting patterns were significant for Q$_{10}$ and R$_{20}$ (p<0.05). Londo et al. (1996) also found Q$_{10}$ values to be higher 16 months after partial harvesting than in controls (+20.1%), but instead noted lower basal rates (-10.5%) and only slightly elevated peak rates (+5%).
Figure 2.5 Mean annual soil carbon dioxide efflux (FCO₂) effect sizes (%) for soil respiration modelled to 10 °C (R₁₀) and 20 °C (R₂₀) comparing harvested treatments (tree-length harvesting – TL, biomass harvesting – BIO) to unharvested controls for a mixed deciduous forest in Central Ontario. Asterisks denote significant post-hoc pairwise test differences between treatment and control values within each year (*p≤0.10, **p≤0.05). Error bars = standard error for differences of means.

Figure 2.6 Mean annual Q₁₀ effect sizes (%) comparing harvested treatments (tree-length harvesting – TL, biomass harvesting – BIO) to unharvested controls for a mixed deciduous forest in Central Ontario. Asterisks denote significant post-hoc pairwise test differences between treatment and control values within each year (*p≤0.10, **p≤0.05). Error bars = standard error for differences of means. ¹Q₁₀ = The response of measured soil respiration to changes in temperature over a range of 10 °C.

2.5 Discussion

2.5.1 Comparing Temporal Changes in Rₛ Effect Sizes to Similar Studies

Model interaction effects were significant for changes to the magnitude of respiration effect sizes between seasons over years (Table 2.3). A transition from negative to positive Rₛ effect size values by autumn 2010, higher FCO₂ rates than the control treatment throughout most of the study period (Fig. 2.2), and recurring seasonal effect size patterns indicated that harvesting increased FCO₂ rates and influenced seasonal biogeochemical soil processes. Londo et al. (1999) found that 1³ year post-harvest Rₛ effect sizes were smallest in summer (<10%) and peaked in autumn (+50 to +65%) following a partial
harvest in a Texas bottomland forest, comparable to average summer (-5 to +5%) and September R5 effect sizes (+39 to +43%) in 2010. Peng and Thomas (2006) also showed a R5 effect size peak in September (+33 to +55%), two months after a summer selection harvest equivalent to the TL treatment. Harvested treatment R5 values remained substantially elevated after 2-3 years (+14 to +19%), similar to 3rd year values from a commercially thinned mixed-conifer forest (+10 to +35%, p≤0.05) ≈125 km east of my study site (Hendrickson et al, 1989) and 7th year values in a thinned hardwood forest in Missouri (+14%; Concilio et al., 2005). Higher 2nd year post-thinning values (+43%) have been reported from mixed-conifer forests in the Sierra Nevada region (Ma et al., 2004; Concilio et al., 2005), whereas other study areas that had also been burned or subject to seasonal moisture limitations showed no change or decreases to FCO2 (Ma et al., 2004; Tang et al., 2005).

Examples from mixed deciduous forests employing similar management techniques as ours have shown different responses. Stoffel et al. (2010) found no change in FCO2 within 2 years of a partial-harvest; they attribute this to minimal forest floor disturbance and minimal and non-significant temperature difference from the control. Their split-plot design targeted gap and non-gap subplots and contrasted them with uncut subplots; while pre-harvest measurements indicated the number of replications were sufficient to account for spatial heterogeneity of R5, they may not have been sufficient to account for the spatial heterogeneity of harvesting treatment effects. In contrast, a chronosequence study using a 10 year baseline as a control in the same forest area as my study (Peng and Thomas (2006) found annual effect sizes had become negative (~20 to ~40%) within 2 to 3 years of harvesting, despite no apparent moisture restrictions to R5. This discrepancy in the same forest system as ours may be related to the timing of data collection and seasonal variations in effect sizes. Their annual FCO2 and temperature values for years 2-6 were averaged across monthly measurements between June and November 2003, while baseline and 1st year values were measured only once in September 2004. Additionally, their mean baseline soil temperatures in September (15 °C) were exceptionally high compared to my control treatment (11.7 °C); when corrected to 15 °C, control treatment values in September were 2-8% higher than mean annual values. Furthermore, substantial inter-annual variation in the control treatment R5 (CV: 9%) was more pronounced for September only (CV: 16%). These factors suggest that both baseline and 1st year measurements from Peng and Thomas (2006) could be somewhat inflated relative to years 2 to 6, accounting for a portion of negative effect sizes. This emphasises the need to account for seasonal and inter-annual variations to accurately define effect sizes, particularly in a “space for time” chronosequence analysis of a spatio-temporally heterogeneous system.
2.5.2 Declining Annual Precipitation and Soil Moisture as a Control on Q\textsubscript{10}, and Peak Respiration

Control treatment Q\textsubscript{20} values in 2010 (3.6) and 2011 (2.5) were consistent with those found in managed temperate forests across North America and China (Boone et al., 1998; Davidson et al., 1998, 2006; Peng and Thomas, 2006; Wang et al., 2006). However, a particularly low value in 2012 (1.7), and declining annual summer R\textsubscript{Smean}, R\textsubscript{20}, and Q\textsubscript{10} values across all treatments indicated a change to an ecosystem-scale factor regulating R\textsubscript{S}. These changes were not related to annual peak temperatures, but may have been driven by annually declining summer precipitation volumes (Table 2.4) affecting soil moisture supplies. Annual Q\textsubscript{10} values in forest soils are correlated with soil moisture (Olajuyigbe et al., 2012), and R\textsubscript{S} is inhibited when available moisture cannot meet biological demands (Davidson et al., 1998, 2006). The shallow, sandy loam soils and hilly topography in the study region are not optimal for moisture retention, and total precipitation for 20 days prior to each measurement date in 2011 and 2012 explained most of the variation in summer soil moisture values. Additionally, R\textsubscript{20} and summer R\textsubscript{Smean} values pooled across all years were correlated with summer soil moisture values (r\textsuperscript{2}=0.12 and 0.08; n=424, p≤0.001); these relationships were strongest in 2012 (r\textsuperscript{2}=0.13, 0.11; n=145, p≤0.001) when soil moisture was lowest. Correlations improved after accounting for the high spatial variability of soil moisture by using R\textsubscript{20} and R\textsubscript{Smean} values averaged by year and treatment (r\textsuperscript{2}=0.79, 0.74; n=9, p≤0.01). Q\textsubscript{10} values demonstrated a similar relationship with soil moisture (r\textsuperscript{2}=0.82; n=9, p≤0.001), while no significant relationships were found for R\textsubscript{10} and autumn R\textsubscript{S} values. These results suggest that declining annual summer precipitation inputs reduced annual soil moisture levels. In turn, this limited peak respiration rates during periods of high evapotranspiration, presumably by restricting R\textsubscript{S} when demands for soil moisture exceeded supply, and contributed to the annual decline in Q\textsubscript{10} values for all treatments over the study period.

Removal of tree cover in harvested treatments may have differently affected respiration and Q\textsubscript{10} values than in the control treatment by reducing evapotranspiration demands and moisture limitations. However, beta coefficient and r\textsuperscript{2} values for linear regressions between R\textsubscript{Smean}, R\textsubscript{20}, Q\textsubscript{10}, and soil moisture values did not differ significantly amongst treatments, either within or across years, and soil moisture values were often lower in harvested treatments than controls. These data suggest that the smaller annual decline in peak respiration and Q\textsubscript{10} for harvested treatments was not related to differences in soil moisture demands by respiration following harvesting. Alternatively, soil moisture samples may have been too shallow (5 cm) to detect harvesting impacts on soil moisture supply and use by roots.
2.5.3 The Dynamic Influence of Temperature on $R_S$ Effect Sizes

Higher soil temperatures in harvested treatments were correlated to canopy openness, indicating that increased soil insolation from canopy thinning might be partially responsible for elevated $R_S$ effect sizes. These temperature differences accounted for 33-41% of $R_S$ effect sizes in 2010, but declining differences and increasing $Q_{10}$ effect sizes substantially reduced the influence of temperature on $R_S$ effect sizes by 2012. These changes may be related to forest recovery; growth rates of shade-tolerant understorey vegetation often increase in response to canopy gaps from selection harvests (Beaudet et al., 2004; Jones et al., 2009). The basal area of understorey trees adjacent to canopy gaps can increase twice as much as canopy trees within 5 years of harvest (Jones and Thomas, 2004), and regrowth of sapling and shrubs can decrease light penetration near the forest floor more rapidly than at canopy height (Beaudet et al., 2004; Domke et al. 2007). In my study, post-harvesting losses of sapling basal area regrew to pre-harvest levels by 2012, and the difference in annual soil temperatures in harvested plots between 2010 and 2012 was 1.02 °C lower for every 1 m$^2$ increase in sapling basal area from 2010 to 2012 (Fig. 2.7a; $r^2=0.45$, n=10, p≤0.05). Additionally, every 1 m$^2$ of total residual understorey basal area (trees <25 cm DBH, saplings, and shrubs) in harvested plots predicted a 0.28 °C decrease in soil temperatures during the summer of 2012 (Fig. 2.7b; $r^2=0.63$, n=10, p≤0.01).

![Figure 2.7 a) Relationship between decreasing annual average soil temperatures and increases to sapling basal area between 2010 and 2012, and; b) Relationship between post-harvest understorey basal area (vegetation <25 cm DBH) and summer soil temperatures in 2012. Corrected for inter-annual differences in control treatment values.](image)

These results reveal that post-harvest soil temperature differences from canopy thinning initially contributed substantially to effect sizes, and understorey regrowth eventually reduced temperature differences amongst treatments by 2012. Even with this decline, $R_S$ remained elevated in harvested treatments, indicating that factors other than temperature were increasingly governing effect sizes during forest recovery. Despite strong evidence of moisture limitations to peak respiration in
2011/2012, there was no substantial influence of soil moisture on effect sizes. Although not well documented, the supply and quality of soil substrates (as root photosynthate supplies, leaf litter, root necromass) can contribute to spatio-temporal variations to $Q_{10}$ (Davidson and Janssens, 2006) by altering seasonal peak and basal respiration rates. $Q_{10}$ represents the product of true substrate temperature sensitivity and the seasonality of moisture and substrate availability; values may be elevated where temperature and substrate supply positively co-vary (Davidson et al., 2006). Therefore, significant increases to annual $Q_{10}$ effect sizes by 2012 suggests that effect sizes were influenced by changes to forest and soil properties during recovery that altered the contribution and utilisation of substrate supplies.

2.5.4 Seasonal Changes to Contributions of $R_R$ and $R_H$ to $R_S$

Dynamic patterns of seasonal $R_S$ and inter-annual $Q_{10}$ effect sizes may have been influenced by post-harvesting changes to environment-driven physiological mechanisms regulating the seasonal contributions of $R_R$ and $R_H$ to $R_S$. Although my sampling design did not distinguish amongst these, a comparison of studies that measured seasonal changes to $R_R$ and $R_S$ in unharvested northern forests revealed that the ratio of $R_R$ to $R_S$ is generally highest in mid-summer ($53\pm11\%$: mean ± SD), when photosynthesis rates and temperatures peak, and lower in autumn ($25\pm11\%$) as photosynthate availability and consumption in roots declines as trees prepare for winter dormancy (Hanson et al., 2000; Högberg et al., 2001; Lee et al., 2003; Bond-Lamberty et al., 2004; Jiang et al., 2005; Yang and Wang, 2006; Sampson et al., 2007; Irvine et al., 2008; Ruehr and Buchmann, 2010). This effect can persist even after correcting for temperature differences using $Q_{10}$ (Widén and Majdi, 2001) or by heating roots excised during different seasons to the same temperature (Jarvi and Burton, 2013), demonstrating that phenology can regulate $R_R$ independent of temperature and by different physiological mechanisms than $R_H$.

2.5.5 Post-Harvest Substrate Supplies and Respiration: Root Senescence and Harvest Residues

Tree death is related to reductions in $R_R$; Högberg et al. (2001) showed that girdled trees can decrease $R_R$ by 50% within 5 days and cease respiring entirely within 2 months once supplies of photosynthates are depleted. Since root biomass is generally proportional to aboveground biomass (Jenkins et al., 2003), the amount of root dieback and associated reduction to $R_R$ is likely proportional to the amount of harvested biomass. Summer $R_{\text{Smean}}$ values averaged by plot were negatively correlated with removed total vegetation basal area (Fig. 2.8a, b, c; 2010, 2011, 2012: $r^2=0.58$, 0.64, 0.43; n=10, p≤0.05) when
R_s is potentially highest, but not during the autumn when R_s was likely lower. This suggests that summer respiration rates were limited by cut tree biomass, decreasing substrate supplies for R and potentially accounting for recurring lower effect sizes in the summer. Ostensibly, this restriction of R should reduce R_s. Nevertheless, FCO₂ rates were substantially higher in harvested treatments than controls by September 2010 and for the duration of the study. Effect sizes were only partially and decreasingly explained by temperatures differences, could not be attributed to soil moisture, and were highest during autumn when R is lowest. Since the other main component of R_s is R_h, it follows that an increase in labile substrates from harvest residues (e.g., root necromass and woody debris leachate) may have stimulated decomposition rates (Olajuyigbe et al., 2012), sufficiently increasing R_h to exceed reductions to R and accounting for a portion of effect sizes.

Figure 2.8 Relationship between total cut tree and sapling basal area and soil carbon dioxide efflux (FCO₂) for R̄ mean [1] values (grey circles) measured in the summer for 2010 (a), 2011 (b), and 2012 (c) for a mixed deciduous forest in Central Ontario; d) Relationship between post-harvest input volumes of fine woody debris (FWD) and soil carbon dioxide efflux (FCO₂) for R̄ mean [1] values measured in the autumn of 2010 (white circles). The dashed slope line excludes an outlier value (black circle). R̄ mean = soil respiration modelled to mean control treatment values.

Studies have shown that decaying fine roots in mixed deciduous forests can lose ≈17-23% of their dry mass within a year of harvesting, while larger roots lose ≈50% within 5 years (Fahey et al., 1988; Fahey and Arthur, 1994). Woody debris decay rates are highly variable, but FWD decays over twice as fast as...
CWD, and nutrient-rich twigs and small branches disappear quickly from the forest floor (Yanai, 1998; Müller-Using and Bartsch, 2009). Leachate from woody debris can contain higher dissolved organic carbon and nutrient concentrations than leaf litter, enriching the adjacent soil (Hafner et al., 2005). Post-harvesting FWD inputs were strongly correlated with $R_{10}$ and autumn $R_{\text{Smean}}$ values averaged by plot in 2010 (Fig. 2.8d; $r^2=0.58/0.57$, n=10, p=0.01), but not in 2011/12 or with summer $R_{\text{Smean}}$ and $R_{20}$ values; this relationship improved substantially after omitting an outlier value from a plot where the transect-based method to measure FWD failed to capture observed new material (Fig. 2.8d; $r^2=0.90/0.91$, n=9, p≤0.001). Since $R_{10}$ and $R_{\text{Smean}}$ effect sizes were highest during the autumn when $R_{\text{H}}$ is typically low, this relationship suggests that $R_{\text{H}}$ rates may be higher in harvested treatments, and therefore more important to defining basal respiration than $R_{\text{H}}$. Whether FWD inputs contributed directly to respiration or functioned as a proxy for some other forest property (e.g., fine root turnover) was unclear. Sampson et al. (2007) proposed that higher basal respiration rates (as $R_{10}$) in forests are regulated by photosynthesis; however, they might be better described by the predominant substrate pool contributing to $R_{\text{S}}$, and differ during recovery from disturbances.

2.5.6 Forest Regrowth and $Q_{10}$

Intensified growth rates from the release of understorey vegetation into new growing space may have contributed to $R_{\text{S}}$ during post-harvest recovery. Fine roots recover rapidly after harvest, often becoming denser within 5 to 10 years than in uncut mature stands (Yin et al., 1989; Idol et al., 2000; Claus and George, 2005), and production is correlated with $R_{\text{S}}$ (Lee and Jose, 2003). Toland and Zak (1994) and Olajuyigbe et al. (2012) both surmise that $R_{\text{H}}$ is more sensitive to temperature relative to $R_{\text{H}}$ due to the stronger response of $R_{\text{S}}$ to temperature in unharvested forest compared to recently cut areas. Wang et al. (2010) found that a higher $R_{\text{H}}$ increased the $Q_{10}$ of $R_{\text{S}}$, and Boone et al. (1998), and Widén and Madji (2001) both report the $Q_{10}$ of fine root respiration alone to be twice that of $R_{\text{S}}$.

Fine root regrowth was not measured. However, $Q_{10}$ values were found to be lower in harvested treatments than controls shortly after harvesting, followed by a significant increase relative to controls during forest recovery over the next two years. A regression analysis indicated that $Q_{10}$ values in harvested plots increased by 0.37 units from 2010-2012 for every 1 m$^2$ of residual understorey woody vegetation (Fig. 2.9; $r^2=0.80$, n=10, p≤0.001). In conjunction with limitations to summer respiration rates by cut tree biomass, these factors collectively support a potential link between dynamic changes to forest structure and $R_{\text{H}}$, and indicate that forest regrowth may be affecting the $Q_{10}$ treatment signal by increasing $R_{\text{H}}$ contributions to $R_{\text{S}}$. 
2.5.7 Differences Between Harvested Treatments

In general, comparable temporal patterns of $Q_{10}$, temperature, and FCO$_2$ effect sizes between the TL and BIO treatments indicate that the response to harvesting disturbance was regulated by similar factors. However, there were some notable differences. Autumn $R_{S\text{mean}}$ effect sizes declined substantially in the BIO treatment by 2012, while the TL treatment value remained elevated above both the control and BIO values (+20% and +18%, $p \leq 0.10$). In contrast, $Q_{10}$ effect sizes in 2012 were significantly higher in the BIO treatment than either the control or TL treatments; this may have been influenced by a significantly higher total understorey basal area in the BIO treatment (+32%, $p \leq 0.05$). Despite these differences, there was no clear evidence that biomass harvesting differently affected $R_s$ than conventional tree-length methods, and discrepancies in $Q_{10}$ and peak respiration may have been due to non-treatment related differences in post-harvest standing biomass, unquantified environmental variables, or simply insufficient sampling.

2.5.8 Potential Implications for Ecosystem carbon dynamics

My results suggest that selection harvesting of northern hardwood forests may initially decrease $R_R$ and increase $R_H$ via changes to respiration substrate pools (i.e., photosynthates and labile harvest residues), decreasing the ratio of $R_R$ to $R_S$. Consequently, a sufficient decline in $R_R:R_S$ might temporarily reduce net ecosystem production (NEP) even when there is no change in $R_S$ relative to uncut controls (e.g., Mattson and Swank, 1989; Weber, 1990; Toland and Zak, 1994; Laporte et al., 2003). In consideration of the expanse of managed forests worldwide, even small, short-term changes to $R_R:R_S$ could appreciably affect patterns of carbon flux between terrestrial and atmospheric pools. Since forest regrowth increases GPP
and therefore \( R_h \) (Brown et al., 1996; Chapin et al., 2002), this may eventually offset elevated \( R_h \) rates that presumably decline as labile harvest residues are consumed with time.

Furthermore, I found that a higher residual basal area of understorey vegetation may contribute to the recovery of \( R_h \). As such, management of forests for carbon sequestration could focus on enhancing regrowth rates to influence the post-harvest recovery of \( R_h \), potentially minimising reductions to NEP. However, the time required for post-harvest FCO\(_2\) dynamics to recover to pre-harvesting levels remains unclear, as does the extent to which this is affected by harvest intensity and forest structure.

### 2.6 Conclusions

Accounting for spatio-temporal dependence in heterogeneous ecosystems is a key requirement for interpreting ecological and biogeochemical processes. Observed measurements of FCO\(_2\) over three growing seasons revealed that partial harvesting in northern mixed deciduous forests can elevate \( R_S \) and decrease \( Q_{10} \) values by increasing soil temperatures and potentially altering available substrate pools. Recurring seasonal variations to harvesting effect sizes and relationships amongst respiration rates, \( Q_{10} \) values, and post-harvest forest properties suggest that stimulation of heterotrophic respiration can compensate for reduced root respiration following harvest. Subsequent understorey regrowth can quickly reduce soil temperatures but may increase \( R_h \), seen as rising \( Q_{10} \) values. Consequently, post-harvest changes to annual \( Q_{10} \) values may serve as a valuable metric to gauge disturbance and recovery.

These findings agree with the conclusion of Peng and Thomas (2006) and several other studies that post-harvest \( R_S \) dynamics are in large part controlled by \( R_h \), but also suggest an important role of \( R_{hi} \), which has potential implications for NEP. However, the specific processes linking \( R_{hi} \) and \( R_h \) to the decomposition of harvest residues, disturbances in stand and soil structure, and forest regrowth remain unclear. Although methodological issues and biases exist, these uncertainties highlight the need for research to better understand the mechanisms behind the seasonal patterns and post-harvesting response of \( R_h \) and \( R_{hi} \) under a variety of management approaches and their influence on terrestrial carbon cycling.
Chapter 3
Soil nutrient and organic matter losses following tree-length and intensive biomass harvests in a northern mixed-hardwood forest

3.1 Abstract

Decomposition of litter and root turnover comprise the primary nutrient input mechanisms for northern hardwood forest soils. Changes to these processes from harvesting can potentially alter soil nutrient pools. To understand the effect of harvest intensity on nutrient dynamics, I investigated the impact of conventional tree-length (TL) and more intensive biomass (BIO) harvests on exchangeable soil organic matter (SOM) and nutrients in a Central Ontario hardwood forest. Soils were sampled from LFH and mineral horizons prior to, one, and three years following harvest. Principal component analysis (PCA) was used to evaluate complex relationships amongst variables through dimension reduction, and extracted principal component (PC) scores were assessed for significant changes using mixed models.

Partial harvesting decreased extractable dissolved organic carbon and nitrogen (DOC/DON), NH₄⁺, and K (19-46%; p≤0.05) and SOM (6-7%; not significant) by year one in the LFH of TL and BIO treatments, while Mg decreased (16-19%) and Fe increased (8-16%) by year three. Total C also declined in both the LFH and mineral horizons (7-16%). Similar, smaller changes occurred in mineral soils, primarily in the TL treatment. PCA of LFH data produced three PCs explaining ≈77% of the variance. PC1 linked SOM, soil moisture, Ca/Mg/K and Fe/Al⁺, and chiefly represented exchangeable cation pools associated with SOM. Soil moisture, Ca/Mg, NO₃⁻, pH, and % conifer cover loaded on PC2, linking it to moisture regime and vegetation cover, while PC3 was defined by labile compounds (DOC/DON, K/NH₄⁺). Post-harvest scores for PC1 were insignificantly lower in harvested treatments, and a significant decrease to both TL and BIO treatment PC3 and DOC values relative to controls was correlated to increasing soil respiration rates. Mineral soil PCA results were similar but less substantial, indicating that harvesting primarily impacted labile and readily exchangeable nutrients in the LFH layer. Nutrient decline was likely due to a combination of elevated decomposition rates, increased immobilization by decomposers, and possible leaching losses.
3.2 Introduction

Temperate forests in North America and Europe have aggraded substantially over the past 150 years due to improved management and reforestation of agricultural fields and pasture, providing a modest terrestrial carbon (C) sink (Caspersen et al., 2000). However, changes to conventional forestry markets, and attempts to mitigate C emissions from fossil fuels, have spurred growth of wood-based energy in recent years (Richter et al., 2009), eliciting a spate of concerns regarding the long-term effects of intensified management on forest soil productivity and carbon storage (Watmough and Dillon 2003; Janowiak and Webster, 201; Thiffault, et al., 2011). Studies of harvesting impacts in temperate forests have reported a wide range of effects, including declining C, nitrogen (N), phosphorous (P), and certain base cation concentrations (K, Ca, Mg) (Yanai, 1998; Yanai et al., 1999; Watmough and Dillon, 2003; Lal, 2005; Kreutzweiser et al., 2008; Thiffault et al., 2011; Zummo and Friedland, 2011). In many cases, losses increase with harvest intensity, such as whole tree and stump extraction (Johnson and Curtis, 2001; Thiffault, et al., 2011), predominant tree cover and soil order (Johnson and Curtis, 2001; Nave et al., 2010), greater physical disturbance of the forest floor (Zummo and Friedland, 2011) and in areas with less productive soils, particularly in regions with poorly buffered soils and acidic parent materials (Watmough and Dillon, 2003). Others report minimal losses of C, N, and Ca (Johnson and Curtis, 2001; Yanai et al., 2003; McLaughlin, 2014), indicating that changes may be dependent on a combination of factors such as soil characteristics, site topography, ecosystem type, climate, and harvest prescription.

The nature of partial harvesting disturbances to soil chemistry tend to be highly variable and clustered due to the heterogeneous distribution of rooting zones, residual woody debris, and physical disturbances from machinery. In the short term, root senescence decreases competition for resources amongst remaining vegetation (Tang et al., 2005) and possibly heterotrophs, while increases to harvest residues such as fine root necromass and woody debris provide a potential source of labile substrates for decomposers, particularly as DOC (Hafner et al., 2005; Zummo and Friedland, 2011; Shabaga et al., 2015). Improved access to nutrients and labile substrates can stimulate microbial activity, increasing rates of decomposition, N mineralisation, and nitrification (Bormann and Likens, 1979; Qualls et al., 1991; Yanai et al., 1999; Cleveland et al., 2004; Hafner et al., 2005; van Hees et al., 2005). This may also alter the dynamics and availability of exchangeable labile C pools and induce a “priming” effect on the rates of decomposition of recalcitrant SOM, particularly where physical breakdown of aggregates and mixing occurs and in soils receiving labile DOC exported from the disturbed LFH (Kuzyakov et al., 2000; Paul, 2007; Blagodatskaya and Kuzyakov 2008; Crow et al., 2009; Zummo and Friedland, 2011), potentially decreasing existing soil organic matter (SOM) pools. Decomposition of SOM may also alter
the sorption of cations to colloids and the stability of metal complexes with DOM (Sollins, 1996), leading to losses of soluble cations via leaching and uptake (e.g., K, Mg, Ca), and potential mobilisation of acid-cations such as Fe and Al. Losses of non-acid cations can increase the saturation of recalcitrant Al and Fe in the cation exchange complex, potentially acidifying the soil solution.

These effects may be differently represented throughout the vertical soil profile. The LFH layer, or forest floor horizon, is a composite of forest litter, fibric, and humic materials of variable thickness serving as the primary source of many soil nutrients, and therefore often contains a high density of fine roots and mycorrhizal mycelium relative to the mineral soil beneath it (Lawrence et al., 1995; Paul, 2007). This pool of nutrients turns over more rapidly compared to more recalcitrant SOM associated with mineral soil deeper in the profile (Chapin et al., 2002), which may differ considerably in content and biogeochemistry from the organic horizon. SOM in the LFH is predominantly formed from turnover of fresh leaf/needle litter, fine roots, and woody debris (Garten, 2009). Sources of SOM in the mineral soil are less clear, but largely generated from root turnover (Rasse et al., 2005; Garten, 2009) and the translocation of dissolved and particulate SOM originating from the LFH (Qualls et al., 1991; Fröberg et al., 2007). Rates of dissolved organic matter (DOM) translocation from the LFH to the mineral soil are often low relative to losses to CO₂ and uptake by plants, even to shallow depths, may vary considerably by location (Fröberg et al., 2007). Additionally, mineral SOM is often more recalcitrant to decomposition due to complex molecular structures and stabilisation with mineral surfaces (Lützow et al., 2006; Kalbitz and Kaiser, 2008). As such, the LFH layer may be more sensitive to ecosystem perturbations from harvesting disturbances than the mineral horizons, influenced by post-harvest fine root and mycorrhizal senescence, woody debris leachate, and SOM disturbance, and expressed as changes in nutrient pools and cycling. Studies of harvesting effects on soil chemistry that do not distinguish between these horizons may therefore be at a disadvantage to detect treatment effects, particularly over short time frames.

Few comparisons of changes to post-harvest soil chemistry have been made between different methods of partial-harvesting management, particularly within the vast range of upland tolerant hardwood forests of eastern North America. Instead, most studies examining the impacts of harvesting for intensified biomass and bioenergy production often contrast standard partial harvest prescriptions for the region with unharvested controls and/or clear-cuts (Kreutzweiser et al., 2008). Furthermore, although many emphasise the role of reduced post-harvesting residue inputs and leaching losses on nutrient decline, few explicitly consider the role of changing biogeochemical mechanisms that may respond to harvesting expressed as unique multivariate patterns amongst various soil chemistry
variables. In this study, I compared the effects of two partial-harvest intensities on soil chemistry relative to unharvested controls prior to, one, and three years after harvest. One treatment consisted of a conventional tree-length selection harvest that retained all crown and branch materials on site, while the other applied a similar but modified method for increased biomass retrieval that removed approximately one-half of the branch and crown materials.

The objectives of this study were to: (i) assess if biomass harvesting reduced soil C and nutrients relative to conventional single-tree selection harvesting methods and unharvested controls based on reduced harvesting residue biomass inputs in a managed mixed deciduous forest in Central Ontario; and (ii) identify potential harvesting disturbance mechanisms based on biogeochemical processes to account for observed changes to soil chemistry. Based on these objectives, I hypothesise that: (i) harvesting will substantially increase woody debris volume relative to controls, with fewer inputs in the BIO treatment relative to the TL; (ii) harvesting will reduce the availability of labile soil C and nutrients relative to controls, but short-term differences between harvested treatments will be insubstantial; and (iii) the magnitude of post-harvest changes to soil chemistry will correlate to measures of harvesting intensity such as woody debris volumes and cut biomass.

3.3 Methods

3.3.1 Study Sites

The study was conducted within the same plot network established in Chapter 2 at Haliburton Forest and Wildlife Reserve. All details, including sample plots, subplots, and treatments are identical to those described in Chapter 2, section 2.3.1.

3.3.2 Forest Mensuration

For each plot, trees >8 cm DBH were tagged and diameter recorded to 0.1 cm prior to harvest in 2009 and after harvesting during the summer of 2010. Volumes of fine woody debris (FWD) were estimated from diameter measurements of downed woody debris pieces 1-10 cm in diameter along five equi-radially distributed transects running 30 m from plot centres. All pieces of downed woody debris >2 m long and >10 cm diameter in the middle were measured and mapped, then used to estimate coarse woody debris (CWD) volumes. Sapling density was estimated from counts of stems (DBH=2-8 cm) within five 50-m² subplots equi-radially distributed 20 m from plot centres.
3.3.3 Soil Sampling and Extraction

Soil samples were collected from five 3-m² soil subplots staggered between sapling subplots. Pre-harvest soil samples were collected in early October 2009 prior to winter harvesting, and one year later in early October 2010. An additional post-harvest set was collected in early October 2012. Separate LFH and mineral soil samples were collected from each subplot. The LFH layer was characterised by poorly consolidated organic materials averaging 4 cm in depth, held together by a dense network of fine roots. Samples were extracted by brushing aside loose litter and carefully separating a 25x25 cm square of sod-like material that readily separated from the underlying mineral soil. Mineral soil samples were then extracted using a dutch auger to a depth of 20 cm. In some cases, soil sample locations were offset to avoid roots, cobble, and woody debris, or where the LFH had been completely removed by harvesting machinery (i.e., on larger skid trails).

Soils were frozen within hours of collection and thawed later for processing. Field-moist mineral soils were sieved to 2 mm. Fine roots, twigs, and leaves (Litter – Oi) were manually separated from LFH samples; the remaining fibric and humic materials, constituting the F (Oe) and H (Oa), were then sieved to 5 mm due to difficulty in passing through smaller screens when moist. Field-moist samples were used to measure DOC, NH₄⁺/NO₃⁻, and total dissolved nitrogen (TDN), as drying can substantially affect the concentrations of some compounds, such as increasing concentrations of DOC and DON 3-10 fold (Jones and Willet, 2006). Soil extracts were prepared from a 5:1 v/w ratio of 0.5M K₂SO₄ to wet soil and agitating on a shaker for 1 h at room temperature (=21 °C). Soil slurries were immediately refrigerated to 4 °C and allowed to settle for 24 h to facilitate filtration, and the supernatant was carefully drawn and filtered using a 0.45 µm whatman filter. Soil pH was measured using an ion selective probe in the soil extracts after filtering. DOC and TDN were measured using a Hach IL-550 TOC/TN analyser, while and NH₄⁺/NO₃⁻ were measured using a Lachet QC8500 automated ion analyser.

Air-dried samples were used to measure total C/N/P and extractable compounds (e.g. PO₄³⁻, Na, Ca, Mg, K, Al, Fe) at the Ontario Forest Research Institute (OFRI). Extracts were processed using Brays method (PO₄³⁻), sodium pyrophosphate (Al/Fe), and ammonium acetate (base cations) and analysed using an IC with quality control applied using ISO standards derived from soil and plant material. Dissolved organic nitrogen (DON) values were estimated from the difference between dissolved total nitrogen (DTN) and combined dissolved inorganic nitrogen (DIN = NH₄⁺ and NO₃⁻ + NO₂⁻).
3.3.4 Statistical Analyses

3.3.4.1 Data Preparation

The results of multivariate methods such as principal component analysis (PCA) can be susceptible to extreme values that disproportionately influence correlation coefficients. Extreme values were identified as those outside 99% of the normal distribution range (i.e., z-scores exceeding 2.58 or -2.58). These accounted for <5% of values amongst several soil chemistry variables (e.g., DOC, DON, Al, Fe, \( \text{PO}_4^{3-}, \text{NO}_3^- \)), ranged from ±3 to ±10, and could not be attributed to human or analytical error. To account for these values without rejecting valid results, “extreme” values were “winsorized” (Tukey, 1968) by being reassigned z-scores of 2.58 or -2.58. This method retained meaningful data and substantially reduced both the coefficient of variation and excessively large correlation coefficients amongst variables.

In the pre-harvest dataset, about 3% of \( \text{PO}_4^{3-} \) values were missing at random due to insufficient sample for analysis. To avoid list-wise rejection of this sample location by SPSS (v.21, IBM), these values were replaced with the mean value for that variable.

3.3.4.2 Principle Component Analysis

Due to the large number of variables in these analyses, I employed multivariate analyses to better understand complex relationships between data. Principal component analysis (PCA) is commonly used as a dimension reduction tool to explore multivariate datasets, extracting a reduced number of principal components (PCs) that represent potential underlying latent variables from co-varying input variables. Using PCA (SPSS v.21, IBM), I explored potential over-arching connections between measured soil and environmental variables to determine if PCs represented biogeochemical processes that affecting multiple variables. Since these processes are often correlated, PCs were rotated to maximise loading using the promax oblique method to account for this dependence rather than orthogonal rotation which assumes complete independence of PCs. Interpretation of results is based on pattern loadings.

Initially, PCAs were conducted separately for pre and post-harvest data. Both produced the similar loading patterns on PCs; however, small differences in the strength of correlations amongst variables influenced which PC they were expressed on, making direct pre/post comparisons of extracted scores for each subject impossible. Therefore, data was pooled for all dates to allow for direct comparisons between pre and post-harvest PC scores via an interaction effect for date and treatment in a linear
mixed model. Additionally, separate PCAs were conducted for the LFH and mineral horizons since these yielded notably different loading patterns and differ in soil forming processes and ecosystem function.

3.3.4.3 Testing for Harvesting Effects

Soil chemistry variables were tested for harvesting effect using an interaction effect between time and treatment (fixed effects) in a linear mixed model (LMM: SPSS v.21, IBM) and a random intercept to account for subject dependence of repeated measures. Post-rotation principal component (PC) scores were assessed similarly.

A post-hoc analysis of LMM soil chemistry variable results was conducted by comparing the mean change in pre and post-harvest values amongst treatments (i.e., change scores); effect sizes were defined by expressing the difference between control and harvested treatment change values as a percentage of the mean pre-harvest control values. For example:

$$\left[ (Post_{(TL \text{ or } BIO)} - Pre_{(TL \text{ or } BIO)}) - (Post_{(control)} - Pre_{(control)}) \right] / Pre_{(control)} \times 100 = \% \text{ effect size}$$

Standard errors for these values were calculated as the pooled standard error of the mean for pre-harvest control and harvested treatment change scores (Morris, 2002). By focusing on interaction effects and the magnitude of change scores rather than simply post-harvest outcomes, this accounts for the effect of both naturally occurring inter-annual variations and potential harvesting disturbances to forest ecosystem and soil biogeochemical processes that govern soil chemistry.

Since PC derived z-scores contain negative values and a mean of zero, these could not be used to determine proportional effect sizes. Consequently, effect sizes are described as pre to post-harvest changes in z-scores (i.e. standard deviations from the mean) for TL and BIO treatments relative to changes in the mean. Standard errors were calculated for differences of means using pooled standard errors for paired comparisons between the control treatment and TL and BIO treatments.

Residuals from the LMM analyses were assessed for homogeneity of variance using Levene’s test and residual plots. Some soil chemistry variables exhibited excessive right-tailed skew and were heteroscedastic. Several dependent variables (DOC, DON, Al, Fe, EP, TP, NO₃⁻) were log-transformed prior to LMM analysis where indicated by the distribution of residuals to fit the assumptions of homogeneity of variance for LMMs (Herbst et al., 2009; Shabaga et al., 2015).
3.3.4.4 Spatial Dependence

Soil subplot variables were tested for spatial independence from plots by inclusion of plot as a random factor in the LMM. Some variables expressed significant plot dependence (e.g., Ca, Mg, pH, PO$_4^{3-}$, NO$_3^-$) while others did not (Al, Fe, NH$_4^+$, DOC, DON, K). Additionally, forest property variables (e.g., Tree BA by species, FWD) were only available at the plot scale. To account for this, a random intercept for plot was included in the final mixed model analyses of soil chemistry and PC scores where it reduced the Akaike Information Criterion score.

3.4 Results

3.4.1 Changes to Forest Structure Following Harvest

Harvesting significantly decreased the tree basal area of both the TL and BIO treatments (27.1% and 27.8%; p≤0.001) relative to the control treatment (p≤0.001) (Table 3.1). Residual forest basal area cover remained predominantly deciduous in all treatments (74-87%), of which sugar maple was the main component. Most harvested trees were >25 cm DBH (canopy trees), and the residual basal area and density of trees <25 cm DBH (understorey trees) did not differ significantly from controls. Sapling basal area (all woody stems 2-8 cm DBH; Table 3.2) declined more substantially in the TL and BIO treatments (20.1%, p≤0.05 and 17.3%, p≤0.10) than in the control (4.4%, p≤0.10) following harvest, but values did not differ significantly amongst harvested treatments.

A significant increase in the number of pieces of coarse woody debris (CWD) was observed in harvested treatments (Table 3.2; TL: 37.0%, BIO: 18.4%, p≤0.05), and values were higher than in the control treatment (TL: 58.9%, p≤0.05; BIO 39.5%, p≤0.10). However, estimated CWD volumes did not increase significantly, likely due to displacement and damage to pre-harvest CWD by machinery at rates similar to accrual. Fine woody debris (FWD) volumes increased significantly in harvested treatments (TL: +113.5 and BIO: +41.9%, p≤0.01), and residual FWD volumes were double those of the control treatment (TL: 230.0%, BIO: +208.2%; p≤0.01). The TL treatment amassed substantially more FWD than the BIO treatment (+92%, p≤0.10), where tops and branches for biomass were recovered as a function of treatment design.

3.4.2 Changes to Soil Chemistry

Many soil chemistry and other edaphic properties increased or decreased significantly post-harvest relative to pre-harvest values across all treatments in both the LFH and mineral horizons, indicating that
results captured inter-annual variations in ecosystem-scale processes affecting soil chemistry. Due to these complex relationships, I focused on interpreting linear mixed model (LMM) interaction effects and the difference in relative changes between treatments rather than absolute values.

Table 3.1 Pre and post-harvest mixed deciduous forest stand properties in Central Ontario, Canada (control – unharvested, TL – tree-length harvest, BIO – biomass harvest, QMD – quadratic mean diameter), ± = standard error of the mean.

<table>
<thead>
<tr>
<th>Tree</th>
<th>Basal Area (m²/ha)</th>
<th>Density (#/ha)</th>
<th>QMD cm</th>
<th>Timing</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>&lt;25 cm</td>
<td>&gt;25 cm</td>
<td>Total</td>
<td>&lt;25 cm</td>
</tr>
<tr>
<td>Pre: 2009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>28.29±1.37</td>
<td>4.32±0.60</td>
<td>23.96±1.74</td>
<td>436±21</td>
<td>247±25</td>
</tr>
<tr>
<td>TL</td>
<td>28.19±1.64</td>
<td>4.71±0.52</td>
<td>23.48±1.47</td>
<td>434±21</td>
<td>261±30</td>
</tr>
<tr>
<td>BIO</td>
<td>28.89±2.58</td>
<td>6.04±0.75</td>
<td>22.86±2.22</td>
<td>490±24</td>
<td>307±18</td>
</tr>
<tr>
<td>Post: 2010</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>28.27±1.37</td>
<td>4.31±0.60</td>
<td>23.96±1.74</td>
<td>434±20</td>
<td>246±25</td>
</tr>
<tr>
<td>TL</td>
<td>20.35±1.63</td>
<td>3.87±0.46</td>
<td>16.49±1.51</td>
<td>332±17</td>
<td>207±21</td>
</tr>
<tr>
<td>BIO</td>
<td>21.05±1.97</td>
<td>5.15±0.79</td>
<td>15.90±1.54</td>
<td>396±25</td>
<td>265±17</td>
</tr>
</tbody>
</table>

Table 3.2. Pre- and post-harvest mixed deciduous forest sapling basal area (woody stems 2-8 cm DBH) and downed woody debris volume in Central Ontario, Canada (control – unharvested, TL – tree-length harvest, BIO – biomass harvest, CWD – coarse woody debris, FWD – fine woody debris), ± = standard error of the mean.

<table>
<thead>
<tr>
<th>Sapling</th>
<th>Basal Area (m²/ha)</th>
<th>CWD (m³/ha)</th>
<th>CWD (m³/ha)</th>
<th>FWD (m³/ha)</th>
<th>Timing</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre: 2009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>1.28±0.36</td>
<td>222±18</td>
<td>51.77±6.51</td>
<td>9.00±1.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL</td>
<td>1.60±0.30</td>
<td>244±29</td>
<td>68.68±9.11</td>
<td>10.04±2.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO</td>
<td>1.56±0.56</td>
<td>248±29</td>
<td>69.67±15.41</td>
<td>14.11±1.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Post: 2010</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>1.22±0.18</td>
<td>210±14</td>
<td>48.26±5.60</td>
<td>6.49±0.75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL</td>
<td>1.28±0.28</td>
<td>334±49</td>
<td>72.26±10.69</td>
<td>21.43±3.53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO</td>
<td>1.29±0.48</td>
<td>294±25</td>
<td>67.01±12.86</td>
<td>20.02±2.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Post 2012</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>1.49±0.32</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TL</td>
<td>1.51±0.60</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIO</td>
<td>1.67±0.24</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Several variables demonstrated proportionally larger changes in one or both harvested treatments compared with controls (Tables AI-II and AI-III), where increases or decreases in harvested treatments were significantly different from control values. In the LFH layer, there were significant interaction effects between treatment and period of measurement, and post-hoc analyses were associated with a decline in K, \(\text{NH}_4^+\), DOC, and DON relative to controls within one year of harvest (19-46%, \(p\leq 0.05\); Fig. 3.1a), while Mg decreased (16-19%) and Fe increased (8-16%) insignificantly by the third year. Soil organic matter (SOM), soil organic C (SOC), and total N declined in both harvested treatments (6-11%) by year one and remained lower by year three (6-10%) relative to pre-harvest control values. Additionally, \(\text{PO}_4^{3-}\) declined (6-14%), and Na and NO\(_3^-\) increased (6-15% and 20-48%) in harvested plots by year one, but the results were not significant. No substantial differences were found between treatments for Ca, Al, total P, soil moisture, the C:N ratio of SOM and DOM, and pH.

The data on soil chemistry values from pre-harvest to one year post-harvest for tree-length (TL) and biomass harvesting (BIO) treatments relative to pre-harvest control values for a mixed deciduous forest in Central Ontario in (a) the LFH layer and (b) the upper mineral soil. Asterisks denote significant post-hoc pairwise test differences for change scores values between harvested and control treatments (*\(p\leq 0.10\), **\(p\leq 0.05\), ***\(p\leq 0.01\)). SOM = soil organic matter. DOC and DON = dissolved organic carbon and nitrogen. Error bars = standard error for differences of means. LFH and mineral soil DOC and DON values and mineral soil SOM and K values were log-transformed prior to analysis, producing uneven error bars after back-transformation.

A similar pattern was found in the upper mineral horizon, but the results were generally not significant and differed somewhat between TL and BIO treatments (Fig. 3.1b, Table AI-III). Within the first post-harvesting year \(\text{NH}_4^+\) and DON declined notably in TL (16% and 25%) and BIO (12% and 20%) treatments; in contrast, NO\(_3^-\) increased considerably in both (37% and 43%). Modest declines to Ca, Mg, and K were found in both harvested treatments (TL: 10-17%; BIO: 12-22%), while larger declines in SOC, DOC, and Al were found primarily in the TL treatment (TL: 24-38%; BIO: 2-14%). By the third post-harvesting year,
harvested treatment SOC values had nearly returned to pre-harvest levels, Al declined (TL: 22%, BIO: 24%), Ca increased above pre-harvest levels (TL: 20%, BIO: 6%), and PO$_4^{3-}$ declined by 25% in the TL treatment only. However, none of these mean differences were statistically significant.

Some similar changes to soil chemistry at the 40-60 cm depth were observed, such as a post-harvest decrease in K for both TL and BIO treatments (36% and 17%), and an increase in NO$_3^-$ (11%) and a decline in DOC and DON (18% and 30%) in the TL treatment. However, extremely high variance and lower samples numbers (n=5 per treatment) prevented accurate determination of any changes to exchangeable soil chemistry pools in deeper soils.

### 3.4.3 Principal Component Analysis

Several forest property variables were screened for inclusion in the PCA. All except for tree basal area (BA) by species were rejected due to low communality values. Poorly represented species were grouped with other similar species (e.g., spruce with hemlock, white birch with yellow birch, red maple with sugar maple). Strong correlations to soil chemistry were found to be inversely related between most deciduous species and yellow birch and conifers; no relationships were found for beech. The combined BA of all conifer and birch species loaded more strongly and inversely to the combined BA of all deciduous tree species (excluding beech and birch). Therefore, the proportion of conifer and birch to total tree BA (excluding beech) was used as a single variable to describe the influence of tree cover, simplifying the analysis and interpretation of results.

Preliminary PCA analyses for both LFH and mineral soil physiochemical variables included SOM, total N, total P, Ca, Mg, K, Na, Al, Fe, DOC, DON, C to N ratio of SOM, NH$_4^+$, PO$_4^{3-}$, NO$_3^-$, % soil moisture (SM), pH, and the conifer to deciduous tree ratio. For both LFH and mineral soils, total P, Na, PO$_4^{3-}$, NO$_3^-$, and C:N exhibited communality values of <0.5 (i.e., correlated poorly with multiple variables) and either displayed complex structure on multiple principal components that did not contribute to interpretation of PC structure, or loaded exclusively on additional PCs that explained minimal variance (<5%). Therefore, these values were excluded from the final PCA models. Fe was also excluded from the PCA of mineral soil for the same reasons but retained for the PCA of the LFH.

#### 3.4.3.1 LFH Horizon

The PCA of LFH soil variables yielded three principle components (PCs) with eigenvalues >1 that explained 76.6% of the total variance in the data with a KMO index score value of 0.75, indicating adequate sampling. Components were rotated obliquely to maximise explained variance for each
component, with providing weighted correlation loading values for each variable to PCs. The first PC was predominantly loaded by SOM, various metal cations, and soil moisture (Table 3.3a); acid cations Al and Fe loaded inversely to non-acid cations (K, Ca, and Mg) and SOM. Although labile soil compounds NH$_4^+$, DOC, and DON were moderately correlated to PC1 ($r=0.44$-$0.55$, $p \leq 0.001$), rotation weighted them largely to PC3. In contrast, most metal cations were moderately correlated to PC3 ($r=0.37$-$0.50$, $p \leq 0.001$), but were primarily weighted to PC1 and PC2. The correlation between the PC1 and PC3 ($r=0.55$, $p \leq 0.001$) following rotation suggests that rotation separated two latent variables initially represented primarily in PC1 and partially in PC3. In contrast, PC2 was orthogonal to both PC1 and PC3, and defined by a decline in base cations (Ca and Mg) and pH with increasing conifer cover, soil moisture, and SOM.

Table 3.3 Principal component analysis loading values for the LFH layer (a) and upper mineral horizon (b) soil chemistry before and after oblique rotation for a mixed deciduous forest in Central Ontario. Values represent weighted loading correlation coefficients based on allocation of eigenvalues between rotated components. Substantial values highlighted in bold with grey background. %SM = gravimetric soil moisture by dry soil mass. % conifer = proportion of conifer trees relative to total tree basal area.

<table>
<thead>
<tr>
<th></th>
<th>(a) LFH</th>
<th>(b) Mineral</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
</tr>
<tr>
<td>SOM</td>
<td>0.73</td>
<td>0.41</td>
</tr>
<tr>
<td>Ca</td>
<td>0.37</td>
<td>-0.73</td>
</tr>
<tr>
<td>Mg</td>
<td>0.57</td>
<td>-0.60</td>
</tr>
<tr>
<td>Al</td>
<td>-0.90</td>
<td>0.22</td>
</tr>
<tr>
<td>Fe</td>
<td>-0.95</td>
<td>-0.07</td>
</tr>
<tr>
<td>K</td>
<td>0.67</td>
<td>-0.05</td>
</tr>
<tr>
<td>NH$_4^+$</td>
<td>0.21</td>
<td>0.05</td>
</tr>
<tr>
<td>DOC</td>
<td>0.06</td>
<td>-0.04</td>
</tr>
<tr>
<td>DON</td>
<td>-0.11</td>
<td>-0.05</td>
</tr>
<tr>
<td>%SM</td>
<td>0.42</td>
<td>0.66</td>
</tr>
<tr>
<td>pH</td>
<td>-0.23</td>
<td>-0.87</td>
</tr>
<tr>
<td>% Conifer</td>
<td>-0.15</td>
<td>0.74</td>
</tr>
</tbody>
</table>
The LMM analysis of the rotated PC1 and PC3 component scores showed a significant interaction effect between harvesting treatment and time ($p \leq 0.01$), and post-hoc analysis of component change scores indicated that values declined significantly in TL and BIO treatments ($p \leq 0.05$) relative to controls for PC3 (0.90-0.98 SD) and marginal declines in PC1 (0.26-0.36 SD, $p > 0.10$; Fig. 3.2b). PC2 component scores showed no substantial treatment effects.

Figure 3.2 Mean change from pre-harvest to one year post-harvest in soil chemistry composite variables derived from principal component analysis (PCA) comparing changes in tree-length (TL) and biomass harvesting (BIO) treatments relative to change in control values for a mixed deciduous forest in Central Ontario. Changes in PCA Z-scores are shown separately for rotated scores in the LFH layer (a) and upper mineral horizons (b). Asterisks denote significant post-hoc pairwise test differences for change scores values between harvested and control treatments (*$p \leq 0.10$, **$p \leq 0.05$, ***$p \leq 0.01$). Standard deviations from the mean.

3.4.3.2 Mineral Horizon

PCA of mineral soil variables also yielded three PCs with eigenvalues $>1$ that explained 80.4% of the total variance in the data, and had a KMO index score value of 0.778. After rotation, PC1 was primarily loaded by Al, SOM, K, DON, DOC, and NH$_4^+$. Base cation loadings were weighted primarily to PC2 (Table 3.3b) where they were inversely associated with conifer cover. Unlike in the LFH, pH did not load on PC2. Instead, pH loaded inversely to percent conifer cover on PC3, indicating pH was not playing a significant role in defining the availability of other variables.

LMM analysis of the rotated PCs showed a significant interaction effect between time and treatment for PC1 ($p \leq 0.01$). A post-hoc analysis showed a significant decline in change scores for the TL treatment (0.74 SD, $p \leq 0.01$; Fig. 3.2b), but not for the BIO treatment. Analysis of other PCs showed no treatment-related effects or trends in change scores.
3.4.4 Comparing LFH and Mineral Horizons

In general, most soil variables were not autocorrelated between horizons for each subplot. Joint inclusion of all LFH and mineral soil variables in a PCA led to the loading of variables onto 6 PCs with eigenvalues >1 that resembled those from separate analyses. However, pH, Ca, Mg, SM, and NO$_3^-$ were weakly to moderately autocorrelated between horizons ($r=0.31$ to 0.52, $n=73$, $p≤0.001$), and loaded on the same PC along with % conifer cover and SOM from the LFH only. Non-significant increasing effect sizes were observed for Na in the LFH layer (<15%), and decreases in the upper (<16%) and lower mineral (<10%) horizons, but changes to Na (or K) in the LFH were not correlated to changes in the mineral horizons. Furthermore, there was no within-horizon correlation between changes to K and Na for the LFH and deep mineral; although changes to K and Na within the upper mineral horizon were strongly correlated ($r=0.83$, $n=73$, $p=≤0.001$), this correlation did not differ between treatments. In contrast, NO$_3^-$ increased substantially but non-significantly in the TL and BIO treatments of the LFH (58% and 24%) and upper mineral horizons (37% and 43%); changes in the deeper mineral soil were insubstantial. Increases to NO$_3^-$ in the LFH predicted increases in the upper mineral soil when averaged by plot across all treatments ($r^2=0.37$; $β1=0.29$, $n=15$, $p≤0.05$), but slope values did not vary by treatment.

In the LFH, rotation of PCs reweighted the loading of labile compounds (NH$_4^+$, DOC, DON) in PC1 to PC3; PC1 retained strong associations between metal cations and SOM, but shared loading of base cations with pH on PC2. Similarly, rotation of mineral soil PCs separated labile components and base cations, retaining the former in PC1 and loading the latter to PC2. In both horizons, distinct treatment related effects were associated with labile compounds (DOC, DON, and NH$_4^+$) and K, but results were only significant for DOC and DON in the mineral horizon.

3.5 Discussion

3.5.1 Reconciling Inter-Annual Changes to SOM in the Reference Treatment and Post-Harvest Declines

I anticipated that harvesting would stimulate shorter-term decomposition and mineralisation rates, increasing the availability of DOM and inorganic N as noted in other studies (Vitousek and Matson, 1985), with some potential losses of total C and N, cations, and nitrate due to leaching and/or increased decomposition rates (Bormann and Likens, 1979; Yanai et al., 1999; Lal, 2005). The data revealed substantial post-harvest changes to soil chemistry, defined primarily by reductions of labile compounds,
including K, DOC, DON, and NH$_4^+$, particularly in the LFH. Some smaller, non-significant changes were associated with soil organic C (SOC) and other cations, such as declining Mg and an increase in Fe by the 3$^{rd}$ post-harvest year. In the upper mineral soil, similar but more modest changes to DOM and cations were much more pronounced in the TL treatment. While mechanical mixing of the LFH into the mineral soil could account for apparent reductions to total C and N in the LFH (Curtis and Johnson, 2001; Yanai et al., 2003), disruption to the forest floor was often minimal and mostly limited to skid trails. Furthermore, even larger declines to mineral soil SOC concentrations (17.5%) were observed than in the LFH (7.6%), discounting the contribution of this mechanism.

Despite these relative declines in harvested treatments, concentrations of SOC, DOM, and several cations in soil samples increased significantly in both the LFH and upper mineral horizons pre to post-harvest across all treatments. DOM in soil leachate can vary considerably by season and year, influenced by phenological events and changes in water flux (McDowell et al., 1998; Solinger et al., 2001). In contrast, estimated pools of SOC in the LFH and 0-15 cm of mineral soils were extremely large (18990 and 72019 kg C ha$^{-1}$), making substantial inter-annual changes unlikely, though not unprecedented. Knoepp and Swank (1997) found considerable inter-annual variations to organic C in A and B horizons of an uncut reference site between 1977-1994, with a coefficient of variation of 18-25% amongst annual averages and inter-annual values differences as high as 41-55% from the previous year. Increases of SOC in the LFH and mineral soils from pre to 1 year post-harvest are in line with this variation (30% and 24%), but large increases to soil pools would require improbable increases to annual SOC inputs (5699 and 17809 kg C ha$^{-1}$).

Apparent post-harvest increases to SOC and related compounds at my site may have also been influenced by sampling technique. In 2010 and 2012, improved separation of the LFH and upper mineral horizons minimised inclusion of the uppermost portion of the mineral soil in LFH samples. Though differences were probably small, increased retention of this organic-rich material in upper mineral horizon samples would also reduce inclusion of dense mineral materials in the LFH, effectively increasing measurements of SOC concentrations in both horizons. Additionally, SOC values in 2012 remained similar to those from 2010 than 2009, further suggesting that the improved technique was in part responsible for higher overall values. Lastly, SOM is associated with adsorption and production of many other soil chemical constituents (i.e., DOM, cations, NH$_4^+$); most were weakly to moderately correlated to SOM pre and post-harvest, indicating sampling differences likely contributed to increases in these as well. Since the improved method was applied equally to all sample locations, it was unlikely to have produced differences between treatments. Consequently, larger increase to SOM and related
compounds in the control than the harvested treatments described relative declines in the harvested treatments.

3.5.2 Linking Changes in Soil Chemistry and PCA-Derived Variables in Harvested Treatments to Biogeochemical Processes

Strong loading of SOM and soil cations on PC1-LFH suggest this latent variable represents cation exchange capacity (CEC) associated with SOM, while strong loading of DOM and NH$_4^+$ on PC3-LFH suggests it represents the products of decomposition and mineralisation processes. Both PCs were strongly correlated, indicating that post-harvest changes to each may be inter-related. In the mineral horizon, DOM loaded strongly with SOM, soil moisture, and Al on PC1-MIN, suggesting that this latent variable represented decomposition by-products from SOM which are often associated with increased acid cation mobility (Sollins, 1996). Using PCA, Filep and Rékási (2011) also found DOM loaded on the same PC as SOM in mineral soils, indicating availability is linked to SOM. Base cations and NH$_4^+$ loaded strongly on PC2-MIN with percent conifer cover, linking it to CEC and base saturation. However, pH, which expressed low variability (CV: 4-7%) and remained unchanged following harvest, loaded separately on PC3-MIN with conifer cover despite being moderately correlated to K and NH$_4^+$. This suggests that the CEC in the mineral soil was not strongly influenced by pH despite high SOM and relatively low silt and clay content (sandy loam), conditions typically associated with a predominance of pH dependent charges on soil colloids.

A moderately strong correlation between PC2-LFH and PC1-MIN (r=0.54, p≤0.001) linked increasing soil moisture and conifer tree cover, base cation deficiency, and lower pH in the LFH horizon to the availability of labile compounds, SOM, and acid cations in the mineral horizon. This indicates that wetter sites are more likely to contain conifer cover, producing an acidic and DOM-rich soil with a greater availability of Fe and Al. However, change scores for PC2-LFH and PC1-MIN were not correlated, demonstrating that these values were linked by the external environment, and changes in one did not immediately effect changes in another. Furthermore, only pH, Ca, Mg, SM, and NO$_3^-$ were auto-correlated between horizons. Changes between all other cations, labile compounds, and extracted PCs were unrelated. Soil moisture and certain labile compounds (especially DOM and inorganic N) have been found to be autocorrelated between organic and mineral horizons of other soils, generally linked by hydrologic connections that periodically mobilise them (Bengston and Basiliko, 2007). A failure to detect autocorrelation of highly mobile compounds between the LFH and mineral horizons in my study suggests a disconnect between these horizons with regard to biogeochemical processes.
Nonetheless, the similarity of treatment effects in each horizon on soil chemistry and PCA-derived variables (i.e., labile compounds and exchangeable cations) point to a common disturbance-based factor. Changes to SOM within each horizon were correlated to changes in K, NH$_4^+$, DOC, and DON ($r$=0.51-0.75, $p$≤0.001), but not between horizons. These patterns may be the product of similar but independently regulated within-horizon biogeochemical processes driven by differing sources of organic inputs and lability of DOM (Qualls et al., 1991; Rasse et al., 2005; Froberg et al., 2007; Garten, 2009). Significant declines to labile nutrients and cations in harvested treatments relative to controls (Figs. 3.1, 3.2) indicates that harvesting affected these biogeochemical cycling dynamics, possibly by altering the CEC, litter inputs, and losses via increased decomposition and leaching rates.

3.5.3 Changes to Leaf Litter Contributions

Annual leaf litter-fall comprises an integral source of nutrient inputs for soil pools in northern temperate forests. Labile compounds such as Na, K, and low molecular weight (LMW) factions of DOM (e.g., sugars, organic acids, proteins, amino acids, etc) can leach rapidly from freshly fallen leaves, contributing to exchangeable pools (Chapin et al., 2002). Harvesting removed about 27-29% of the deciduous tree basal area, and presumably reduced litter-fall similarly. Since the post-harvest soil samples were collected one to two weeks after the initiation of leaf-fall in early October, I considered the potential impact of this event on differences to labile nutrient pools.

Studies of northern temperate forests suggest average annual rates of DOC and DON leaching from the litter (Oi) to the humic (Oa) horizon are approximately 155.6 and 5.9 kg·ha$^{-1}$·yr$^{-1}$ (using data aggregated by Michalzik et al., 2001). Much lower litter DOC flux rates of 16.2 kg·ha$^{-1}$·yr$^{-1}$ were measured within my study site area in 2011 (Rudz, 2013), comparable to 32.5 kg·ha$^{-1}$·yr$^{-1}$ found by Solinger et al., (2001) in 1997. However, both these latter values were measured during dry years; a substantial increase in DOC flux during the wetter 1998 year (113.6 kg·ha$^{-1}$·yr$^{-1}$) and inconsistent seasonal patterns led Solinger et al. (2001) to conclude that DOM leaching was primarily regulated by water flux at annual and bi-weekly scales. Additionally, they found DOC and DON flux from the Oa to be much higher than from litter (236.8 and 8.2 kg·ha$^{-1}$·yr$^{-1}$), supporting the hypothesis by Zsolnay (1996) and McDowell and Likens (1988) that older, partially decomposed SOM is a more important source of DOM flux to depth than fresh litter.

The mean size of the exchangeable DOC and DON pools in the F+H (Oe+Oa) horizon in the control treatment of my study were 164.1 and 24.1 kg·ha$^{-1}$, based on an average depth of 4 cm and bulk density of 0.15 g·cm$^{-3}$. DOC and DON leaching rates of 155.6 and 5.9 kg·ha$^{-1}$·yr$^{-1}$ (Michalzik et al., 2001) are
theoretically sufficient to replace half of the DON and the entire DOC pool on an annual basis, corresponding to a weekly exchange rate of 3.65% and 0.95% of the entire exchangeable DOC and DON pools. However, it is unlikely that the exchangeable pool is consistently ephemeral, particularly in the autumn when rates of nutrient uptake by plant roots are low due to phenological cessation of photosynthesis, transpiration, and reduced temperatures, inhibiting root respiration (Shabaga et al., 2015). Additionally, over 50% of the leaves remained on trees, minimising the influence of fresh litter inputs, and there were no major rain events during the two weeks prior to sample collection. Lastly, even assuming higher leaching rates from fresh litter, 100-150% of the exchangeable pools of K, NH$_4^+$, and DOM would need to be replaced to account the magnitude of treatment effect sizes in the LFH layer (i.e., 26%-46% relative decline in DOM). Since this is unlikely from a short period of litter leaching, differences in litter inputs, at best, account for a small portion of effect size. Therefore, declining nutrients in harvested treatments are probably better explained by other mechanisms.

3.5.4 Nutrient Losses from Run-Off and Leaching to Depth

Harvested forest areas are often more prone to increased run-off due to changes in hydrological dynamics, such as increased interception of precipitation with soil, snow-fall accumulation, evapotranspiration, and compacted and damaged soil structure, particularly where there is more topographic relief (Murray and Buttle, 2003; Monteith et al., 2006; others). This may increase erosion of fine sediments relative to undisturbed areas (Kreutzweiser and Capell, 2001) that function as nutrient retention sites and the dissolution of mobile soil chemical components into soil solution, resulting in nutrient losses from overland flow and/or leaching losses to deeper mineral soils (Bormann and Likens 1979; Yanai et al., 2003). If these mechanisms were responsible for the decline of K, DOM, and NH$_4^+$ in harvested treatments, I would anticipate three possible outcomes: 1) comparable declines to Na, which has a lower strength of adsorption to colloids than K and NH$_4^+$, 2) declines to NO$_3^-$, which is poorly retained in young forest soils with low anion exchange capacity, and; 3) changes to soil moisture storage and accumulation of leached compounds (e.g., Na, NO$_3^-$, DOM) in deeper soils relative to control treatments.

I did not gauge run-off, leachate flux, or changes to soil infiltration rates and conductivity. However, soil moisture values did not change or differ significantly amongst treatments in the upper or lower mineral horizons, suggesting infiltration and drainage rates did not differ between treatments. Furthermore, declines to DOM and cations (i.e. K and NH$_4^+$) in the LFH were not correlated to changes in the mineral horizon, and Na actually increased in the LFH and only decreased modestly in the upper mineral soil.
Lastly, although increases to NO$_3^-$ in the LFH predicted increases in the upper mineral soil, rates did not vary by treatment. These patterns suggest that harvesting disturbances did not affect the transport of cations and DOM from or between horizons. Therefore, potential increases run-off rates and leaching losses probably did not contribute substantially to declines in harvested treatments.

### 3.5.5 Harvesting Disturbance Effects on SOM and DOM Dynamics

The mechanisms that drive the production, availability, and decomposition of DOM in forest soils following harvesting disturbances are complex and remain poorly understood (Yanai et al., 2003). In this study, harvesting treatments were primarily associated with substantial declines to labile nutrients (i.e., K and NH$_4^+$) and organic substrates such as root exudates and decomposition by-products (i.e., DOC and DON). Smaller declines to SOM were also found. Pre to post-harvest changes to the concentrations of these compounds were correlated to changes in SOM, suggesting that labile soil chemistry dynamics were being governed by biological mechanisms such as production of root exudates, nutrient mineralisation and assimilation, and oxidation of organic C.

#### 3.5.5.1 Mycorrhizal DOC Exudates

Högberg and Högberg (2002) found that girdling Scots pine trees in a northern Swedish forest significantly reduced soil extractable DOC (≈45%) in the F and H horizons relative to controls, but did not affect DON, reducing the C:N ratio (≈25%) of DOM. They linked this decline to senescence of ectomycorrhizal roots and mycelia, and surmise that exudates from mycorrhizal activity are responsible for up to half of DOC production in forest soils. A similar decline in extractable DOC (42-46%) was observed in the LFH layer of my study site, but the C:N ratio of DOM only declined by 10-12% due to a concomitant decline in DON (26-30%). Though my study forest differed considerably, ectomycorrhizae are widespread throughout temperate and boreal forests (Paul, 2007), as are other mycorrhizal associations such as vesicular-arbuscular mycorrhizae with sugar maple (Brundrett and Kendrick, 1988). Assuming a similar relationship between roots and all mycorrhizae, this suggests that up to a third of DOC losses in my study could potentially be attributable to a reduction in root/mycorrhizal activity.

Some studies suggest that mycorrhizae may also inhibit decomposers activity in soils. Labile C is generally considered the primary limiting resource for microbial activity; by obtaining labile C directly from tree roots, mycorrhizae are generally not substrate-limited relative to decomposers relying upon soil C pools, theoretically increasing their relative resource assimilation efficiency (Högberg et al., 2003). Additionally, some mycorrhizae may utilise allelopathic compounds to further reduce competition with
saprophytes (Duchesne et al., 1988; Hörgberg et al., 2003; Paul, 2007). Senescence of mycorrhizae and roots could therefore reduce resource competition for decomposers. Although reduced production of DOC exudates by mycorrhizae and roots may decrease labile soil C inputs, a decline to the C:N ratio of remaining DOM and potential increases to labile C inputs from substantial additions of mycelial and root necromass (and other harvest residues) may compensate for these losses (Hörgberg and Hörgberg, 2002).

### 3.5.5.2 Changes to Decomposition Rates

An increase to decomposition and mineralisation rates following harvest may also account for declines in total C, DOM, and other nutrients. While DOM is typically considered a by-product of organic matter mineralisation, low molecular weight (i.e., labile) fractions of DOC are a preferred substrate source for heterotrophic micro-organisms, contributing disproportionately to soil CO$_2$ efflux (FCO$_2$) from decomposition (van Hees et al., 2005). Heterotrophic activity in forest soils is typically constrained by soil temperatures, availability of resources (i.e., moisture, nutrients, and bioavailable C substrates), and competition with vegetation (Chapin et al., 2002). Changes to soil and ecosystem properties from harvesting may alter these constraints, increasing access to new sources of labile C from harvest residues and elevating soil temperatures from reduced canopy cover, increasing FCO$_2$ and nutrient uptake from heterotrophic activity and contributing to SOC losses (Toland and Zak, 1994; Londo et al., 1999; Hafner et al., 2005; Chatterjee et al., 2008; Olajuyigbe et al., 2012; Shabaga et al., 2015). Soil CO$_2$ efflux has been shown to increase with soil organic C lability and availability and declining C:N ratios (Prescott, 2000; Davidson and Janssens, 2006; Laganière et al., 2012), particularly where substrate quality co-varies with temperature (Davidson et al., 2006), and harvesting of trees can alter microbial communities and increase the proportion of active (labile) C in soil pools, enhancing mineralisation of SOC to CO$_2$ and turnover of soil C pools (Chatterjee et al., 2008).

In a concurrent study of changes to FCO$_2$ from the same soil sampling locations in 2010, in chapter 2 and Shabaga et al. (2015), I concluded that elevated heterotrophic activity accounted for higher rates of FCO$_2$ in harvested treatments than unharvested controls. Using these same measurements of FCO$_2$, I found that the magnitude of pre to post-harvest decline of DOC values in harvested treatments predicted increases to FCO$_2$ values in autumn 2010 ($r^2$=0.11, n=50, p≤0.05). This relationship improved considerably when values were averaged by plot to reduce noise associated with spatial heterogeneity, ($r^2$=0.59, n=10, p≤0.01). A similar but weaker relationship was found for SOM ($r^2$=0.31, n=10, p≤0.10), suggesting that reductions to DOC and SOM were the product of increased decomposition rates.
3.5.5.3 Harvest Residues as Sources of Labile C and Stimulation of SOM Decomposition Rates

Harvesting substantially increased CWD (37% and 18%) and FWD residues (114% and 42%) in TL and BIO treatments. Since root biomass is generally proportional to aboveground biomass (Jenkins et al., 2003), root dieback following harvesting likely produced root and mycorrhizal necromass proportional to cut basal area (28%). These post-harvest residues contain nutrient-dense tissues (e.g., needles, leaf buds, cambium, mycelium) that turn over rapidly (weeks to months), particularly for fine roots and woody debris, twigs, and small branches (Yin et al., 1989; Yanai, 1998; Müller-Using and Bartsch, 2009).

Decaying woody debris can emit leachate containing DOC, organic and inorganic N, and other nutrients in higher concentrations than leaf litter (Hafner et al., 2005; Rudz, 2013), and widely distributed post-harvest clusters of woody debris have been associated with soil nutrient enrichment and increased CO$_2$ efflux and decomposition rates (Toland and Zak, 1994; Londo et al., 1999; Lee et al., 2003; Belleau et al., 2006; Thiffault et al., 2006; Sullivan et al., 2008; Olajuyigbe et al., 2012; Rudz, 2013; Shabaga et al., 2015). Turnover of fresh root biomass inputs and associated microbial and fungal exudates may release high concentrations of bioavailable DOM into the forest floor (Qualls et al., 1991; Cleveland et al., 2004; van Hees et al., 2005).

In Chapter 2 and Shabaga et al. (2015), I estimated that elevated soil temperatures accounted for up to 34-41% of the difference in post-harvest FCO$_2$ between harvested and control treatments at my study site in 2010, and a strong correlation between FCO$_2$ and FWD inputs (Fig. 2.8a; $r^2=0.58$, p≤0.01) led me to surmise that increases to labile soil C from harvest residues may have contributed to the remaining portion. Higher soil temperatures may have also increased rates of litter decomposition, and more direct interception of precipitation from canopy openings could facilitate leaching of bioavailable SOC to the F and H horizons. Yanai et al. (2003) and others have suggested that litter decomposition rates under clear-cuts may actually be lower than in unharvested forest due to soil moisture constraints. However, soil moisture values did not vary between treatments, and post-harvest soil respiration rates in 2010 were not constrained by moisture (Chapter 2; Shabaga et al., 2015). FCO$_2$ was not correlated to DON, NH$_4^+$, or NO$_3^-$, but pre to post-harvest declines to NH$_4^+$ were correlated to FWD input volumes (Fig. 3.3c; $r^2=0.53$, n=10, p≤0.01), suggesting increasing inputs affected N dynamics. An influx of labile C to soils can result in rapid immobilisation of inorganic N (Magill and Aber, 2000; Hafner et al., 2005), especially from source material with a high C:N ratio such as woody debris, root necromass, leaf litter leachate. However, it is unclear if FWD contributed directly to enhanced decomposition and immobilisation, or functioned as a proxy for other harvest residues (i.e., roots, mycelia, etc.).
Figure 3.3 Relationship between soil carbon dioxide efflux (FCO₂) for \( R_{\text{mean}} \) values measured in the autumn of 2010 and pre to post-harvest changes in (a) DOC concentrations and (b) %SOM in the LFH horizon averaged by plot; relationship between post-harvest input volumes of fine woody debris (FWD) and pre to post-harvest changes in \( \text{NH}_4 \) concentrations in the LFH horizon averaged by plot (c). All results for a mixed deciduous forest in Central Ontario. \( R_{\text{mean}} \) = soil respiration modelled to mean control treatment values.

3.5.5.4 Mechanisms of SOC Loss Through Enhanced Mineralisation of SOC and Organic N

Collectively, these results suggest that the availability of labile C may have been more limiting to decomposition than N, and that potential post-harvest sources of labile C were linked to increasing decomposition rates and uptake of inorganic N. Chatterjee et al. (2008) found that lab incubated soil samples collected from managed coniferous forest sites lost more than twice as much organic C to FCO₂ after four months soils from than unmanaged sites, indicating that harvesting activities increase the proportional size of “active” short-lived C pools relative to decay resistant C pools. An increase in labile C may also stimulate both the decomposition of more recalcitrant SOM via substrate priming effects (Kuzyakov et al., 2000; Paul, 2007; Zummo and Friedland, 2011), particularly if soil temperatures are also elevated. Since the C:N ratio of SOM (18-20:1) for both the LFH and upper mineral horizons was below the 25:1 ratio generally considered the threshold for N immobilisation (Paul, 2007), enhanced decomposition of SOM may have similarly stimulated mineralisation rates of soil organic N which declined at nearly the same rate.
I propose that declines to SOM and DOM, NH$_4^+$ (and probably K to some extent) in harvested treatments can be accounted for by a combination of two biogeochemical mechanisms: 1) declining DOC exudate production by mycorrhizal roots due to root senescence, and 2) stimulation of SOM and DOM mineralisation and nutrient assimilation rates by heterotrophic microbiota following increases to labile C pools from harvest residues, elevated soil temperatures, and release from competition and/or suppression with/mycorrhizal roots. Leaching losses were probably minimal but may also have contributed to declines, particularly for more mobile constituents such as K. Effect sizes were largest in the LFH layer at the soil surface where physical disturbances were most prominent and the soil had more direct contact with fresh litter and harvest residues (e.g., woody debris, fine roots). A lower fine root density, less physical disturbance, and a larger proportion of recalcitrant SOM in the mineral soil may account for similar but reduced effect sizes relative to the LFH.

3.5.6 A Post-Harvest Carbon Flux Budget

Many studies have noted changes to SOC following harvest, including increases or decreases to both the LFH and/or mineral soil (Johnson and Curtis, 2001; Lal, 2005). A meta-analysis by Johnson and Curtis found a significant increase to SOC (25%) in mineral soils of conifer dominated saw-log operations attributed to mixing of organic materials into the soil. They also found a significant decline in SOC in mineral soils following whole-tree harvests (6%), and a non-significant decline in saw-log harvests in hardwood forests (7%). Overall, results were highly variable and did not show significant differences with time since harvesting. A more recent meta-analysis by Nave et al. (2010) found substantial and significant declines to SOC pools in the LFH (36%) of hardwood forests, and a large decline in SOC of the upper mineral horizon of brunisol/inceptisol soils (25%) within the first 5 years that recovered between 6-20 years. In general, conifer forests showed no decline in SOC for mineral soils. In both meta-analyses harvest methods were mixed between clear-felling and thinning.

Post-harvest SOC losses in the forest floor and mineral soil have often been attributed to a combination of increased decomposition rates and decreased litter inputs and NPP over extended recovery periods, based on the Covington curve. Using chronosequence methods, Covington (1981) found a dramatic loss of forest floor materials (50%) within 20 years of harvest, followed by recovery. A conceptual model based on this sequence of change became known as the Covington curve and was widely used to predict SOC losses from both the LFH and mineral soils, despite that it was specific to the forest floor. Reassessment of the original Covington study area decades later did not find the same declines predicted by the curve, questioning the results of similar chronosequence studies and highlighting that
undefined factors such as differing harvesting methods and mixing of the LFH into the mineral soil may be influencing results (Yanai et al., 2003). A comprehensive understanding of the abiotic and biogeochemical mechanisms behind these changes remains unclear (Yanai et al., 2003), particularly over short intervals (i.e., 1-5 years post-harvest).

3.5.6.1 Quantifying SOC Pools

In this study I predicted and observed declines to SOC pools in the harvested treatments relative to the control treatment. Losses averaged across both harvested treatments (7.6% LFH and 17.5% upper mineral) were within the ranges noted by Johnson and Curtis (2001) and especially Nave et al., (2010). However, they were much larger than anticipated from a modest disturbance over a short recovery period, and exhibited high spatial heterogeneity and large temporal pre to post-harvest variance associated with inter-annual variation in ecosystem processes and sampling techniques. The LFH did not appear to mix appreciably into deeper mineral soil following harvest, and declines were linked to increased post-harvest decomposition rates, suggesting SOC losses may be accounted for by mineralisation and FCO₂. I attempted to account for SOC losses by producing a hypothetical C budget based on measured changes to SOC and FCO₂, estimates of soil DOC inputs from woody debris leachate, and estimates of FCO₂ produced from decay of fine roots and mycorrhizal necromass. Since SOC losses were over-represented due to extreme values, even after log transformation, for the purposes of this budget model I conservatively trimmed all pre/post sampling difference values to an arbitrary cut-off value of ±1.5 standard deviations. This approach considerably reduced estimated proportional C losses in the LFH (3.0%) and upper mineral soils (4.5%), yet still predicted substantial mass losses of 530 and 2917 kg C ha⁻¹, of which DOC comprised 41 and 68 kg C ha⁻¹.

3.5.6.2 Estimated Harvest Residue C Inputs

Estimates of live fine root biomass in northern hardwoods range from 2500-4400 kg C ha⁻¹ (Burke and Raynal, 1994; Jackson et al., 1997), and rapidly decaying fine roots lose ≈17-50% of their dry mass within the first year of death (Fahey et al., 1988; Burke and Raynal, 1994). Assuming a proportional increase in fine root necromass as cut BA (28%), and a 25% loss of root necromass C to respiration within the first year (Burke and Raynal, 1994), fine root decomposition might contribute as much as 85-150 kg ha⁻¹ to respired C. Since fine roots from uncut trees were also probably damaged from machinery during operations, this estimate is likely under-representative of fine root necromass. Larger roots may have also contributed, but since they live longer and decompose slower than fine roots following harvest (Fahey et al., 1988), and most were found deeper within the profile (>20 cm), I excluded them from...
consideration. Fewer studies have attempted to estimate mycorrhizal biomass. Using measurements of fungal biomarkers from in-growth mesh bags, Wallander et al. (2001) estimated that mycorrhizal biomass to comprise between 800 to 2700 kg ha\(^{-1}\) in a Swedish conifer forest. Assuming a similar ratio of mycorrhizae to root biomass in my study area, and nearly complete turnover during the post-harvest growth season, I estimate that decomposing mycorrhizal necromass may have provided 74-131 kg C ha\(^{-1}\) to respired soil C.

Fine roots were widespread and primarily located throughout the LFH layer at my site. In contrast, woody debris inputs were clustered, making it more difficult to accurately estimate the extent to which leaching of DOC influenced the results. Regardless, some soil samples were collected near or under slash piles, and in Chapter 2 and Shabaga et al. (2015) I found that FWD was correlated to \(\text{FCO}_2\), suggesting that contributions may have contributed to (or acted as a proxy for) increased decomposition rates. Using woody debris leaching rates measured by Rudz (2013) in my study area, pre-harvest CWD contributed an estimated 12-17 kg C ha\(^{-1}\) yr\(^{-1}\) as DOC to the LFH, higher than 11 kg C ha\(^{-1}\) yr\(^{-1}\) in a deciduous forest converted from pasture 30 years prior (Hafner et al., 2005; Kuehne et al., 2008). Since my study site has only been used as a managed forest, I would anticipate higher woody debris volumes and therefore higher leachate flux. After harvest, TL and BIO treatments produced an estimated 21-23 kg C ha\(^{-1}\) yr\(^{-1}\) of DOC leachate; higher than pre-harvest values, but considerably lower than 147 kg C ha\(^{-1}\) yr\(^{-1}\) estimated by Mattson et al. (1987) following a clear-cut of a mixed forest. The volume of new FWD inputs was 38% that of CWD, but decay rates have been shown to be twice as high (Müller-Using and Bartsch, 2009). Based on this, estimates of DOC flux from FWD were about half those of CWD before (5-7 kg C ha\(^{-1}\)) and after harvest (10-11 kg C ha\(^{-1}\)). Together, new post-harvest FWD and CWD inputs produced an estimated additional 7-12 kg C ha\(^{-1}\) of DOC leachate.

3.5.6.3 C Exports from Soil Respiration and Rapid SOC Recovery

Based on the results from Chapter 2 and Shabaga et al. (2015) and measurements of \(\text{CO}_2\) efflux from incubated soil samples (data not shown), increases to heterotrophic respiration rates following harvest emitted an estimated additional 1830 kg C ha\(^{-1}\) relative to the unharvested control treatment during the snow-free period (April and October 2010). In total, estimates of C losses from decomposition of fine roots and mycorrhizal biomass could account for 9-15% of increases to heterotrophic respired C. When estimated total C soil losses from SOM pools and inputs from woody debris leachates were also considered, post-harvest increases to \(\text{FCO}_2\) from heterotrophic respiration accounted for about half of total estimated C losses. Since losses were likely over-estimated, even after a highly conservative
correction, this suggests that post-harvest stimulation of decomposition rates could account for most soil C losses within the first post-harvest year.

By the third post-harvest year SOC had recovered to pre-harvest values in the mineral soil, and remained similarly lower in the LFH layer. In chapter 2 and in Shabaga et al. (2015) I found that FCO$_2$ in my study area was only correlated to increased FWD in the first post-harvest year (2010), and that the difference in FCO$_2$ between harvested treatments and controls during autumn 2012 were half those of 2010. Since soil respiration after leaf drop tends to be predominantly from heterotrophic activity (Chapter 2 and Shabaga et al, 2015), these results suggest that an initial burst of heterotrophic activity following harvest may decline rapidly as labile C from harvest residues are consumed. The lack of LFH recovery is consistent with this finding as well as numerous studies noting that the forest floor C pools remain lower than mature stands for years following harvest, in part due to reduced litter inputs (Covington, 1981; Yanai et al., 2003). The recovery of mineral SOC suggests that losses were rapidly replaced by residues, likely from turn-over of decaying fine roots and other translocated SOM inputs from the LFH. Since this recovery was quite rapid, and the flux of lost and recovered C so large, this lends further credence to the prediction that even conservatively corrected losses were over-estimated.

### 3.5.7 Evidence for Enhanced Post-Harvest Nitrification Rates

Disturbed forests can increase rates of nitrification and leaching losses from associated acidification (Bormann and Likens, 1979), whereby nitrification is stimulated by increased N mineralisation rates and availability of NH$_4^+$ for nitrifiers, elevated soils temperatures, and reduced competition with plants (Paul, 2007). Vitousek and Matson (1985) found elevated rates of N mineralisation, NH$_4^+$ concentrations, and nitrate production in the upper mineral soil of a harvested pine forest, and that removal of post-harvest woody residues in whole tree harvests produced lower N mineralisation rates and soil NO$_3^-$ concentrations relative to stem-only harvesting. They surmise that harvest residues provided labile C substrates for heterotrophs, increasing N mineralisation rates and available NH$_4^+$ for nitrification. In contrast, I found reduced levels of NH$_4^+$ accompanying elevated levels of NO$_3^-$ in both the LFH and upper mineral horizons of harvested treatments relative to controls. Pre to post-harvest declines to NH$_4^+$ were weakly correlated to increasing NO$_3^-$ concentrations ($r^2=0.11$, $n=48$, $p=0.05$ in the LFH of the harvested treatment, but not in the control treatment or mineral soil. The overall increase in NO$_3^-$ only accounted for 0.9-1.4% of reductions to NH$_4^+$, but since NO$_3^-$ typically has a very short residence time in most soils due to leaching and rapid uptake, assessment of the role of nitrification on losses of NH$_4^+$ are unlikely to be captured by net changes to extractable NH$_4^+$ and NO$_3^-$ pools.
Although the addition of harvesting residues with a high C:N ratio may potentially inhibit nitrification (Paul, 2007), an abundance of available N relative to C in SOM and DOM can offset constraints to heterotrophs. The C:N ratios of SOM (LFH: C:N = 18-20, mineral: C:N = 17-18) and in the dissolved phase (LFH: C:N = 5-8, mineral: 15-18) were relatively high in my study site, and did not vary substantially between treatments. Higher post-harvest concentrations of DON in the LFH horizon were correlated to higher NO$_3^-$ levels in both the LFH and mineral horizons ($r^2=0.79$ and 0.63, $n=10$, $p=\leq0.01$), but DON from the mineral horizon was not correlated to NO$_3^-$. Similarly, a lower C:N ratio of DOM in the LFH was correlated to NO$_3^-$ in both the LFH ($r^2=0.36$, $n=10$, $p=\leq0.10$) and mineral horizons ($r^2=0.65$, $n=10$, $p=\leq0.01$). This indicates that N availability was probably not limiting for nitrifier activity, that harvesting increased N mineralisation rates and successive nitrification in the LFH horizon, and NO$_3^-$ supplies in the mineral horizon were influenced by production in the LFH.

The post-harvest increase in mineralisation and nitrification rates was likely a product of increased availability of labile C from harvesting residues stimulating microbial activity and changes to soil temperatures. Summer soil temperature were moderately correlated to NO$_3^-$ in the LFH ($r^2=0.21$, $n=59$, $p=\leq0.001$) and mineral soil ($r^2=0.15$, $n=57$, $p=\leq0.01$). Although there was no relationship between NO$_3^-$ and woody debris, increasing post-harvest NO$_3^-$ values were strongly predicted by a lower residual combined tree and sapling basal area in harvested plots for both the LFH and upper mineral soils (Fig. 3.4a, b; $r^2=0.66$ and $r^2=0.86$, $n=10$, $p=\leq0.01$), but not in control plots. When considered by species there was no correlation between the residual BA of deciduous cover and NO$_3^-$, yet a higher residual conifer BA predicted lower NO$_3^-$ levels in both the LFH and mineral horizons for all treatments ($r^2=0.41$ and $r^2=0.50$; $\beta_1=-0.14$ and -0.04; $n=15$, $p=\leq0.05$). This effect was stronger when only harvested plots were considered ($r^2=0.60$ and $r^2=0.82$; $\beta_1=-0.22$ and -0.07; $n=10$, $p=\leq0.01$). Furthermore, post-harvest NO$_3^-$ concentrations were negatively correlated to the BA of cut conifer trees in both the LFH and mineral horizons ($r^2=0.50$ and 0.84; $n=10$, $p=\leq0.05$). In contrast, NO$_3^-$ levels increased in both the LFH and mineral soil with cut deciduous BA (Fig. 3.4c, d; $r^2=0.44$ and 0.41, $n=10$, $p=\leq0.05$).

These results suggest that post-harvest nitrification rates were increased by elevated soil temperatures and the intensity of tree removal. Ostensibly, the latter was due to increased labile C supplies from harvesting residues such as decaying roots influencing N mineralisation rates, particularly for deciduous trees. Additionally, areas with a higher proportion of conifers may limit nitrification, especially following harvest. Nitrification is an acidifying process, and rates often depend upon availability of NH$_4^+$ and may decline with soil pH (Schlesinger, 1997). Ste-Marie and Paré, (1999) found that nitrification was more prevalent in areas of deciduous cover and nearly absent in some conifer stands, and determined in large
part by soil pH. Several other studies have noted lower rates of nitrification in conifer dominated stands, sometimes linked to lower pH (<5) or the presence of allelopathic compounds in plant residues produced exclusively or in higher quantities by conifers, such as terpenoids and tannins (Killham, 1990; Schlesinger, 1997; De Boer and Kowalchuk, 2001).

Figure 3.4 Relationships between post-harvest NO$_3^-$ concentrations and residual post-harvest tree and sapling basal area averaged by plot in the (a) LFH horizon (b) and mineral horizons; and compared with the basal area of cut deciduous trees for the (c) LFH horizon (d) and mineral horizons. All assessed in a mixed deciduous forest of Central Ontario.

I did not find a direct link between NO$_3^-$ and deciduous cover or pH, but PC2-LFH values, defined by increasing acidity, soil moisture, and conifer cover, were negatively correlated to NO$_3^-$ in the LFH and mineral horizons across all treatments ($r^2=0.34$ and 0.43, n=15, p≤0.05). Conifer cover and NH$_4^+$ were inversely loaded on PC2-MIN, indicating supplies were limited where conifer cover was higher, and PC3-MIN linked higher conifer cover to lower pH. My data therefore indicates that nitrification rates increased in response to tree harvesting intensity, and was either positively influenced by environmental conditions that favour deciduous dominated stands or inhibited by conditions favouring conifer dominated stands.
3.5.8 Changes to Cation Exchange Dynamics

An increase to SOM decomposition rates following harvest may also account for declining cations in the LFH layer. Changes to pH and the decomposition of organic compounds may liberate acid metal cations (e.g., Al, Fe) by increasing solubility and degrading chelates binding them to SOM and DOM into the soil solution (Sollins, 1996; McLaughlin, 2014), altering exchangeable pool dynamics. Acid cations have a higher strength of adsorption to colloid surfaces than soluble non-acid cations (e.g., K, Na, and NH$_4^+$). This leaves non-acid cations susceptible to displacement and leaching loss, potentially reducing non-acid cation saturation and increasing saturation of Fe and Al in the exchangeable soil pool.

I observed significant reductions to readily displaced cations in the LFH layer, such as K and NH$_4^+$, and a modest and non-significant decline to Mg. The third post-harvest year saw a non-significant increase to Fe effect sizes, while Mg and K remained lower than in controls despite evidence of recovery to K. Patterns in the upper mineral horizon were similar but weaker. There was no indication of soil Ca loss, which agrees with the conclusion by Mclaughlin (2014) that partial harvesting practices in mixed hardwood forests do not significantly decrease pools of extractable Ca in the short term. Since pH did not vary between treatments before or after harvest, and was not sufficiently acidic (pH ≈4.3-4.8) to solubilise acid cations (e.g., Fe, Al), mobilisation of Fe from acidification cannot account for changes. However, post-harvest declines to SOM predicted increases to Fe ($r^2=0.40$, p≤0.05; n=10), and increasing soil FCO$_2$ in autumn 2010 predicted increases to Fe and Al in harvested treatments (Fig. 3.5a; $r^2=0.80$, p≤0.001; and $r^2=0.39$, p≤0.05; n=10); non-significant decreases to Ca, Mg, and K were also predicted by soil FCO$_2$ ($r^2=0.28$, 0.29, and 0.32, p=0.08-0.12; n=10). Furthermore, increasing post-harvest FWD inputs predicted declines to PC1-LFH (Fig. 3.5b; $r^2=0.71$, p≤0.01; n=10), which corresponded to similar predicted declines in K and NH$_4^+$ values ($r^2=0.56$, p≤0.01, and $r^2=0.38$, p≤0.05; n=10), and increases to Fe values ($r^2=0.59$, p≤0.01; n=10).

Since cations often form complexes with DOC (Sollins, 1996), concurrent declines to DOC suggest apparent losses may be due to restriction from the exchange complex and/or leaching. However, a deficit of evidence for cation leaching to depth and an observed increase in exchangeable Fe, which adsorbs strongly to DOC ligands, makes this unlikely. Instead, a strong correlation between PC1-LFH (i.e., CEC) and PC3-LFH (i.e., labile compounds) and correlations between changes to cations, PC1-LFH, and FCO$_2$ indicates that the CEC may have been altered in harvested treatments due to increased decomposition of SOM, particularly in the LFH. Additionally, increasing Fe and Na, both of which have a low biological demand, suggest that relative declines to non-acid cations such as K, NH$_4^+$, and Mg may be
related to increases in biological assimilation. Vegetation and root regrowth begins rapidly following harvest (Yin et al., 1989; Shabaga et al., 2015), and cation uptake by plant roots can be inhibited in acidic soils, particularly where anions are in relative short supply. In the absence of changes to soil pH, an increase in $\text{NO}_3^-$ production from nitrification may facilitate uptake of macronutrient cations by plant roots (Kirkby, 1981; Nadelhoffer et al., 1984). However, higher $\text{NO}_3^-$ concentrations have also been associated with increased leaching of non-acid cations in acidic soils (Likens et al., 1994). Therefore, despite lack of evidence for enhanced leaching of cations from harvested areas, declines in $\text{NH}_4^+$, K, and Mg may be attributable to a combination of increased uptake by decomposers and plants as well as leaching losses.

Figure 3.5 Relationships between pre to post-harvest changes in Fe concentrations in the LFH horizon and (a) change in soil carbon dioxide efflux ($\text{FCO}_2$) for $R_{\text{Smean}}$ values averaged by plot measured in the autumn of 2010 and, (b) post-harvest PC1-LFH values (in standard deviations from the mean) and inputs volumes of fine woody debris (FWD) averaged by plot in a mixed deciduous forest of Central Ontario. $R_{\text{Smean}} = $ soil respiration modelled to mean control treatment values.

3.5.9 Differences Between Harvested Treatments

Harvesting deposited 92% more CWD and FWD in the TL treatment than the BIO treatment. Decreases to woody debris inputs may impact long-term soil nutrient pools (Thiffault et al., 2011). However, three years of post-harvest evaluation showed no indication of increased impacts on nutrient pools associated with increased biomass retrieval. In general, harvesting produced similar patterns of change to the soil chemistry to both harvested treatments. Although the TL treatment demonstrated stronger effects on soil chemistry in the upper mineral horizon, this may have been related to the heterogeneity of soil chemistry and influenced by extreme values. Correlations between soil chemistry and woody debris may have been representative of variations in individual plot harvest intensity rather than a direct effect of woody debris retention. Some relationships were similar to those seen with cut tree basal area,
although others varied, suggesting a need for further investigation into the role of woody debris harvest residues on soil chemistry relative to other harvest residues (i.e., root and mycorrhizal necromass and regrowth).

3.6 Summary and Conclusions

Despite an abundance of study, a mechanistic understanding of harvesting disturbance intensity on soil nutrient and carbon dynamics remains unclear. This is due in large part to the spatiotemporal complexity of forested ecosystems, producing system specific results and conditions, and potential inconsistencies in sampling methods. This study examined the effects of a method of forest management specifically designed to minimise ecosystem impacts, yet was able to detect modest post-harvest losses of SOM and a substantial decline to labile compounds and cations such as DOM, NH$_4^+$, and K and an increase to NO$_3^-$ in the forest floor. Smaller, similar changes were found in the upper mineral horizon. Increases to NO$_3^-$ were strongly correlated between horizons and to increased removal of deciduous tree biomass, indicating that even low impact harvesting may induce nitrification commonly associated with more intense harvesting practices. Use of PCA connected increasing acidity and % conifer cover to lower NO$_3^-$ independent of harvesting, and parsed remaining soil chemistry into two correlated underlying components representing CEC and labile compounds. The latter was also correlated to elevated post-harvest soil respiration rates, and linked enhanced SOM decomposition and N immobilisation to declining CEC and cation declines. Estimated increases to heterotrophic respiration following harvest accounted for most SOC losses and estimated C fluxes from decaying harvest residues, but high spatial variation in soil C hampered the accuracy of estimates. Substantial K losses and modest declines in Mg and increases to Fe in the LFH three years after harvest suggest some loss of base saturation, but I found no clear indication of Ca or Na losses or changes to pH, and mineral pools remained relatively unaffected. Base cation losses may have been through decomposer immobilisation and uptake by understorey regrowth, but despite a lack of evidence, leaching cannot be discounted as a pathway of loss. Harvesting treatment effects were statistically indistinguishable between two different partial-harvest intensities. This agrees with the conclusion by Mclaughlin (2014) that variable intensity partial-harvesting practices in mixed and hardwood forests do not significantly decrease pools of extractable Ca over 10 year periods, though this effect may be site dependent.

Therefore, I conclude that partial harvesting in mixed northern systems can produce increases to NO$_3^-$ and losses of SOM and K via increased nitrification and decomposition rates, and that modified selection harvesting for additional woody biomass by increased retrieval of smaller diameter wood does not
present an elevated risk for loss of vulnerable nutrients in the shorter term, particularly base cations. However, few studies of harvesting disturbances have persisted beyond a single harvest cycle (Raulund-Rasmussen et al., 2008), and chronosequence studies have proven unreliable at detecting the magnitude of post-harvest changes to soil C (Yanai et al., 2003), challenging our understanding of long-term nutrient supply and C dynamics and the reliability of predictive models (Thiffault, et al., 2011). Additionally, few studies explicitly consider changes to underlying biogeochemical mechanisms that may respond to harvesting. As such, further study assessing post-harvest changes to decomposition rates, leaching losses, root uptake, and ion exchange following multiple successive harvests is essential to properly evaluate the risk of long-term changes to soil C and nutrient retention.
Chapter 4
The Influence of Skid Trail Use Intensity on Soil Compaction, Respiration, and Carbon and Nutrient Pool Losses in a Managed Northern Mixed Deciduous Forest

4.1 Abstract

Skid trials comprise up to 20-40% of many managed forest areas and are subject to wide variations in disturbance intensity. Despite the potential for accelerated carbon (C) and nutrient losses following use, they are underrepresented in studies of forest soil respiration as CO$_2$ efflux (FCO$_2$) and biogeochemistry. To address this, I assessed changes to soil FCO$_2$ and chemistry on primary and tertiary skid trails relative to adjacent cut forest between May and October following a winter partial-harvest in a Central Ontario mixed hardwood forest. Soils of primary skid trails were highly mixed and compacted relative to forest controls and tertiary trails, with rates of FCO$_2$ substantially lower than from adjacent harvested forest controls (≈36%, p=≤0.01), despite higher soil temperatures (+2.5°C, p=≤0.01). After accounting for temperature differences, predicted FCO$_2$ values on primary skid trails were half those of controls. The absence of roots and estimated associated respiration accounted for the majority of this difference (≈73%), while reduced pore space from compaction leading to periodic moisture saturation and lower C availability for heterotrophs probably accounted for the remainder. On tertiary trails, FCO$_2$ from ruts was also lower than adjacent forest controls (18%, p=≤0.10) despite higher soil temperatures (+0.7 °C, p=≤0.01), while values were slightly higher on trail centres (10%, p<0.10). Correction for soil temperatures differences negated higher centre values and predicted even lower FCO$_2$ from ruts, suggesting tertiary ruts were more influenced by compaction and/or root damage than centres.

Soil C and N values on primary skid trails were substantially lower than controls in May (50%), probably due to reduced SOM inputs from litter-fall and root turnover from previous years. Certain base cation concentrations (K and Mg) were also much lower (30-40%), and values for total C:N and cations did not change substantially between May and October. In tertiary sites, total C and N values were also considerably lower in ruts than in adjacent forest controls (19-27%) in May, and modest declines by October (5-11%) were lower than that of declines in controls (12-23%). In contrast, declines in total C and N for primary and tertiary trail edges during this period were 7-11% greater than for controls, suggesting slightly increased rates of decomposition despite no difference in FCO$_2$. However, C losses across all treatments were difficult to quantify due to high spatiotemporal variability of data, and highlight the importance of technique and sampling adequacy. Overall, recurrent and higher intensity
use of primary skid trails had a much greater impact on soil FCO$_2$ and chemistry than intermittent tertiary trail use, primarily due to lack of tree root regrowth and compaction effects.

4.2 Introduction

Terrestrial stores of soil organic carbon (SOC) are largely regulated by disturbance to soils and ecosystems from land-use changes such as conversion from forest to agriculture, reforestation, forest aggradation, and urbanisation (Houghton, 1999, 2003), altering rates of net primary production, decomposition, and soil respiration dynamics (Chapin et al., 2002; Chapter 2 and Shabaga et al., 2015). Soil respiration ($R_S$) is a product of respiring heterotrophic organisms decomposing litter and soil organic matter (SOM) and the roots of trees and other vegetation, and comprises the largest source of global terrestrial CO$_2$ efflux (FCO$_2$) (Heimann and Reichstein, 2008; Subke and Bahn, 2010). In managed forests, harvesting of trees may elicit changes to FCO$_2$ as a function of tree root senescence, changes to soil moisture and temperature, and fluctuations in available labile soil organic carbon (SOC) pools favoured by decomposers, implicated in “priming” decomposition of more recalcitrant soil C (Kuzyakov et al., 2000; van Hees et al., 2003; Paul, 2007; Zummo and Friedland, 2011; Chapter 2 and Shabaga et al., 2015). Increased SOM mineralisation rates from disturbances associated with land-use changes may therefore contribute to reduced soil C pools and accumulating atmospheric carbon dioxide (CO$_2$; Houghton, 1999, 2003; Shevliakova et al., 2009), and increase leaching losses of SOC and cations (including base cations K, Ca, Mg, Na) by reducing the soil adsorption capacity (Borman and Likens, 1979; Covington, 1981; Sollins, 1996; Yanai et al., 2003; Paul, 2007; McLaughlin, 2014; Chapter 3; others).

Skid trails are roadways used to remove harvested wood from cut-blocks, and comprise a considerable proportion of managed forest area. In the province of Ontario, provincial silvicultural guidelines recommend that total trail coverage not exceed 20% in selection harvests and 30% for shelterwood and thinning harvests in mixed deciduous forests (OMNR, 2010). Trail coverage of 18-38% has been reported for thinned western coniferous forests and partially-harvested New York hardwood forests (Nyland and Gabriel 1971; Froehlich et al., 1981). Trails often follow a herringbone or vascular pattern, with larger and more heavily used primary skid trails branching into narrower and more lightly used secondary and tertiary trails, often defined by the number of passes by machinery (e.g., primary: 12+ passes, secondary 4-8, tertiary 1-3; McNabb et al., 2001). Disturbance effects from harvesting are often concentrated on skid trails where soil temperatures can be higher than adjacent forest, moisture levels are more variable, soils are more susceptible to erosion, and roots can be damaged or severed. Furthermore, soils
are often compacted from machinery: this can inhibit new root growth and reduce soil pore space and rates of gas exchanges, such as diffusion of atmospheric oxygen into soil and $\text{FCO}_2$ (Ballard, 2000; Startsev and McNabb, 2009; Novara et al., 2012). Some studies indicate that compaction of soil to bulk densities >1.5 g cm$^{-3}$ may also reduce SOC decomposition (De Neve and Hofman, 2000), competing with disturbance effects that might stimulate decomposition rates and $\text{FCO}_2$. In many soils, most compaction occurs after the first few passes; however, primary trails typically experience higher overall compaction rates than tertiary trails, and changes to soil structure can vary greatly amongst and within ecosystems (McNabb et al., 2001; Ezzati et al., 2014; Naghdi and Solgi, 2014).

Since skid trail networks develop in response to demarcation of cut-block areas and variations in landscape topography that prohibit machine access, they sometimes run along low lying moist areas out of necessity. Soil bearing strength declines sharply with increasing moisture, making these areas especially sensitive to disturbances such as mixing, compaction, and rutting, although high soil moisture content can reduce compaction where air-filled porosity is limited (McNabb, 1994). Best management practices and government regulations often recommend or require avoidance of trail development and use in such areas, or mandate use only during drier months or when soils are frozen and have a higher structural strength, resisting damage to roots, disturbance of the forest floor, and rutting (Ballard, 2000; Duckert et al., 2009; OMNR, 2010). Regardless, it can sometimes be difficult to anticipate the presence of ephemeral springs and other moist areas and prevent excessive soil disturbance from occurring, particularly on heavily utilised trails and in areas of high relief and restrictive access. Furthermore, sometimes trail installation and use can alter local surface hydrology, turning trails into ephemeral streams.

Despite their wide coverage and propensity to disproportionate disturbance effects, skid trails have been relatively under-studied with regard to impacts on forest biogeochemical processes. Most studies have focused on compaction and erosion of skid trail soils, others on nutrient run-off, but I am unaware of any that specifically attempt to measure changes to $\text{FCO}_2$ rates and pools of SOC and base cations as related to biogeochemical processes. In light of this, the objectives of this study were to: (i) compare the effect of two different skid trail intensities on rates of $\text{FCO}_2$ and pools of soil organic carbon and base cations relative to adjacent forest harvested using single-tree selection in a mixed deciduous forest in Central Ontario; (ii) compare changes to SOC and base cations before and at the end of the post-harvest growing season; and (iii) identify key mechanisms by which disturbances influence biogeochemical processes that account for observed patterns of $\text{FCO}_2$ and soil chemistry. With consideration to these objectives, I hypothesise that: (i) primary trails will be substantially more compacted and produce lower
rates of FCO$_2$ than tertiary trails and adjacent forest due to reduced gas exchanges and root contributions; (ii) tertiary trails will be minimally compacted relative to primary trails, and rates of FCO$_2$ will be similar to controls; (iii) soil C and nutrient content will be lower on primary trails than tertiary trails and controls due to frequent re-use and subsequent reductions to inputs of forest residues over prolonged periods, but similar between tertiary trails and adjacent forest; and (iv) soil C and nutrients will decline in all treatments including harvested controls during the post-harvest growing season.

4.3 Methods

4.3.1 Study Site

The study was conducted within the Haliburton Forest and Wildlife Reserve (44°55'N, 78°50'W), a privately owned and commercially managed forest within the Great-Lakes St. Lawrence (GLSL) forest region of Central Ontario. The humid continental climate has a mean annual temperature of 5.0 °C and 1074 mm of precipitation with low monthly variation and 280 mm as snow (Environment Canada, 2015). Upland vegetation is dominated by sugar maple (Acer saccharum Marsh), American beech (Fagus grandifolia L.), yellow birch (Betula alleghaniensis Britt.), and eastern hemlock (Tsuga canadensis Britt.). The area has been managed for 50+ years using various intensities of partial harvest, most recently single-tree selection in 15 to 25 year harvest cycles. Soils overlie granite-gneiss Precambrian Shield bedrock and are shallow (0.5 – 2 m deep) and acidic (pH 4.2 – 6.2) Dystric Brunisols with organic-rich surface horizons and textures ranging from sandy loam to loamy sand. The topography comprises undulating hills and partially exposed bedrock, interspersed with numerous small wetlands. This study focused on well-drained upland areas where commercial harvesting would typically occur but some areas were wetter than others.

4.3.2 Experimental Design

Plots were established in the study area following commercial harvest between January and March of 2012. Trail installation and harvesting were conducted using regional Ontario silviculture guidelines (OMNR, 1998) for selection harvest practice: ≈25-30% of tree basal area were removed, including mixed sizes, boles only, all stems >17 cm diameter at breast-height (DBH) with a target top diameter of 18 cm. Eighteen split plots were installed in random locations set up along primary (n=9) and tertiary (n=9) skid trails within a 2 km$^2$ harvested upland forest area. Plots contained four soil sampling locations running in a line perpendicular to the trail and into the forest (Fig 2.1), with each sampling location comprising a
different treatment: the trail centre (Centre), a trail rut (Rut), the edge of forest about 20-30 cm from the trail (Edge), and 5 m from the trail in the forest (Control).

To capture both heterotrophic and root respiration ($R_S$), collars were installed to a depth of 2-3 cm in April 2012 and allowed to equilibrate with the environment until the first set of measurements in May 2012. Soil CO$_2$ efflux was measured by enclosing collars with a 1.5 litre PVC chamber connected via Tygon® tubing to a customised Infrared Gas Analyzer (IRGA) field kit (S151 CO$_2$ Analyzer; Qubit Systems). The chamber atmosphere was equalised to atmospheric pressure via a relief valve and circulated using an air pump flowing at 150 ml min$^{-1}$. Contents were allowed to equilibrate for several minutes until CO$_2$ concentrations readings stabilised in the chamber, then measurements of chamber CO$_2$ concentrations were recorded for 3 to 5 minutes and repeated when rates appeared unstable. The short measurement period minimised chamber CO$_2$ concentrations, avoiding alteration of diffusion rates of CO$_2$ from soils (Davidson et al., 2002). Air temperatures in the chamber were recorded prior to measurement and soil temperatures were recorded using a probe inserted to a 5 cm depth beside the soil collar.

FCO$_2$ and air and soil temperatures were measured every three weeks between May and October 2012. To minimise daytime soil temperature differences, FCO$_2$ was measured between 10 am and 4 pm on consecutive days. The number of sampling points (n=72) and distribution over a large area sometimes necessitated a 2 day collection period. Measurements were avoided within 24 hours of significant rain events to prevent FCO$_2$ “flushing” effects (Laporte et al., 2003). Rates of FCO$_2$ were determined by using chamber CO$_2$ headspace concentrations to calculate changes in the mass of CO$_2$ produced by area over time and expressed as µmol CO$_2$ m$^{-2}$ s$^{-1}$.

4.3.3 Determining Q$_{10}$ and Modelling Temperature-Adjusted Respiration Rates

The Q$_{10}$ of respiration was calculated using the van’t Hoff equation method employed by Linder and Troeng (1981). A linear regression equation was defined for each subject between the natural logarithm of soil FCO$_2$ and temperature (°C) measurements:

$$\ln(R_S) = \beta_0 + \beta_1 \times Temperature \ °C$$

(1)

The $\beta_1$ coefficients were used to calculate Q$_{10}$ values:

$$Q_{10} = e^{(\beta_1 \times 10)}$$

(2)
Q_{10} can be used to model FCO\textsubscript{2} rates at various temperatures. This approach was used to standardise measured FCO\textsubscript{2} values to 10 °C (R\textsubscript{10}), producing “basal” respiration rates (Davidson et al., 2006; Acosta et al., 2008):

\[ R_{10} = R_S \times Q_{10}^{\left(10-T\right)/10} \]  \hspace{1cm} (3)

To correct for temperature differences between treatments and sampling locations while maintaining seasonal temperature based patterns of R\textsubscript{S}, I used R\textsubscript{10} and Q\textsubscript{10} values to predictively model FCO\textsubscript{2} rates (R\textsubscript{Smean}) standardised to the mean control treatment temperature value from each measurement date.

\[ R_{Smean} = R_{10} \times Q_{10}^{\left(T_{mean}-10\right)/10} \]  \hspace{1cm} (4)

To compare changes to respiration associated with trail use and harvesting, the difference between mean treatment values were used to determine the *effect size* of skid trail treatments. The magnitude of effect sizes were calculated as a proportion of the mean control value (except where otherwise indicated). For example:

\[ \frac{\left(R_S^{(treated)} - R_S^{(control)}\right)}{R_S^{(control)}} \times 100 = \% \text{ effect size} \]  \hspace{1cm} (5)

### 4.3.4 Soil sampling and analysis

Soil samples were collected within 1 m of FCO\textsubscript{2} soil collars locations in early April 2012 following winter harvesting, and again in early October 2012. The forest floor, where present, was carefully separated from the mineral soil surface, and soil samples were extracted using a soil corer to 20 cm. In some cases, soil sample locations were offset to avoid roots, cobble, and woody debris.

Soil samples were sealed in plastic bags, frozen within hours of collection, and thawed later for processing. Samples were air dried and sieved to 2 mm prior to measuring SOC, total N, and extractable base cations (e.g. Na, Ca, Mg, K) at the Ontario Forest Research Institute (OFRI). A total C/N analyser was used to determine concentrations of soil organic carbon (SOC) and total N. Extracts were prepared using ammonium acetate to assess base cation concentrations, and analysed using an ICP with quality control applied using ISO standards derived from soil and plant material.

To compare changes in soil chemistry associated with recovery of trails over the growing season, the difference between mean values for May and October were used to determine the *effect size*. The
magnitude of effect sizes were calculated as a proportion of the May value for each treatment to
distinguish relative change (except where otherwise indicated). For example:

\[(\text{SOC}_{\text{October}} - \text{SOC}_{\text{May}})/\text{SOC}_{\text{May}} \times 100 = \% \text{ effect size}\]

Bulk density samples were extracted using a 5 cm diameter soil corer to a depth of 10 cm. Soils were
weighed, dried, and weighed again. Soil porosity was estimated from bulk density using an assumed
mineral particle density for granite (2.65 g cm\(^{-3}\)) and an organic material density of 1.25 g cm\(^{-3}\) (Brady
and Weil, 2010).

4.3.5 Statistical Analysis

4.3.5.1 Data Preparation

All FCO\(_2\) data (R\(_S\), R\(_{10}\), and R\(_{\text{Smean}}\)) were log-transformed prior to analysis to fit the assumptions of
homogeneity of variance for LMMs (Herbst et al., 2009; Chapter 2 and Shabaga et al., 2015). The mean
and standard errors were back-transformed and represented in units of µmol m\(^{-2}\) s\(^{-1}\). Back-
transformation produced uneven sized standard errors due to log transformations.

Much greater variability existed for soil chemistry data, producing extreme values that were identified
as those outside 99% of the normal distribution range (i.e., z-scores exceeding 2.58 or -2.58). These
ranged from Z=±3 to ±10, and could not be directly attributed to human or analytical error. The results
of parametric analyses such as LMM can be susceptible to extreme values that produce
heteroscedasticity, disproportionately influencing means. In addition to these extreme variables within a
set of measurements, extreme differences between time points in repeated measure analyses can also
act as outliers, disproportionately influencing outcomes. To account for these values without rejecting
valid results, “extreme” values were “winsorized” (Tukey, 1968), being reassigned z-scores of 2.58
or -2.58. This method reduced skew and improved the homogeneity of variance, assessed using
Levene’s test and residual plots. The product of these trimming methods reduced overall effect sizes and
standard errors while retaining values that appeared as outliers but were otherwise real measurements.
Furthermore, it reduced correlation coefficients amongst variables artificially inflated by outliers.

4.3.5.2 Hypothesis Testing

Principal component analysis was used to assess correlative relationships amongst soil chemistry
variables (SPSS v.21, IBM). Soil chemistry and FCO\(_2\) variables were tested for treatment effects using
interaction effects between time and treatments (skid trail type and position) in a linear mixed model
(LMM: SPSS v.21, IBM) and random intercepts to account for subject dependence of repeated measures and plot dependence. Univariate (ANOVA) multiple comparison tests and pairwise post-hoc tests were used to interpret simple effects associated with significant interactions. Significance tests used Fisher’s unrestricted least significant difference (LSD) method rather than more conservative corrections due to the low number of treatment groups and to better understand complex interaction effects without unnecessary loss of power (Saville, 2003).

4.4 Results

4.4.1 Soil Bulk Density and Moisture

Bulk densities between 0-10 cm varied significantly between primary and tertiary skid trail sites and locations (Table 4.1). Soils on primary skid trails (centre: 1.23 g cm$^{-3}$, rut: 1.16 g cm$^{-3}$) were significantly more dense than the forest control (0.56 g cm$^{-3}$; p≤0.001). Tertiary skid trail values (centre: 0.57 g cm$^{-3}$, rut: 0.63 g cm$^{-3}$) were also higher than adjacent forest controls (0.48 g cm$^{-3}$) but differences were not statistically significant. Primary site forest edge treatment values were also higher than adjacent controls (0.78 g cm$^{-3}$; p≤0.05), while tertiary edge and control treatment values were essentially the same. Since higher soil organic matter (SOM) content can substantially reduce the bulk density of forest soils due to a lower material density and improved porosity (Perie and Oumet, 2007), and values varied considerably between skid trails and treatments, I attempted to correct for differences in SOC. The slope of a regression between log-transformed SOC and log transformed bulk density values ($r^2=0.65$, $\beta_1=-0.99$, n=72, p≤0.001) was used to adjust bulk densities based on differences in SOC between each sampling location and the mean SOC value for the forest control treatment. This correction reduced bulk density values on primary trails considerably, but values remained higher on trails (centre: 0.93 g cm$^{-3}$, rut: 0.83 g cm$^{-3}$, p≤0.01) and edges (0.66 g cm$^{-3}$; p>0.10) than forest controls (0.50 g cm$^{-3}$).

Soil samples from the 0-5 cm depth horizon were collected for each set of respiration measurements to determine gravimetric soil moisture values of the upper soil surface. Values for forest controls were 4.5x higher than primary skid trails, and 1.4x higher than tertiary trails. Differences were significant between skid trails and treatments within each skid trail type. Although bulk density was not measured for 0-5 cm, I was able to estimate values from gravimetric soil moisture (0-5 cm) averaged across May and June (similar to mean 0-10 cm moisture values) using a linear regression equation ($r^2=0.91$, $\beta_0=5.383$, $\beta_1=-0.803$, n=72, p≤0.001) derived from 0-10 cm log-transformed bulk density and log-transformed gravimetric moisture values. In turn, these bulk densities were then used to calculate volumetric soil
moisture and total porosity for 0-5 cm samples; these variables were not correlated to either 0-5 cm gravimetric moisture or estimated bulk densities, ensuring data independence.

Table 4.1 Soil bulk density and total porosity for 0-5 cm and 0-10 cm depths amongst treatment position groups (A=trail centre, B=trail rut, C=forest edge, D=adjacent forest controls) in primary (P) and tertiary (T) skid trail plots in a mixed deciduous forest in Ontario during the year 2012. Also estimated % water-filled porosity for 0-5 cm depths for June 2012 and the average over 2012 between May and August.

<table>
<thead>
<tr>
<th>Depth</th>
<th>Position</th>
<th>Bulk Density (g cm⁻³)</th>
<th>%Total Porosity</th>
<th>% Water-filled porosity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0-5 cm</td>
<td>P-A</td>
<td>1.26 ± 0.05</td>
<td>48.2 ± 1.8</td>
<td>75.1 ± 6.7</td>
</tr>
<tr>
<td></td>
<td>P-B</td>
<td>1.16 ± 0.06</td>
<td>51.9 ± 2.5</td>
<td>64.9 ± 7.0</td>
</tr>
<tr>
<td></td>
<td>P-C</td>
<td>0.34 ± 0.04</td>
<td>84.7 ± 1.4</td>
<td>42.6 ± 2.2</td>
</tr>
<tr>
<td></td>
<td>P-D</td>
<td>0.30 ± 0.05</td>
<td>86.1 ± 1.8</td>
<td>47.8 ± 2.4</td>
</tr>
<tr>
<td></td>
<td>T-A</td>
<td>0.34 ± 0.04</td>
<td>84.5 ± 1.8</td>
<td>42.1 ± 2.0</td>
</tr>
<tr>
<td></td>
<td>T-B</td>
<td>0.33 ± 0.03</td>
<td>85.1 ± 1.1</td>
<td>46.0 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>T-C</td>
<td>0.23 ± 0.03</td>
<td>88.9 ± 1.0</td>
<td>44.1 ± 3.9</td>
</tr>
<tr>
<td></td>
<td>T-D</td>
<td>0.26 ± 0.03</td>
<td>87.9 ± 1.2</td>
<td>46.9 ± 3.3</td>
</tr>
<tr>
<td>0-10 cm</td>
<td>P-A</td>
<td>1.23 ± 0.07</td>
<td>49.7 ± 2.9</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>P-B</td>
<td>1.16 ± 0.07</td>
<td>52.8 ± 3.0</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>P-C</td>
<td>0.78 ± 0.08</td>
<td>67.3 ± 3.2</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>P-D</td>
<td>0.56 ± 0.07</td>
<td>76.3 ± 2.6</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>T-A</td>
<td>0.57 ± 0.09</td>
<td>75.7 ± 3.7</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>T-B</td>
<td>0.63 ± 0.10</td>
<td>73.3 ± 3.7</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>T-C</td>
<td>0.49 ± 0.08</td>
<td>79.0 ± 3.4</td>
<td>NA</td>
</tr>
<tr>
<td></td>
<td>T-D</td>
<td>0.48 ± 0.09</td>
<td>79.2 ± 3.8</td>
<td>NA</td>
</tr>
</tbody>
</table>

Estimated volumetric soil moisture values (0-5 cm) declined considerably and similarly across all treatments from spring to late summer, and there was notably lower than average precipitation during the growing season of 2012. Levels peaked briefly in early June following heavy rains, and were slightly lower on primary trails (45-54%) and tertiary trails (48-56%) than forest controls (60-62%). However, estimated total porosity was about twice as high in tertiary sites and forest controls (85-89%) as primary
trails (48-49%). As such, water-filled pore space on primary trails was consistently higher than all other treatments throughout the year (65-75% vs 43-48%, p≤0.001), and was essentially saturated (95%) during early June while all other treatments retained remained between 56-73%.

4.4.2 Soil Respiration, Temperature, and Moisture

4.4.2.1 Temperature and Q10

The results of a linear mixed model analysis demonstrated that FCO2 varied significantly between treatments for both skid trail types, and treatment differences between skid trail types were not quite significant (Table 4.2). Measurements of soil respiration (Rs) as FCO2 averaged across the growing season were considerably lower in the centre and ruts of primary skid trails (35-38%, n=63, p≤0.01) than in forest controls and forest edges (Fig. 4.1). Similarly, FCO2 in ruts of tertiary skid trails were substantially lower (18%, n=63, p≤0.05) than forest controls, but trail centre values were actually higher than both forest controls (10%, n=63, p>0.10) and ruts (35%, n=63, p≤0.001). Forest edge FCO2 values did not differ notably from forest control values for either skid trail type.

FCO2 was significantly correlated to soil temperature using a natural log transformation (ln-FCO2) when pooled across all treatments and skid trails (r²=0.17, n=504, p≤0.001). When values were pooled by skid trail and treatments, stronger relationships emerged for forest control treatments in both skids trail types (r²=0.38-0.47, n=252, p≤0.001) and centres and ruts on tertiary skid trails (r²=0.53 and 0.30, n=252, p≤0.001). However, temperature remained a weak predictor of FCO2 for primary skid trails centres and ruts (r²=0.15 and 0.10, n=252, p≤0.001). Relationships improved considerably when they were evaluated for each individual sampling location (median r²=0.65, n=7, p≤0.05), accounting for the spatial heterogeneity and dependence of soil respiration (Chapter 2 and Shabaga et al., 2015).

In contrast to FCO2, soil temperatures were significantly higher in centres and ruts of both primary and tertiary skid trails than in forest controls (p≤0.001; Fig. 4.2). Temperatures on primary skid trails were already substantially elevated by May (centre=3.0 °C, rut=3.3 °C) and peaked in July (centre=5.1 °C, rut=3.5 °C) before becoming similar to forest controls in October. Tertiary skids trails exhibited a similar pattern of smaller differences, with insignificant differences in May, values peaking in August (Centre=1.6 °C, Rut= 1.8 °C) before declining below forest controls in October (Centre= -0.57 °C, Rut= -0.78 °C). Taking these differences into account, estimates of soil respiration corrected to mean temperature values in the forest control treatment (R_smean; Fig 4.1) predicted even lower FCO2 values on primary skid trails (centre: -47%, rut: -43%, p≤0.01) and tertiary ruts (-22%, n=63, p≤0.05) relative to adjacent forest.
Figure 4.1 Mean soil CO$_2$ efflux (FCO$_2$) values for Rs$^1$ and Rsmean$^2$ comparing differences amongst treatment position groups (A=trail centre, B=trail rut, C=forest edge, D=adjacent forest controls) in primary (P) and tertiary (T) skid trail plots in a mixed deciduous forest in Ontario during the year 2012. $^1$Rs = Measured soil respiration; $^2$Rsmean = soil modelled respiration estimated from mean control treatment temperature values.

Figure 4.2 A comparison of relative temperature (°C) differences between the forest control (D) treatment and each of the trail centre (A), trail rut (B), and forest edge (C) treatments for primary (P) and tertiary (T) skid trail plots between May and October in a mixed deciduous forest in Central Ontario during the year 2012.
Table 4.2 Linear mixed model significance test results of main and interaction effects for soil carbon dioxide efflux (FCO₂) from measured soil respiration (Rₛ), soil respiration modelled at mean control treatment temperature values (Rₛmean), the response of Rₛ to temperature over a 10 °C range (Q₁₀), and soil temperatures (Temp) for a mixed deciduous forest in Central Ontario. Also shown are results for soil bulk density (BD) to 10 cm depth and bulk density corrected for differences in soil carbon content (BD_adj). Significant results in bold.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Source</th>
<th>Significance (p-value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>Rₛ</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rₛmean</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Q₁₀</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Temp</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BD</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BD_adj</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>0.631</td>
</tr>
<tr>
<td></td>
<td></td>
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<tr>
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<td></td>
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<td>0.005</td>
</tr>
<tr>
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<tr>
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</tr>
<tr>
<td></td>
<td></td>
<td>&lt;0.001</td>
<td>0.016</td>
</tr>
<tr>
<td>Position*Skid trail type</td>
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<td>0.013</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.022</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&lt;0.001</td>
<td>0.029</td>
</tr>
</tbody>
</table>

Figure 4.3 Mean Q₁₀ values comparing differences amongst positions (A=trail centre, B=trail rut, C=forest edge, D=adjacent forest controls) in primary (P) and tertiary (T) skid trail plots in a mixed deciduous forest in Central Ontario during the year 2012.

The rate of change in FCO₂ over a 10 °C rise in temperatures (Q₁₀) was best described as exponential, and varied considerably by position on primary skids trails but not tertiary trails. Primary skids trails experienced a decline in FCO₂ from May to early June following extensive rains. This produced outliers in FCO₂ and temperature models that led to overestimation of seasonal Q₁₀ values and inflated standard errors; therefore, these data were removed from estimation of Q₁₀ values. On primary skid trails, Q₁₀ values (Fig. 4.3) varied significantly between trails and forest control (Centre: 1.8, Rut=1.5, Control=2.7, n=36, p≤0.01), with forest edge values falling in-between both (2.2). In contrast, Q₁₀ values in tertiary trail treatments were lowest in the forest control (2.3), but differences from other treatments (2.4-2.7) were insignificant.
4.4.2.2 Soil Moisture and Bulk Density

Gravimetric soil moisture (0-5 cm depth) and FCO₂ values pooled for all sampling locations were not correlated. When values were pooled by skid trail and treatments, moisture values were moderately correlated to declining ln-FCO₂ for primary trails only ($r^2=0.14$, $n=90$, $β1=-0.03$, $p≤0.001$). For volumetric soil moisture, pooled primary trail values ($r^2=0.13$, $n=89$, $β1=-0.027$, $p≤0.01$) predicted much greater declines to ln-FCO₂ than pooled primary forest treatment and tertiary site values ($r^2=0.06$, $n=263$, $β1=-0.005$, $p≤0.01$). Estimates of water-filled porosity for 0-5 cm were a better predictor of ln-FCO₂ than soil moisture when pooled across all treatments ($r^2=0.13$, $n=360$, $β1=-0.010$, $p≤0.001$), particularly in early June ($r^2=0.16$, $n=72$, $β1=-0.16$, $p≤0.001$). Similarly, ln-FCO₂ rates pooled across all treatments declined with increasing bulk density values ($r^2=0.07$, $n=360$, $β1=-0.42$, $p≤0.001$); again, this relationship was much stronger during early June ($r^2=0.46$, $n=72$, $β1=-1.22$, $p≤0.001$) but not present for other months or when pooled by treatment.

4.4.3 Soil Chemistry

The results of linear mixed model (LMM) found significant differences between skids trail types and dates for all soil chemistry variables, and significant differences between treatment positions for SOC, total N, and Mg (Table 4.3). A lack of a significant interaction effect between treatments and skid trails and dates suggests that the treatment response was similar on both trail types, and changes during the growing season did not differ significantly across treatments.

4.4.3.1 SOC and Total N

SOC was significantly ($p≤0.001$) higher in tertiary sites (forest control: May=10.1%, October=7.7%) than primary sites (forest control: May=6.4%, October=5.8%), and values declined across all treatments in both trail types over this period (Fig. 4.4). Overall declines were generally larger on tertiary sites than primary ones, decreasing by 24-33% ($p≤0.01$) on tertiary skid trail centres, edge, and control treatments, and by 11% ($p≤0.10$) in ruts. In contrast, SOC declined minimally on primary trail centres and ruts (<5%, $p>0.10$), while edge and control treatment values declined more substantially (25%, $p≤0.10$; 14%, $p>0.10$). SOC was considerably lower on primary skid trails than in forest controls for both May and October (50% and 44%, $p≤0.001$). On tertiary sites, skid trail values were also lower than forest controls in both May and October (18% and 16%, $p<0.10$).

Total N expressed a similar but somewhat weaker pattern of decline than SOC; as a result, the C:N ratio decreased similarly between all treatments from May to October for both primary (3%, $p≤0.05$) and
tertiary (5%, \(p \leq 0.01\)) sites. The C:N ratio was significantly (\(p \leq 0.01\)) higher on primary skid trails in both May and October (18.8 and 18.1) than in forest controls (17.4 and 16.7) but did not differ amongst treatments in tertiary plots.

Table 4.3 Linear mixed model significance test results of main and interaction effects for soil chemistry, including soil organic carbon (SOC), total nitrogen (TN), potassium (K), calcium (Ca), magnesium (Mg), and the extracted principal component produced following principal component analysis of all variables combined (PC1) in a mixed deciduous forest in Central Ontario. Significant results in bold. \(^1\)Intercept not significant since values were centred at a mean of zero.

<table>
<thead>
<tr>
<th>Independent Factor</th>
<th>DF</th>
<th>SOC</th>
<th>TN</th>
<th>K</th>
<th>Ca</th>
<th>Mg</th>
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</tr>
</thead>
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<tr>
<td>Intercept</td>
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<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>(1.000)</td>
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<tr>
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<td>0.001</td>
<td>(&lt;0.001)</td>
<td>0.092</td>
<td>0.198</td>
<td>0.045</td>
<td>0.008</td>
</tr>
<tr>
<td>Skid (trail type)</td>
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<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
<td>0.018</td>
<td>(&lt;0.001)</td>
<td>(&lt;0.001)</td>
</tr>
<tr>
<td>Date (measurement date)</td>
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<td>0.001</td>
<td>0.016</td>
<td>0.002</td>
<td>(&lt;0.001)</td>
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<tr>
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<td>0.360</td>
<td>0.024</td>
<td>0.641</td>
<td>0.414</td>
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</tr>
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<td>Skid *Date</td>
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<td>0.022</td>
<td>0.006</td>
<td>0.291</td>
<td>0.013</td>
<td>0.005</td>
<td>0.010</td>
</tr>
<tr>
<td>Position*Skid</td>
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<td>0.443</td>
<td>0.322</td>
<td>0.576</td>
<td>0.293</td>
<td>0.977</td>
<td>0.950</td>
</tr>
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<td>0.776</td>
<td>0.574</td>
<td>0.219</td>
<td>0.447</td>
<td>0.851</td>
<td>0.908</td>
</tr>
</tbody>
</table>

4.4.3.2 Cations

Base cations K, Ca, and Mg followed similar patterns of change as SOC from May to October. Values decreased substantially in tertiary edge (37-39%, \(p \leq 0.001\)) treatments, but more modestly in forest control (13-33%, \(p \leq 0.10\)) and tertiary trail treatments (11-18%, \(p > 0.10\)). In primary sites, K and Mg declined considerably in both edge and forest control treatments, (K=25-33%, \(p \leq 0.001\); Mg=11-19%, \(p > 0.10\)), but declines were negligible on primary skid trails. Ca did not change notably on either primary trails or forest area treatments, and tertiary values were substantially higher than in primary sites in both May (110%) and October (60%). In contrast, Na increased similarly and substantially across all tertiary treatments (mean all treatments: 40%, \(p \leq 0.001\)) but did not change much in primary treatments (7%; \(p > 0.10\)).
### 4.4.3.3 PCA

All soil chemistry variables displayed a high degree of intra-correlation, and the use of PCA led to the grouping of all variables on a single principal component. The LMM indicates that differences were significant amongst treatments, skid trails, and dates irrespective of other factors.

Figure 4.4 Mean soil (a) % SOC, (b) mg K per kg\(^{-1}\) dry soil, (c) mg Ca per kg\(^{-1}\) dry soil, and (d) mg Mg per kg\(^{-1}\) dry soil values comparing differences amongst treatment groups (A=trail centre, B=trail rut, C=forest edge, D=adjacent forest controls) in primary (P) and tertiary (T) skid trail plots in a mixed deciduous forest in Central Ontario during the year 2012.
4.5 Discussion

4.5.1 Compaction of Trails

Primary trails saw considerable use, with tens of passes by machinery during both the winter and spring, and intermittently recurring use during previous harvests over the past decade or longer. The surface lacked any vegetation or LFH, and soils were extensively mixed and compacted, with mounding of soil in the centre and ruts ranging from 5-30 cm deep in places. Tertiary trails were only used between 2-4 times during initial extraction in winter when soils were generally frozen. No rutting was apparent; however, the surface of the soil in tread impact zones (i.e., “ruts”) was slightly depressed relative to centres and forest edges, and the LFH remained mostly intact, though some disturbance was evident.

Soil bulk density values (0-10 cm depth) on primary trails were similar between centres and ruts (1.23 and 1.16 g cm\(^{-3}\)), and showed evidence of substantial compaction relative to adjacent harvested forest (0.56 g cm\(^{-3}\); p≤0.01). Values were comparable to those found by other studies (average 1.21-1.37 g cm\(^{-3}\); McNabb et al., 2001; Ezzati et al., 2014; Naghdi and Solgi, 2014) but considerably higher than very disturbed non-skid trail locations noted by Zummo and Friedland (0.83 g cm\(^{-3}\); 2011). Tertiary trails were much less affected by compaction, with values slightly higher in ruts than centres (0.63 g cm\(^{-3}\) and 0.57 g cm\(^{-3}\)) and considerably higher than controls (0.48 g cm\(^{-3}\)), though differences were not statistically significant. Values were comparable to non-skid trail specific locations noted by Zummo and Friedland (2011) in unharvested and lightly-disturbed post-harvest areas in a similar mixed-forest in New Hampshire (0.52-0.63 g cm\(^{-3}\)), but low relative to unharvested and tertiary trail values reported by several studies in boreal and temperate forests (undisturbed: 0.73-1.11 g cm\(^{-3}\); tertiary: 0.83-1.22 g cm\(^{-3}\)) (McNabb et al., 2001; Ezzati et al., 2014; Naghdi and Solgi, 2014).

These aggregated results from several studies show that compaction reduced bulk densities (0-10 cm) by an average of 11% on tertiary trails; in comparison my tertiary trail sites were 19-31% lower than adjacent harvested forest, indicating a greater degree of compaction following use. However, Shetron et al. (1988) found much higher post trail-use compaction effects in the 0-5 cm depth range, with bulk densities increasing from 0.42 g cm\(^{-3}\) in unharvested areas to 0.77 g cm\(^{-3}\) on low use trails (+83%). Higher rates of compaction at 0-5 cm depths (15-19%) were also been noted in some sites by McNabb et al., (2001), but results were not consistent. Estimated 0-5 cm bulk density values for my tertiary trails were somewhat more compacted than 0-10 cm values (+37%; p≤0.05) relative to forest controls (0.41 g cm\(^{-3}\) vs. 0.30 g cm\(^{-3}\)). Regardless, post-use tertiary trail bulk densities were considerably lower than those reported in most other studies despite similar number of machine passes, which were more similar to
values found on primary trails in my study. It is likely that several reasons account for these differences, but the most important are probably related to seasonal patterns of use and considerably lower pre-use bulk density values (50-75% of average values from other studies).

In most studies, trail use largely occurred in summer. In contrast, harvesting and tertiary trail use in my study had been completed by March, when the ground was still covered in snow and soils partially frozen, providing much greater soil strength and resilience to damage. Differences in SOM content and upper soil structure probably also played a large role in defining discrepancies in pre-use bulk densities. Higher SOM and root densities are often associated with lower bulk densities, and I observed a strong relationship between these variables where exponential increases in SOM expressed an exponential decline in bulk density ($r^2=0.65$, n=72, p≤0.001). Tertiary trails in my study contained 11-13% SOM from 0-10 cm and showed considerable fine root densities within the upper 5 cm. SOM values and forest type in non-trail forest areas (12-15%) were similar to those reported by Zummo and Friedland (9-13%; 2011) may therefore account for comparable bulk densities (0.52-0.63 g cm$^{-3}$) that are much lower than those described elsewhere. Lower SOM content and less developed upper soil structure were likely responsible for substantially higher pre-use bulk densities in other studies. Despite a cooler boreal forest environment, McNabb et al. (2001) noted much lower SOM values of <4%, and although SOM values were not stated by Ezzati et al. (2014) and Naghdi and Solgi (2014), values were likely low due to the warmer Mediterranean climate.

These same conditions also contributed to the substantial difference between tertiary and primary trail bulk densities. In addition to carrying more frequent and heavier loads and re-use between harvesting cycles, primary trails were also used after March when snow had melted and soils had thawed, long after tertiary trails had ceased being used. Furthermore, primary trails contained less SOM (7-8%) than tertiary trails (11-13%) and few if any roots, which to some extent may have also contributed to lower resilience to compaction.

4.5.2 Influences on Patterns of Skid Trail FCO$_2$

4.5.2.1 Primary Trails: Root Density, Temperature, and FCO$_2$

Overall, primary skid trails produced 35-37% less FCO$_2$ than forest controls during the entire growing season. Although I did not measure root densities, observations from sampling and spot checks showed that soils were sometimes quite shallow (<20 cm) and roots were largely absent within 20 cm of the surface. Consequently, minimal contributions by roots to soil respiration probably influenced lower rates
of FCO₂. Typically, 50% of soil respiration during the growing season is accounted for by roots in unharvested mixed forest systems (Hanson et al., 2000), but contributions can vary considerably by season (Chapter 2, Shabaga et al., 2015). Since root biomass is proportional to the biomass of trees (Jenkins et al., 2003), the contribution of roots to forest soil respiration after a selection harvest (25-30% reduction to tree basal area) is probably closer to 35-38%. If roots were not contributing to soil respiration on primary trails, a proportionally lower rate of FCO₂ on primary skid trails would be observed, assuming heterotrophic respiration rates remained similar to forest controls. Furthermore, this difference would probably be higher during periods of peak photosynthetic activity (mid-summer) when root respiration is higher, and lower during early spring and autumn when root respiration is typically lower (Chapter 2, Shabaga et al., 2015).

Primary trails produced 41% less FCO₂ than controls in July, 17% less in May just before leaf-out, and 11% less in October following leaf-drop. Overall, primary skid trails produced 35-37% less FCO₂ than forest controls during the entire growing season, and seasonal fluxes suggest that differences in root respiration played a clear role in differentiating FCO₂ between skid trails and forested controls. A lower sensitivity of soil respiration to temperature on primary skid trails relative to adjacent forest controls (Q₁₀: 25-36% lower) also suggests a lack of root respiration response. Wang et al. (2010) found that a higher proportional contribution of root respiration to overall soil respiration increased Q₁₀, and Boone et al. (1998), and Widén and Madji (2001) both found the temperature sensitivity of fine root respiration alone to be twice as high as that of overall soil respiration. Others have concluded that root respiration is more sensitive to temperature than heterotrophic respiration due to higher total soil respiration Q₁₀ values in unharvested forest than recently cut areas (Toland and Zak, 1994; Olajuyigbe et al., 2012; Chapter 2 and Shabaga et al., 2015).

The difference in FCO₂ between primary trails and controls increased even further when differences in temperature were considered. Primary trails were generally around 6 m wide and received direct insolation for a portion of each the day, depending on the orientation of the trail. Consequently, average annual temperatures were substantially higher on primary skid trails (centre: 2.6 °C, rut: 2.3 °C, p≤0.001) than in forest controls. Increasing soil temperatures stimulate soil respiration (Lloyd and Taylor, 1994; Davidson et al., 2006; Chapter 2 and Shabaga et al., 2015), and when FCO₂ values were corrected to mean control treatment temperatures using Q₁₀ values, primary skid trail values were 43-47% lower than those of the control treatment. Overall, this suggests that an absence of root respiration contributions could account for up to 73-85% of differences in FCO₂ between primary skid trails and controls. The balance of this difference was likely due to high levels of compaction.
4.5.2.2 Primary Trail: Compaction Effects on Soil Moisture and FCO\(_2\)

The bulk density of soil often increases following harvesting operations due to compaction from tire contact and skidding of cut trees. This reduces the air-filled pore-space relative to non-compacted forest soils, which in turn decreases rates of soil gas exchanges such as FCO\(_2\) on primary trails relative to less compacted areas (Laporte et al., 2003; Frey et al., 2009). McNabb et al. (2001) showed that recently compacted skid trail soils in a boreal forests with bulk densities over >1.2 g cm\(^{-3}\) had one-half the air-filled porosity (16%) of those with bulk densities <1.2 g cm\(^{-3}\) (32%), potentially limiting FCO\(_2\). Novara et al. (2012) found soil columns mechanically compacted to a bulk density of 1.5 g cm\(^{-3}\) produced 37% less FCO\(_2\) than soils compacted to 1.1 g cm\(^{-3}\).

Primary trails had a much lower estimated total porosity at 0-5 cm (48-52%) than forest controls (86-88%) and tertiary sites (84-85%), reducing the potential total soil pore space available for gas exchanges relative to all other treatments. A regression analysis indicated that increasing total porosity for 0-5 cm depths predicted higher FCO\(_2\) values when averaged over the entire growing season \((r^2=0.16, \beta_1=1.06, n=72, p\leq0.001)\). However, this relationship was undoubtedly confounded with soil moisture. FCO\(_2\) declined by 27% on primary skid trails in early June relative to May values, coinciding with heavy rains prior to measurement. In contrast, FCO\(_2\) rates doubled in forest control treatments. The occurrence of leaf-out in early June and increased associated root respiration may account for a portion and timing of differences in FCO\(_2\) between forested areas and primary trails. However, a decline in FCO\(_2\) and a much stronger relationship between FCO\(_2\) and total porosity in early June \((r^2=0.45, \beta_1=3.08, n=72, p\leq0.001)\) indicates that the inhibition of gas exchanges by compaction may have been exacerbated by poor moisture drainage. Highly exposed primary trails directly intercept precipitation that is otherwise filtered by the forest canopy and the highly porous LFH layer. Volumetric soil moisture levels were similar between primary trails and all other treatments during early June. However, volumetric soil moisture values had increased by 48% relative to May on primary trails, but only by 15-26% in forested controls, indicating greater infiltration of precipitation on primary trails. Furthermore, due to the lower total porosity on primary trails these areas had a much higher water-filled porosity (\(\approx95\%\)) than controls or tertiary trails (56-73%), effectively preventing gas exchanges in saturated soils. By late June, water-filled pore space had declined to 60-75% and FCO\(_2\) values increased to twice those of May values on primary skid trails, indicating that drainage has substantially relieved restrictions on gas exchanges.

The link between soil moisture and FCO\(_2\) is complex and typically site/region specific, making it difficult to consistently predict or model (Davidson et al., 2006; Chapter 2 and Shabaga et al., 2015). Startsev et
al. (1998) also found compaction from harvesting reduced rates of FCO$_2$; they found no differences between primary and tertiary trails, but there was little differences in bulk density between them. In my study, a regression relationship predicted an exponential decline in FCO$_2$ with increasing bulk density, and the relationship between declining FCO$_2$ and increasing volumetric soil moisture was strongest on primary skid trails. Increasing water-filled pore space also predicted declines in FCO$_2$ ($r^2=0.21$, n=72, $p \leq 0.001$), but in all cases, the relationship between the predictor variable and FCO$_2$ was best described as a threshold between low and high values. During early June, the mean FCO$_2$ rates for areas with bulk densities $>0.90$ g cm$^{-3}$ were 67% lower than those $<0.90$ g cm$^{-3}$; in comparison, rates were only 26% lower when averaged across the entire growing season. Similarly, FCO$_2$ was 45% higher for water filled porosities of $<80\%$ in June, and 35% higher for water filled porosities of $<60\%$ when averaged over the course of the growing season. The lowest FCO$_2$ values were consistently from primary skid trails, and no linear or threshold relationships with porosity/moisture were apparent when only the less compacted soils of tertiary skid trails or harvested forest controls were considered. These results therefore indicate that compaction at levels found on primary skid trails accounted for a portion of the difference in FCO$_2$ between primary trails and forest controls due to reduced pore space, particularly following precipitation events.

4.5.2.3 Tertiary Trails: Temperature, Compaction, and FCO$_2$

Tertiary trails exhibited a similar but much weaker pattern of FCO$_2$ and temperature differences from controls than primary trails. Trails were not as wide as primary trails (3-4 m) and vegetation less disturbed at edges, producing narrower canopy gaps and with less direct insolation relative to primary trails. Regardless, soil temperatures were significantly higher on tertiary trails than controls (Centre: +0.71 °C, Rut: +0.75 °C, $p \leq 0.01$). FCO$_2$ values were considerably lower in tertiary ruts than forest controls (18%) in spite of higher soil temperatures, but centre values were modestly higher than controls (10%) and significantly higher than in ruts (35%; $p \leq 0.05$). Differences in soil temperatures between ruts and the centre were negligible, indicating lower FCO$_2$ in ruts could be attributable to higher compaction than in centres. However, differences in bulk densities were small and well below threshold values that influenced FCO$_2$ on primary trails (0.9 g cm$^{-3}$), suggesting other factors were be involved.

Direct contact with tires may have caused more intensive localised damage to roots of adjacent trees and shrubs under ruts than under centres or edges, reducing root respiration contributions and ostensibly FCO$_2$. Considering that the LFH horizon remained largely intact and compaction was limited, tree root senescence was unlikely to be substantially greater than in adjacent cut forest. In contrast, any
similar declines from disturbances in the trail centre appeared offset by elevated temperatures, yielding higher \( \text{FCO}_2 \) than ruts and controls. Controlling for temperature differences using \( Q_{10} \) further lowered rut values relative to controls (22%), and reduced the differences between centre and control values to negligible levels. Therefore, increases to centre values were probably a function of higher temperatures, while lower rates in ruts were presumably linked to reduced root respiration and compaction.

### 4.5.3 Large Declines to SOM During the Growing Season

Total soil organic C (SOC) and N declined from May to October amongst most treatments. Declines were highest in tertiary sites (11-33%), lower in primary edge and control treatments (25% and 15%), and negligible on primary skid trails (<5%). While soil SOC losses and increased \( \text{FCO}_2 \) have been noted to occur following harvest due to increased decomposition rates and leaching losses (Bormann and Likens, 1979; Covington, 1981; Toland and Zak, 1994; Londo et al., 1999; Johnson and Curtis, 2001; Yanai et al., 2003; Hafner et al., 2005; Chatterjee et al., 2008; Olajuyigbe et al., 2012; Chapter 2 and Shabaga et al., 2015), apparent losses were probably too large to be accounted for by increases to heterotrophic activity and leaching alone.

Instead, naturally occurring spatial variations in SOC pools and non-specific and unintentional differences in sampling methods between dates may account for a portion of this apparent decline. Measured inter-annual variations in mineral SOC as high as 41-55% from the previous year have been reported (Knoepp and Swank 1997). In Chapter 3, I found substantial but statistically insignificant increases to soil C (24-30%) in unharvested forest control plots following re-measurement one year later, and attributed this to subtle but important differences in soil extraction methods; specifically, differences in the separation of the LFH from the mineral soil between sampling periods. When differences between harvested treatments and unharvested controls were considered, the data indicated a decline of \( \approx 18\% \) in SOC in harvested sites, though this estimate was considered excessive.

In this study, all soil samples (spring and autumn) were processed by the same technicians during the same period, and analysed using identical methods. Although the LFH layers (where present) were separated from the mineral soil during extraction, accurate field-based separation of these horizons can be hampered by high variability in LFH thickness and SOM content with depth. This may have led to inadvertent inclusion of more humic materials during spring sampling that were more effectively separated or coincidently missed during autumn, contributing to apparent declines. Consequently, my analysis focused primarily on relative differences between controls and other treatments within skid
trail sites rather than absolute differences. In spite of this, large post-harvest upper mineral soil losses of SOM (25%) within short periods have been recorded by studies in areas similar to my study site (Nave et al., 2010), and analysis showed large losses as statistically significant, suggesting relative losses may be accurate.

4.5.4 Effect of Skid Trail Use on Soil Biogeochemical Processes

My data presented two differing patterns of SOC losses between trails and positions. In the first, primary and tertiary trail values edge values declined substantially more between May to October than control values (primary: 25%, p≤0.05 vs. 15%, both p>0.10; tertiary: 33% vs 24%, both p≤0.01), suggesting higher apparent SOC losses than forest controls, though differences between edge and control treatments were not significant. In the second, SOC did not change substantially on primary skid trails (0-5% loss) relative to forest edge and control treatments, while values declined considerably on tertiary centre treatments (26%) but much less so on tertiary ruts (10%). This suggests that some mechanism may have been effecting higher SOC losses at trail edges, such as higher decomposition rates.

Although FCO₂ values for edge treatments did not differ from forest controls, root damage at the trail edge may have decreased root respiration values. An increase in labile substrates from new root necromass may have stimulated heterotrophic activity following disturbance, compensating for root respiration losses (Toland and Zak, 1994; Chatterjee et al., 2008; Chapter 2 and Shabaga et al., 2015). More substantial reductions to SOC in primary and tertiary edge treatments relative to forest controls may therefore reflect enhanced decomposition following disturbance of edges due to plant root damage, microbial priming from mixing of organic and mineral materials, and improved air exchanges from increased exposure of the soil profile adjacent to ruts (Kuzyakov et al., 2000; Paul, 2007; Blagodatskaya and Kuzyakov 2008; Zummo and Friedland, 2011). Soil respiration rates for primary site edges were lower than forest controls in mid-summer (-9%) when contributions of root respiration to FCO₂ peaks, and higher in May and October (+20% and +9%) when root contributions are lower than heterotroph contributions (Chapter 2 and Shabaga et al., 2015). Furthermore, edge Q₁₀ values were somewhat lower than forest controls (-14%, p=>0.10), suggesting some decline in root respiration activity relative to forest controls (Wang et al., 2010). Since soil respiration rates averaged across the growing season were similar to forest controls, this indicated that any declines to root respiration were offset by increases to heterotrophic activity.
Tertiary edge sites showed a more complex pattern of seasonal $\text{FCO}_2$: rates were lower than controls in spring (13%) but rose over the course of the season, becoming higher by summer (7%) and peaking in autumn (17%), suggesting that root respiration was probably not reduced relative to control treatments, but there may have been increasing heterotrophic rates, particularly later in the season. In contrast to primary trails, tertiary trails were likely either previously unused or not utilised for at least one harvest cycle (15-20 years), and modest physical disturbances did not strip the LFH or mix soil thoroughly. Physical disturbances to trail edges were much less severe than on primary trail sites, suggesting less root damage, and compaction was more pronounced in tertiary ruts than centres, where the soil surface was slightly depressed in some areas relative to the centre or edges and bulk densities were slightly higher. Relatively little disturbance between trails and harvested adjacent forest may account for the similarity of respiration between treatments, while minimal decline in SOC in ruts may be the result of reduced heterotrophic activity from compaction relative to other treatments. Unlike primary skid trails, $Q_{10}$ values were higher on trails and edges than in the forest control, but differences were not significant and unlikely to represent substantial differences in root respiration contributions as in primary sites. Instead, they may have simply been an artifact of spatial heterogeneity.

Patterns of SOC loss from May to October in edge treatments were similar between primary and tertiary sites, despite that tertiary edge treatments were less impacted by skid trail disturbance than at primary sites. However, SOC was substantially lower on primary skid trails than tertiary trails or forest controls in both May and October, indicating previous losses associated with a different pattern of use. Forest cut-blocks are re-visited at 15-25 year cycles in this forest, allowing decades between disturbances. Tertiary trails are specific to these cut-blocks and may not be re-used in successive harvests, allowing for vegetative and soil restoration. In contrast, primary trails are often semi-permanent, and are frequently reused for different cut-blocks in the same area. As such, they may only experience a few years and modest regrowth of vegetation in-between use, primarily as herbaceous plants and shrubs, minimising new SOC inputs from litter and roots. Additionally, usage is more intensive due not only to a higher number of passes by machinery, but also by intermittent passage of larger equipment (loaders, forwarders, etc.) not found on tertiary trails. Consequently, soils of primary skid trails contained no LFH layer and an insubstantial number of roots (dead or alive) within the upper 20 cm of soil. Soils were thoroughly mixed and heavily compacted, and reduced pore-space appeared to limit gas exchanges and drainage and probably contributed to lower rates of $\text{FCO}_2$ than controls. Ruts on primary trails differed from centres only by their concave topographic position, making them more likely to collect surface water following precipitation, while edges were often adjacent to freshly exposed vertical profiles along
the sides of ruts where some severed fine roots were evident. Furthermore, strongly disturbed and mixed soils in sufficiently warm and moist conditions tend to lose stores of SOC rapidly from increased decomposition and leaching and/or runoff losses. Therefore, substantially lower SOC values on primary skid trails than forest controls or tertiary sites was largely a legacy of reduced SOM inputs and continued decomposition of existing SOM, not due to a sudden loss associated with disturbance.

Lastly, decomposition rates are in part driven by substrate quality, often loosely defined by the proportion of more readily decomposed low molecular weight carbon compounds and the C:N ratio of SOM (Chapin et al., 2002). A lack of fresh SOM inputs to primary trails may have depleted the labile soil C pool relative to forested areas, reducing heterotrophic activity (van Hees et al., 2005). Minimal changes to SOC on primary trails from May to October, a higher C:N ratio, and significantly lower respiration rates and $Q_{10}$ values than in forested areas were therefore likely due to a combination of little to no root respiration, inhibition of gas exchanges from compaction, and lower decomposition rates due to degraded substrate quality. More substantial declines in SOC on tertiary trails and forested areas were probably associated with a combination of stimulated decomposition rates of higher quality substrates from root necromass and priming effects (Chapter 2, 3), and possible over-estimation of losses due to measurement errors.

4.5.5 Cation Losses

Patterns of base cation losses resembled those of SOC with higher losses in edge treatments than in forest controls, but changes were not significantly different. Declines to base cations between May and October were predicted by declines to SOC (i.e. through assessing change scores) in in both primary and tertiary sites (K: $r^2=0.38$ and 0.73; Mg: $r^2=0.59$ and 0.66; Ca: $r^2=0.37$ and 0.45; n=36, p≤0.001). Although relationships were stronger for tertiary sites than primary sites and overall losses higher, beta coefficients were higher for primary sites, suggesting spatial heterogeneity may have produced more noise in the primary sites. Use of principal component analysis (PCA) loaded change scores for SOC, K, Mg, and Ca onto a single principal component (PC1) that explained 81% of all variance. As such, cation decline appeared to be linked to SOC loss. A similar pattern was found in Chapter 3 assessing post-harvest declines to SOM and base cations in both the LFH (PC1-LFH) and mineral horizons (PC2-MIN). However, the inclusion of other covariates in that study led to more complex PCs that were not directly comparable to the one derived from this study.
Organic matter serves as a key medium for cation exchange capacity (CEC) in soil, particularly where soils contain little clay such as those in the study area. Therefore, decreases to SOM can reduce the CEC of soils. An increase to SOM decomposition rates following harvest may also account for cation decline by degrading hydroxyl and carboxyl functional groups in SOM and DOM that retain cations binding them to SOM and DOM into the soil solution (Sollins, 1996; McLaughlin, 2014), altering exchangeable cation pool dynamics. Losses were thus probably due to leaching and run-off following OM declines, as well as physical removal of SOM and bound base cations on skidded logs.

4.5.6 Implications of Patterns and Intensity of Trail Use on Forest C Pools and Cycling

Several papers have reported highly varied results regarding post-harvest patterns of FCO$_2$, with some noting increases, decreases, or no change at all (Chapter 2 and Shabaga et al., 2015). In part this may be due to insufficient distinction between compacted and denuded skid trail areas and cut but relatively intact forest soils in experimental designs. Laporte et al., (2003) found scarified surfaces to have lower rates of FCO$_2$ than cut forested areas. They suggest that in addition to lower rates of root respiration, compaction may have contributed to lower FCO$_2$, though bulk density was not assessed. I found substantially higher rates of FCO$_2$ in harvested forest plots than uncut controls in Chapter 2, but few sampling locations were located on heavily used skid trails. Values from primary skid trails were substantially lower than cut forest areas, while tertiary skid trail ruts saw more modest declines to FCO$_2$. Therefore, some of the discrepancies amongst studies assessing post-harvest FCO$_2$ may be attributable to a failure to block for differences between trails and cut forest.

My results indicate a strong need to consider the unique contributions of skid trails areas when assessing overall CO$_2$ efflux from managed forests. Since gross primary production and associated root respiration may be reduced immediately following harvest, and the contribution of heterotrophic organisms decomposing fresh root necromass and woody debris likely increases (Chapter 2 and Shabaga et al., 2015), an overall decline in CO$_2$ efflux from recently cut areas might not actually represent a net decrease in C flux to the atmosphere. Most of the FCO$_2$ from primary trails is probably from heterotrophic organisms, and represents net C losses. In Chapter 2 and in Shabaga et al. (2015) I demonstrated that higher decomposition rates in non-trail cut areas following harvest could account for an increase in FCO$_2$, hypothetically reducing the ratio of root respiration to total soil respiration. In Chapter 3 I was able to link estimates of these elevated annual heterotrophic contributions CO$_2$ efflux in harvested areas to soil C losses. If the overall CO$_2$ efflux from the forest now indicates a higher
proportion of CO$_2$ from decomposition, this suggests the area has the potential to function as a net C source, even if the overall efflux has decreased.

Furthermore, heavily used primary trails exhibited considerably lower SOC than tertiary trails or harvested forest. Bulk density was highest on primary trails and increases were strongly correlated to decreasing SOC, linking compaction and SOC losses over time. Consequently, primary trails may not only function as modest C sources, but also areas of low C storage. The results of this study were unable to determine the long-term fate of C on primary trails. However, evidence suggests that continued or intensified use may further deplete C pools, trail type might predict losses based on level of use and compaction, and that newly developed primary trails will also undergo C losses.

This raises questions regarding the potential for increased trail development and usage in these systems under intensified harvesting for biomass. Demand for wood biomass for bioenergy is rapidly growing within the tolerant hardwood region of Ontario due to decline in traditional wood markets for the region (OMNR, 2009; Richter et al., 2009; Zhang et al., 2010; Wolf et al., 2014; Thiffault and Paré, 2016). Pilot projects have been implemented that increase rates of woody biomass extraction from the same cut-blocks relative to conventional selection silviculture. However, increased trail usage due to larger load masses and/or frequency of loads from additional biomass retrieval may exacerbate the impacts described in this chapter, largely from increased compaction of trails i.e. reduced SOM inputs, sustained C and nutrient losses over time, and function as a likely net-source of C).

In light of the vast extent and variability of skid trail areas in managed forests, estimates of forest C pools, sinks, and sources need to consider decreased C storage and potential net C emissions associated with skid trails as well harvested forest. Since these vary depending on skid trail type, topographic position, and history and frequency of use, this highlights the importance of accounting for different contributing disturbance components when considering the overall forest C balance.

4.6 Conclusions

The impacts of physical disturbances on forest biogeochemistry are frequently acknowledged, but the spatiotemporal heterogeneity of the source and intensity of the disturbance signal makes it difficult to assess. In contrast, skids trails present easily identifiable and discrete disturbed forest areas that vary more consistently with regard to disturbance intensity based on frequency of use. Due to the substantial skid trail coverage in many forests, neglecting to consider the unique contribution of these areas to biogeochemical processes and gas exchanges may result in misleading estimates of FCO$_2$ and soil C and
nutrient losses; the results of this study stress the importance of these areas to overall post-harvest forest soil dynamics. By directing my analysis on comparisons of two skid trail intensities to more modestly disturbed adjacent forest, I was able to directly observe the intensified effects of skid trail disturbances on soil respiration and soil carbon and base cation chemistry. As anticipated, heavily used primary trails exhibited much smaller soil C and base cation pools and lower rates of soil respiration than lightly used tertiary trails or harvested forest controls, which were attributed to differences in organic inputs, decomposition rates, root activity, and reduced gas exchanges from compaction effects. Substantial decreases to SOC in all other treatments, more pronounced along trail edges, suggest stimulation of decomposition rates may be related to SOM and base cation losses (Chapter 3). However, a high degree of dispersion in the data and large seasonal declines indicate potential issues with repeated sampling methods that might plague many studies, giving the impression of improbably high rates of C loss from decomposition. Furthermore, significantly lower SOC on primary trails than all other treatments and controls was most likely an artifact of cumulative losses associated with previous use and not due to rapid and disproportionate losses following disturbance. These phenomena may contribute to the mis-application of the Covington Curve model to explain C losses via decomposition following soil disturbances (Chapter 3; Covington, 1981; Yanai et al., 2000 and 2003). Studies that neglect to account for historical patterns of land-use and inter-annual variations in measurements, particularly chronosequences, may presume much greater C losses from disturbance than are actually occurring.
Chapter 5
Summary and Conclusions

5.1 Summary of Research

Forest ecosystems function as a carbon (C) sink and reservoir of nutrients, but rely heavily on internal recycling of nutrients between biomass and soils to sustain productivity. Extraction of biomass threatens to reduce C and nutrient pools, while harvesting disturbances can disrupt terrestrial biogeochemical processes, altering rates of organic matter decomposition and nutrient cycles. As such, anticipating the response of these systems to harvest intensity is paramount to the maintenance of both ecosystem health and sustainable industry alike. In order to develop better guidelines to meet these objectives, we require a comprehensive understanding of the mechanisms governing disturbance-based nutrient dynamics and C storage.

Although numerous studies over several decades have investigated these phenomena, our current understanding of the impacts of land-use on soil C storage and fertility remains under-developed and over-generalised. Considerable variability and disagreement amongst results reveals an underlying theme of insufficient characterisation of conditional properties that may be influencing the outcomes, with potential misidentification of causal mechanisms. These include pre and post-harvesting forest stand dynamics, detailed descriptions of silvicultural methods, gauging the intensity of disturbance to soils and forest stand structure, topographic and other environmental properties, differences in phenology between vegetation and decomposers, and accounting for the spatial organisation and type of disturbances (e.g. scarified vs. intact soil, compaction and/or mixing of soils on trails). As such, generalisations about the mechanisms and biogeochemical processes responsible for changes (or lack thereof) may not accurately represent the unique regional or local conditions contributing to observed results. Causal relationships are especially difficult to establish in these uncontrolled environments; however, opportunities exist to assess several independent variables either directly or as proxy data to better link changes in dependent variables to changes to biogeochemistry and forest structure.

In this dissertation, the hypothesis that the level of harvesting disturbance influenced decomposition rates, altering soil chemistry and respiration, was tested by comparing the impacts of two differing selection harvest methods on rates of soil efflux of CO$_2$ (FCO$_2$) and changes to soil SOM and nutrient pools. Harvested treatments differed primarily in post-harvest woody biomass residue retention, and
both pre and post-harvest results were compared to unharvested controls. I attempted to minimise environmental variation between treatments by focusing on well-drained upland areas with predominantly deciduous forest cover. However, due to the heterogeneous nature of the landscape, pre-harvest forest structure (e.g. distributions of species, age, and size class) and other environmental parameters varied somewhat between harvesting plots. Furthermore, phenological variations between the activity of vegetation and decomposers indicate a need to account for temporal patterns that have not been well documented. To address these concerns, several key soil and forest stand covariates were assessed pre and post-harvest: downed woody debris volumes, tree and sapling basal area by species, and soil temperature, moisture, and texture. These unique conditions also led to each plot experiencing a different level of harvest intensity (i.e. cut basal area and DWD inputs) based on Ontario Ministry of Natural Resources and Forestry (OMNRF) selection harvest prescriptions. Broader-scale disturbance effects were considered by contrasting soil differences between two skid trail use intensities and selection harvested forest, considering changes to bulk density, soil temperature, and soil pore water. Measurements of FCO$_2$ were collected during representative periods of each growing season for several years, accounting for phenological activity and potential post-harvest recovery.

5.1.1 Evidence of Enhanced Post-harvest Decomposition Rates and Nitrification

The results of Chapter 2 indicated that harvested areas expressed significantly higher rates of FCO$_2$ relative to unharvested controls, and effect sizes fluctuated in a seasonally recurring pattern. Increases to soil temperatures in harvested plots accounted for up to 41% of elevated FCO$_2$, and decreasing summer rates of FCO$_2$ in harvested plots were correlated to cut tree basal area while increasing autumn rates were linked to fine woody debris volumes. Since respiration rates during the growing season for autotrophic activity are highest in summer and lowest in autumn, this suggested that soil respiration from roots had declined, while respiration by decomposers had increased sufficiently to more than compensate for these losses. A significantly lower sensitivity of respiration to temperature ($Q_{10}$) in harvested treatments than the control treatment during the first post-harvest year also indicated reduced root respiration contributions.

This argument is strengthened in Chapter 3. Harvested plots experienced substantial losses of soil organic carbon (SOC) and labile soil chemistry components such as dissolved organic C (DOC) and N, K$^+$, and NH$_4^+$. Changes were most strongly pronounced in the root-dense LFH horizon, where losses of soil DOC and SOC were correlated to autumn rates of FCO$_2$, but similar, smaller losses were also observed in the upper mineral horizon. Little change occurred in deeper mineral soils; combined with no change to
highly soluble Na, this suggests leaching was not substantially contributing to losses. Consequently, increased decomposition and assimilation of available nutrients was the most probable explanation for these declines. Since autumn FCO$_2$ rates were also correlated to post-harvest inputs of fine woody debris volume, this suggested that microbial priming by labile C inputs from harvest residue inputs may have stimulated this decomposition. Inputs of FWD may have contributed both directly through leaching of labile C and/or functioned as a proxy for fine root and mycorrhizal necromass. A C budget for the study area found that estimation of total FCO$_2$ from decomposers during the first post-harvest growing season (based on results from Chapter 2) could account for over half of all SOC losses and estimated DOC leachates from DWD and root/mycorrhizal necromass.

Although large post-harvest increases to soil NO$_3^-$ were not significant, values were strongly inversely correlated to residual combined tree and sapling basal area in harvested plots for both the LFH and upper mineral soils. Increases to NO$_3^-$ were also strongly correlated between horizons and to increased removal of deciduous tree biomass. Other studies have linked labile C inputs from harvest residues to nitrification rates in clear-cuts (Vitousek and Matson, 1985), and to the presence of deciduous vegetation (Ste-Marie and Paré, 1999). These results indicate that even low impact harvesting in hardwood stands may induce nitrification commonly associated with more intense harvesting practices.

Unlike more labile soil chemistry, minimal declines in Ca and Mg and increases to Fe and Al were observed, and did not become apparent until the 3$^{rd}$ post-harvest year. These changes were also correlated to autumn FCO$_2$, suggesting that decomposition affected availability. Since SOM functions as an important component of the soil cation exchange complex, decomposition may have led to release of adsorbed cations through degradation of chelates and losses through assimilation by microorganisms and plant regrowth or leaching. Evidence for the latter was lacking since no change to the concentration or eluviation of highly soluble Na in the exchangeable complex was observed throughout the soil profile. Soluble base cations removed from the soil solution may then have been supplanted by poorly soluble acid cations. These results agree with the conclusion by Mclaughlin (2014) that variable intensity partial-harvesting practices in mixed and hardwood forests do not significantly decrease pools of extractable Ca over 10 year periods. However, this effect may be site dependent; despite poorly buffered soils and a history of acid deposition, plots may have been at low short-term risk due to large quantities of SOM.
5.1.2 Influence of Skid Trail Use on Soil Properties

Skids trails and logging roads comprise a substantial portion of managed forest area, even in partial-harvest systems. Yet little research has been conducted to assess their role in forest C budgets and nutrient dynamics. My results indicated that extensive use led to much lower FCO$_2$ on primary skid trails, despite higher soil temperatures. Substantial compaction, extensive mixing, and frequent re-disturbance equally affected ruts and trail centres, and appeared to inhibit root development. A lack of root respiration was estimated to account for most of the difference in FCO$_2$ between primary trail and adjacent harvested forest. The remaining deficit was attributed to compaction, particularly following rain events. Reduced soil porosity led to periods of soil saturation due to poor drainage, inhibiting FCO$_2$. In comparison, tertiary trails exhibited minimal compaction and change in soil respiration, and small differences between centres and ruts could be attributed to patterns of use and modestly elevated soil temperatures.

In Chapters 2 and 3 my results showed substantially higher rates of FCO$_2$ and modest losses of SOM in harvested forest plots relative to uncut controls, but few sampling locations were located on heavily used skid trails that covered a large portion of these cut-blocks. In contrast, rates of FCO$_2$ on primary skid trails were much lower than those of adjacent cut forest areas; SOM pools were also considerably lower, but decreased little during the growing season. However, low SOC and nutrients on primary trails were probably not related to recent use, and instead represented a legacy of loss from repeated prior disturbances. Rates of FCO$_2$ and SOM losses on tertiary skid trail ruts were also modestly lower than harvested forest, but much less so than for primary trails. Laporte et al., (2003) also found scarified surfaces to have lower rates of FCO$_2$ than cut forested areas, suggesting that lower rates of root respiration and compaction may have contributed to lower FCO$_2$.

5.1.3 Recovery and Relation to Pre and Post-harvest Forest Structure

Three years of post-harvest analysis provided an opportunity to determine if there were early indications of site recovery. Physical damage to vegetation reduced sapling and shrub volumes following harvest, but these had regrown by the third post-harvest year. This regrowth was linked to decreasing temperatures in the harvested treatment. Similarly, a depressed sensitivity of soil respiration to temperature in the harvested treatments ($Q_{10}$) increased significantly within three years to exceed control treatment values. This increase was correlated to the volume of post-harvest understorey vegetation, suggesting root regrowth was increasingly influencing the soil respiration signal. Furthermore, the correlation between FCO$_2$ and DOC/SOM had disappeared and soil SOM losses had
stabilised by this time. Yet $\text{FCO}_2$ and basal respiration rates remained higher than controls despite declining temperature differences. This suggests that while decomposition rates likely remained elevated in harvested sites, they were probably becoming increasingly relevant to defining the post-harvest respiration signal.

5.1.4 Implications of “Intensified” Biomass Harvesting Compared to Conventional Harvesting

No significant differences in soil chemistry and $\text{FCO}_2$ were apparent between harvested treatments, except for $Q_{10}$ values in the third post-harvest year. In general, the biomass treatment exhibited insignificantly higher rates of summer $\text{FCO}_2$, while the TL treatment exhibited higher autumn rates. The TL treatment accrued substantially more woody debris following harvesting, while the biomass treatment retained considerably more under-storey vegetation. The former was by design, and may have resulted in higher decomposition rates due to greater labile C inputs. The latter was incidental; however, in conjunction with a significantly higher $Q_{10}$ than other treatments by the third post-harvest year, it suggests that retention of more understorey biomass may accelerate post-harvest recovery of root respiration and possibly NPP.

Overall, this study did not detect any substantial effect of increased biomass retrieval on soil function or C and nutrient pools. However, the short-term results of this study cannot dismiss concerns over long-term effects of increased biomass removal on soil nutrient pools. A nutrient budget constructed by Phillips and Watmough (2012) estimated that selection harvesting in the same region reduced nutrients in aboveground biomass by 30%. Though most of these are estimated to recover between harvest cycles from weathering and atmospheric deposition, low inputs of Ca and K generally predicted mass balance losses, indicating that they are at risk for long-term loss from biomass recovery using conventional silvicultural methods. The authors note that increased recovery rates from biomass harvesting may intensify losses of base cation, and suggest that additional CWD retrieval may exacerbate this.

My results indicate that both CWD and FWD inputs were reduced by half from biomass harvesting. A partnered study evaluating the recovery of harvesting residues in the same plots found that the modified harvesting treatment increased total biomass retrieval per ha by 13% relative to conventional harvesting (Wolf et al., 2014), increasing aboveground nutrient losses from these sites. Assuming a similar biomass to basal area conversion ratio and concentrations of nutrients to those noted by Phillips and Watmough (2012), this would result in an additional 18.5 Mg ha$^{-1}$ of recovered wood biomass, increasing nutrient losses from aboveground biomass from 30% to 37%. This assessment may yet under-
estimate increased nutrient losses; these exports are mostly comprised of smaller branch stems which have a higher nutrient density than stems (Phillips and Watmough, 2012; Thiffault and Paré, 2016). Consequently, this type of retrieval may have disproportionate impacts on nutrient losses over time, a factor that needs to be considered in long-term models of losses through biomass harvest.

Lastly, the potential impacts of differences in operational activities in biomass harvested areas relative to conventional harvesting were not specifically considered in this study. Heavier and/or more frequent loads hauled by skidders and other operational equipment (loaders, forwarders, etc.) may also increase the extent and intensity of physical soil disturbance. Though differences are small, the cumulative impacts of these effects over successive harvest-cycles and periodic re-use of primary trails for cut-blocks harvested on different harvesting cycles may exacerbate compaction, mixing, and rutting disturbances, and associated influence on soil function and nutrient retention. My research indicates that trails edges may emit more CO$_2$ from decomposition than harvested forest, and beyond certain a certain degree of compaction primary trails likely become net C sources deficient in nutrients relative to adjacent forest soils. However, more detailed operational data comparing the intensity of trail use is necessary to better evaluate the disturbance thresholds necessary to effect changes.

5.2 Study Limitations

5.2.1 Inter-Annual Variability in Soil Chemistry

Several key limitations to the effectiveness of the study methods became apparent following data collection. Firstly, inter-annual variations to soil respiration and especially soil chemistry complicated assessment of change over time. Despite an annual decline in FCO$_2$ across all treatments, the respiration treatment signal was clear. In comparison, soil nutrients were more challenging to interpret: values increased in all treatments, but primarily in the control. This may have been due to actual increases or an artifact of subtle differences in sampling methodologies. Since many other studies have expressed similar or larger changes in soil chemistry in both undisturbed and harvested forests, I accommodated this by comparing relative differences between treatments. This demonstrated that there were relative losses in harvested compared to controls. Whether this represented real losses competing with other factors producing ecosystem scale gains across all treatments, or a suppression of broader ecosystem-scale mechanisms increasing concentrations of nutrients in harvested treatments relative to controls, was not completely clear. However, the relationship between declining DOC and SOM values with increasing FCO$_2$ and declines to NH$_4^+$ with increasing FWD volumes are highly suggestive of bona-fide losses due to enhanced decomposition and uptake by organisms.
This limitation may have been easier to dismiss by careful assessment of pre and post-harvest bulk densities of soil samples to determine if changes in concentrations reflected changes in actual pools. Relative differences in the sample bulk densities and soil nutrient concentrations during resampling may have occurred due to subtle differences in technique, such as consistency in the separation of the LFH and mineral horizons. However, this potential bias would have influenced all treatments relatively equally. Furthermore, evidence from Chapters 3 and 4 indicates that bulk densities of non-trail harvested forest soils were quite very low and indistinguishable from control treatment values, and compaction effects on tertiary trails were negligible relative to harvested forest. Lastly, since few sampling locations of harvested plots in Chapter 3 were on primary trails, it is unlikely any differences in compaction effected meaningful change in measurements of soil chemistry, and certainly not commensurate with the magnitude of effect sizes.

Another limitation of the study lies in the short (3 year) post-harvest period of assessment relative to the long-term questions being considered. Few studies of harvesting disturbances have persisted beyond a single harvest cycle (Raulund-Rasmussen et al., 2008), and chronosequence studies can be unreliable at detecting the magnitude of post-harvest changes to soil C (Yanai et al., 2003) due to high spatial variability in soil properties and incorrect assumptions about prior land-use history. The same may hold for other variables, such as soil respiration. For example, Peng and Thomas (2006) conducted a chronosequence study on patterns of post-harvest soil respiration and recovery over ten years in the same forest area as my study, yet their results differed considered from my own. While they did note a large increase in FCO₂ within weeks of harvest, their results found a strong decline in FCO₂ within the first 3 years. By using a single set of 1st year posted harvest and baseline measurements collected during an unseasonably warm autumn and other values collected during the previous year, their results were confounded by inter-annual and seasonal variations, and reveal the weakness of substituting space for time. Though my study only considered a short post-harvest period, FCO₂ remained elevated and SOM/base cations lower at 3 years post-harvest. My plots have since been re-mensurated and soil re-sampled at 5 years post-harvest, and samples are currently undergoing analysis. Further re-evaluations are planned to continue into the next scheduled harvesting cycle due to ongoing observation by the OMNRF, providing what is probably the first long-term evaluation of soil biogeochemistry following selection harvesting in the southern extent of the mixed hardwood forest region of Ontario.
5.3 Proposed Causal Mechanisms and Prediction of Responses

5.3.1 Linking Harvest Intensity and Disturbances to System Responses

Several papers have reported highly varied results regarding post-harvest patterns of FCO$_2$ and soil C and N, with some noting increases, decreases, or no change at all (Chapter 2; Chapter 3; Shabaga et al., 2015). In part, this is due to the heterogeneity of forest and soil properties; the large number of potential covariates (e.g. moisture, temperature, texture, tree root proximity, tree species type and % cover, microtopography) makes it difficult to block on many of these in studies. However, this spatial variability can also facilitate testing of covariance with dependent variables by stratifying the distribution of measured values across a broader range of response.

In most studies, a general set of post-harvest attributes are applied to an ecosystem and tested as a nominal factor in the analysis of response variables. Some studies have described broad relationships between temperature and moisture to FCO$_2$ in both harvested and unharvested areas; differences in insolation and evapotranspiration play a role in this, but since most consider clear cut treatments, the effect of canopy openness on changes to soil biological activity has not been thoroughly investigated (Mattson and Swank, 1985; Raich and Schlesinger, 1992; Simmons et al., 1996; Widén and Madji, 2001; Davidson et al., 2006 Peng and Thomas, 2006; Sampson et al., 2007; Olajuyigbe et al., 2012). Others have related changes in soil C and nutrient pools (or lack thereof) following harvest to differences in forest species cover, type of harvesting method (e.g. thinning, clear cutting with slash retention vs. whole tree harvesting), and soil taxonomy, but the extent of these effects are limited to qualitative categorical interpretation (Johnson and Curtis, 2001; Nave et al., 2010). Others still have looked at changes to soil C and N mineralisation rates and forest floor and mineral soil inputs from harvesting residues, using these to model gains, losses, and transformations of primarily C, P, and N in both undisturbed and disturbed environments through time series studies and chronosequences (Aber et al., 1978; Covington, 1981; Vitousek and Mattson, 1985; Yanai, 1992, 1998; Yanai et al., 2000). In some cases, assessment of post-harvest live fine root density estimates and harvesting residues have been linked to changes in FCO$_2$, nitrate concentrations, and changes in soil C, but no direct relationship assessing a rate of change between them have been conclusively demonstrated (Vitousek and Mattson, 1985; Mattson and Swank, 1989; Chatterjee et al., 2008; Olajuyigbe et al., 2012).

Based on these results and from many prior studies, estimates of ecosystem-scale biogeochemical processes and mechanisms of soil nutrient cycling have been developed and used to predict the effects of harvesting on many aspects of soil function. However, little consideration has been given to directly
linking measures of harvest intensity for specific disturbance outcomes measured as plot-scale changes to various aspects of forest structure and associated environmental covariates (i.e. soil temperature, moisture, and compaction) to changes in response variables for the purposes of prediction. I investigated several potential covariates and factors related to harvesting disturbance intensity in my study to attempt to gauge changes in soil biogeochemistry to system responses.

5.3.1.1 Measures of Harvest Intensity

Higher levels of canopy openness in harvested plots were correlated to post-harvest soil temperatures, providing one of the most important measures of system response to harvesting. Higher soil temperatures in harvested treatments relative to controls accounted for up to 41% of elevated FCO₂ effect sizes, proving to be an important causal mechanism behind treatment effects on FCO₂. Temperature explained 27-46% of overall variance in FCO₂ across all treatments when pooled by year; this increased to an average of 75-91% when considered by subplot. However, no substantial relationship between temperature and FCO₂ was present for any single measurement period. Additionally, soil temperature expressed a very low spatial variability (as the coefficient of variation – CV); while values were slightly higher in harvested treatments, overall differences were negligible.

Similarly, canopy gaps and openness were higher in harvested treatments and expressed higher overall variability, but differences in CV were also not substantial between treatments. This homogeneity was surprising considering that canopy gaps are generally considered heterogeneously distributed, but indicates that soil temperature differences in harvested areas may be consistent and easy to predict from changes in cover over larger areas. This may have been related to gap size, which was not investigated during this study.

Soil moisture demonstrated much higher spatial variability, and while related to the distribution of SOM and various nutrients in general, did not account for variation in treatment effects. Therefore, while post-harvest changes to soil moisture may be influential in forest systems experiencing seasonal deficits, it appears to have little impact in humid climates with consistent precipitation such as central Ontario.

This left several other covariates to consider, such as nutrient limitations and introduction of labile C substrates. Availability of nutrients such as NH₄⁺ and K⁺ did not appear to be a limiting factor for decomposers or trees since post-harvest decreases were noted in harvested treatments where FCO₂ was higher, and attributed to assimilation. Variance in post-harvest FWD inputs at the plot scale explained considerable variance in basal and autumn FCO₂ rates as well as in declining NH₄⁺. Since I did not measure leaching of labile C or other nutrients from woody debris it is difficult to suggest whether it
directly influenced decomposition rates. Instead, FWD values may have functioned as a general proxy for harvest intensity, including introduction of other residues such as fine root and mycorrhizal necromass that turn over in weeks to months (Fahey et al., 1988; Burke and Raynal, 1994; Högberg and Högberg, 2002). The correlation between post-harvest FWD inputs and NH$_4^+$ losses suggests that labile C from leachates may have been a limiting component for microbial activity, which became primed from fresh substrate availability, leading to increased assimilation of other nutrients to meet demands.

Similarly, cut tree basal area provided another metric of disturbance that showed a strong negative influence on summer and peak respiration rates, ostensibly through lower root respiration. A lack of relation to nutrients suggests that spatial variation in nutrient availability at the plot-scale was not limiting tree growth, or that all plots were similarly limited. Nitrate levels in both the LFH and mineral horizons were also strongly linked to changes in forest structure. Lower total residual tree and sapling basal area was correlated to higher nitrate concentrations, as was an increase in cut deciduous biomass. Increasing residual conifer basal area was particularly associated with lower soil nitrate levels. While post-harvest changes to forest structure, conifer cover, and harvesting residues have been broadly linked to changes in N mineralisation and nitrification rates (Chapter 3), I am unaware of any study showing a direct link to a continuous measure of harvesting intensity.

Both cut tree basal area and post-harvest woody debris inputs were linked to pre-harvest conditions; plots with a greater density and basal area of trees within harvesting prescription guidelines (i.e. related to size classes and species) were more intensely harvested. Therefore, despite initial attempts to reduce heterogeneity in forest structure and soil properties by restricting the study to upland deciduous sites, spatial variations in certain covariates proved fortuitous to understanding effect sizes. As such, measurements – or even modelled estimates – of woody debris inputs and cut and/or residual post-harvest basal area may provide a useful metric of harvest intensity to predict change biogeochemical processes and in soil function. However, these results may vary considerably amongst silvicultural systems, and be more applicable to partial-harvesting prescriptions. Beyond a certain threshold of biomass extraction these linear relationships may change or disappear, instead governed by different biogeochemical mechanisms. Large differences in removal rates and the occurrence of progressive thinning events in other silvicultural systems, such as clear-cutting and shelterwood harvesting, may exceed the linear thresholds identified in my study.
5.3.1.2 Skid Trails as Unique Disturbance Zones

My research revealed substantial differences in soil edaphic properties between heavily compacted and scarified skid trails, and areas that were harvested but relatively un-compacted with an intact forest floor. This identified skid trail areas as a key over-arching disturbance factor that may strongly influence soil properties and biological response following harvest. Other studies assessing post-harvest changes to soil properties have acknowledged this to varying degrees (Chapter 4), but to my knowledge, none have specified it as an empirical factor in an overall analysis of harvesting disturbances. A portion of discrepancies amongst studies assessing may therefore be attributable to a failure to block for differences between trails and cut forest.

Skid trail coverage in partial harvest systems may range from 10-30%, and the level of disturbance can vary considerably between primary to tertiary trails. My results showed that primary trials were substantially compacted, with much higher bulk densities than on tertiary trails, which varied minimally from non-trail harvested areas. Tertiary trails experienced a similar number of machine passes to those reported in the literature (2-4), yet were far less compacted and showed minimal damage to the LFH relative to levels described by others. In part, this may have been due to harvesting in winter when soils were frozen and much less susceptible to damage, while primary trails continued to see use for transport of logs left in landings after soils had thawed in spring. In comparison, other studies have shown similar bulk densities and rates of compaction between tertiary and primary trails in boreal and temperate deciduous forests, though most also had much higher pre-use bulk densities and used when soils were not frozen (Chapter 4).

Primary trail soils also demonstrated much lower overall soil respiration values and SOM/nutrient content than tertiary trails or harvested forest. Although soil moisture was not implicated in effect sizes on harvested areas, primary trails were strongly influenced by precipitation events that led to saturation and substantial temporary reductions in FCO$_2$. Since FCO$_2$ efflux appeared to mostly be from heterotrophic activity, primary trails likely represented a C source due to lack of root biomass and activity. Despite this, relatively low SOM/nutrient content was likely due to a history of recurring prior use, depleted by decomposition and erosion from runoff over many years.

Therefore, skid trail hierarchy alone may not consistently describe the level of compaction and associated disturbance to soils, as this likely varies considerably by soil type, region, and prior history of use. Yet there is consistent evidence that intense compaction and prolonged disturbance can fundamentally influence soil properties and function, and must be considered when evaluating the
extent of harvesting disturbance impacts. As such, a failure to effectively stratify sampling locations amongst skid trails and disturbed but otherwise intact soils in harvested forest may account for a large proportion of variability in study results due to non-representative experimental designs. This is a particular concern for chronosequence studies that may inadvertently collect unrepresentative samples. For example, over-representation of primary trails with low SOM due to a long-history of re-use may overstate SOM losses following harvest, potentially accounting for the appearance of rapid and substantial losses. Alternatively, under-representation may lead to overstatement of C stocks in managed forests.

5.3.1.3 Re-Evaluating Harvesting Impact Assessments

In consideration of the phenomena described in the preceding sections, research on harvesting disturbances in heterogeneous forest systems would benefit from the following approaches: 1) incorporation of statistical tools that better account for small-scale subject level dependence (i.e. random intercept models); 2) collection or estimation of appropriate covariate data that will allow models to adjust for differences (e.g. soil temperature and moisture, woody debris, and vegetation basal area), and; 3) an increase in the number of replicates to provide more representative sampling and statistical power with regard to the variance in the data.

5.3.2 Implications for NPP and Carbon Budgets

It is important to consider the different contributions of disturbance types when assessing overall CO$_2$ efflux from managed forests and NPP. Since gross primary production and associated root respiration may be reduced immediately following harvest, and the contribution of heterotrophic organisms decomposing fresh root necromass and woody debris likely increases, an overall decline in FCO$_2$ from recently cut areas might not represent a net decrease in C flux to the atmosphere. For example, primary trails may represent areas of net C losses. In Chapter 2 and in Shabaga et al. (2015) I demonstrated that higher decomposition rates in non-trail cut areas following harvest could account for an increase in FCO$_2$, hypothetically reducing the ratio of root respiration to total soil respiration. In Chapter 3 I was able to link estimates of these elevated annual heterotrophic contributions to CO$_2$ efflux in harvested areas to soil C losses. If the overall FCO$_2$ from the forest now indicates a higher proportion of CO$_2$ from decomposition, this suggests the harvested area has the potential to function as a net C source, even if the overall efflux has decreased. Since these rates likely differ between skid trail type and history/frequency of use and harvest intensity, this highlights the importance of accounting for different contributing components to FCO$_2$ when considering the overall forest C balance.
5.4 Developing a Predictive Framework: Forecasting Post-harvest Responses from Harvesting Disturbance Type and Intensity

In chapter one, I defined a conceptual model of anticipated harvesting disturbances that may influence biogeochemical processes in soils (Fig.1.1). During these studies, I tested the influence of several of these hypothesised disturbances on response variables, such as FCO$_2$ and various edaphic physiochemical properties. Several key results were able to directly link measures of harvest intensity and disturbance to soil function and biogeochemical processes.

- Canopy openness was correlated to soil temperatures, which predicted almost half of all increases to FCO$_2$ in harvested areas
- Post-harvest FWD inputs were correlated to higher rates of FCO$_2$ in autumn and losses of NH$_4^+$
- DOC and SOM losses were also correlated to rates of FCO$_2$ in autumn
- Declines to SOM, DOC, K, and NH$_4^+$ were all correlated
- Cut tree basal area was correlated to lower summer FCO$_2$ rates
- Post-harvest understorey basal area predicted higher post-harvest NO$_3^-$ concentrations and increases to Q$_{10}$ over three years
- Bulk Density predicted SOC

Similarly, certain pre and post-harvest indicators may also to predict recovery rates. Understorey regrowth predicted decreases to soil temperatures after two years, and a higher post-harvest understorey basal area may also predict the recovery of root respiration over time, observed as rising Q$_{10}$ values. Consequently, post-harvest understorey basal area and changes to annual Q$_{10}$ values may serve as a valuable metric to predict and gauge disturbance and recovery.

While most of these measures related continuous measures, skid trail type provided a categorical measure that may simplify estimation of impacts. Primary trails were generally compacted beyond a threshold level that predicted much lower FCO$_2$ and concentrations of SOC and total N. Tertiary trails were more variable, but for the most part statistically indistinguishable from harvested forest with regard to most measures, with the exception of soil temperatures. However, since trail centres produced higher and ruts lower FCO$_2$, the net effect of soil temperatures on biological activity was complex. For the purposes of modelling and C and nutrient pool/flux estimates, primary trails are the main area of consideration, and the properties of tertiary trails cannot be generalised at this time. Consequently, primary trails can be broadly noted as a distinct area that predicts smaller SOC and
nutrient pools and $\text{FCO}_2$, but likely functions as a net C source. One caveat to this simplified structure is the temporal influence of precipitation events leading to soil pore saturation on $\text{FCO}_2$.

Table 5.1 List of variables related to harvest intensity and environmental conditions identified or proposed during this study that may be predictive of forest response to harvesting disturbance level and type. BA = Basal Area.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stimulants</strong></td>
<td></td>
</tr>
<tr>
<td>Canopy Openness</td>
<td>Increased soil temperatures and overall $R_S$</td>
</tr>
<tr>
<td>Volume of Harvest Residues (i.e. roots and DWD)</td>
<td>Likely increased labile C availability, higher $R_W$ from decomposition; nutrient losses</td>
</tr>
<tr>
<td>$Q_{10}$ and Residual Understorey BA</td>
<td>Regrowth of roots; higher $R_R$</td>
</tr>
<tr>
<td>% Cut Deciduous Tree BA</td>
<td>More cut deciduous = higher nitrification rates</td>
</tr>
<tr>
<td><strong>Constraints</strong></td>
<td></td>
</tr>
<tr>
<td>#Machine Passes + Skid Trail Area</td>
<td>Compaction of soil beyond a bulk density of 0.9 g cm$^{-3}$ restricted gas exchanges, led to soil saturation from rain events, and inhibited root growth, reducing root density and $R_R$. High potential for function as net C source. Also ensured substantially lower SOC/N and base cation concentrations. May vary depending on frequency of prior use</td>
</tr>
<tr>
<td>Bulk Density</td>
<td>SOC and moisture content</td>
</tr>
<tr>
<td>Cut Basal Area</td>
<td>Root dieback, decline in $R_S$</td>
</tr>
<tr>
<td>Sapling BA Regrowth</td>
<td>More $R_S$, but reduces soil temperatures and overall $R_S$</td>
</tr>
<tr>
<td>% Conifer cover</td>
<td>Higher conifer cover = lower nitrification rates</td>
</tr>
<tr>
<td><strong>Proposed</strong></td>
<td></td>
</tr>
<tr>
<td>Topographic Wetness Index, Soil Texture, Drainage Class</td>
<td>Moisture availability, gas exchanges. Can exacerbate effects of compaction on reduced gas exchanges. May contribute to emissions of $\text{CH}_4$ and $\text{N}_2\text{O}$ (Winsborough, 2015; unpublished data).</td>
</tr>
</tbody>
</table>

Collectively, these results provide strong evidence for increased post-harvest decomposition and nitrification rates stimulated by introduction labile C of fresh harvesting residues. Additionally, they indicate that soil root activity was initially depressed by harvesting, but showed some evidence of recovery by the third year following harvest. The direct relationships between some of these and measures of harvest intensity suggest that we might be able to use easily measured and/or estimated post-harvest residual forest properties to predict changes in soil C and inorganic N storage, and possibly even NPP. These include harvested basal area and woody debris residue volumes, residual forest understorey biomass, canopy openness, and skid trail area. In conjunction with other variables known to impact productivity rates and soil chemistry (e.g. climate, tree species, drainage/topography), I have
defined a list of predictive variables for future evaluation of harvesting effects on soil and forest function, eventually leading to improved predictive models (Table 5.1).

5.5 Unresolved Questions and Future Directions

Several unanswered questions remain at the conclusion of this dissertation. Strong correlations between variables of harvest intensity (FWD, cut basal area) and effect sizes for SOM, certain nutrients, and seasonal FCO$_2$ provided a compelling rationale for increased decomposition rates based on priming of microbiota with labile C and reduced root respiration; this was the most logical conclusion based on these results and prior scientific theory. However, no actual measurements of root respiration, decomposition rates, or fluxes of labile C from hypothesised sources (e.g. FWD and roots) were conducted, nor were measurements of changes to fine root density in harvested areas or skid trails, leaving the causal mechanisms uncertain. A lack of nutrient flux measurements throughout the vertical soil profile made it challenging to determine if apparent losses were from uptake or leaching. Additionally, low sample numbers at the plot scale (n=15) limited statistical power to detect effects.

Some of these concerns are more readily addressed in future research than others. Effective separation of root respiration from heterotrophic activity remains a challenge unlikely to be resolved without novel methods. However, relative differences in decomposition rates could be measured using the cellulose paper or cotton strip assay methods (Startsev et al., 1998; McLaughlin et al., 2000) and lysimeters could be used to collect leachates from soils at various depths. Mini-rhizotron cameras provide a minimally invasive means of assessing fine root growth, but methods to determine root necromass are destructive and may influence the response variables in question.

Assessment of soil microbial biomass and nutrient content from the same depths may facilitate fractionation of nutrient amongst biological and soil pools. Lysimeters placed under FWD and root systems could help resolve questions over flux of labile fractions of C (or other nutrients). Collected leachates from harvest residuals could also be used to “fertilise” soil samples in the lab to determine if it stimulates FCO$_2$ and produces greater loss of SOM mass than unfertilised controls. Lastly, the high degree of spatial variability of many variables indicates an increase in replicates is necessary to more convincingly link measures of harvest intensity to soil biogeochemistry.
References


Appendix I

Table AI Mean annual soil carbon dioxide efflux (FCO₂) in µmol m⁻² s⁻¹ from measured soil respiration (Rₛ) and soil respiration modelled at mean control treatment temperature values (Rₛ\text{mean}), 10 °C (R₁₀), and 20 °C (R₂₀), the response of Rₛ to temperature over a 10 °C range (Q₁₀), temperature values in °C (Temp.), % canopy openness (Light), % gravimetric soil moisture values (SM) in summer, and average total precipitation (Precip.) in mm for 20 days prior to FCO₂ measurements in summer for a mixed deciduous forest in central Ontario. SE = standard error of the mean.

<table>
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<tr>
<th></th>
<th>Control</th>
<th>TL</th>
<th>BIO</th>
<th>Control</th>
<th>TL</th>
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<td>35.4±10.5</td>
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</table>
**Table** Al-I. II Mean pre-harvest, one, and three year post harvest LFH layer soil chemistry values for control (CTRL), tree-length (TL), and biomass harvesting (BIO) treatments for a mixed deciduous forest in Central Ontario. SOM = soil organic matter. DOC and DON = dissolved organic carbon and nitrogen. All variables measured as mg per kg of dry soil except SOM and TN which represent the % of soil dry mass. Asterisks denote significant post-hoc pairwise test differences between harvested and control treatment values (*p≤0.10, **p≤0.05). Standard errors of the mean (SEM) are represented by ±. Ca, Mg, Na, Al, Fe, DOC, DON, and NO3⁻ values were log-transformed prior to calculating SEM, producing uneven error bars after back-transformation.

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<th>1 Year Post-Harvest</th>
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*(a) Data not presented due to low sample size or technical issues.*
Table Al-III. Mean pre-harvest, one, and three year post harvest mineral soil chemistry values for control (CTRL), tree-length (TL), and biomass harvesting (BIO) treatments for a mixed deciduous forest in Central Ontario. SOM = soil organic matter. DOC and DON = dissolved organic carbon and nitrogen. All variables measured as mg per kg$^{-1}$ of dry soil except SOM and TN which represent the % of soil dry mass. Asterisks denote significant post-hoc pairwise test differences between harvested and control treatment values (*p≤0.10, **p≤ 0.05). Standard errors of the mean (SEM) are represented by ±. SOC, K, Ca, Mg, DOC, DON, PO$_4^{3-}$, and NO$_3^-$ values were log-transformed prior to calculating SEM, producing uneven error bars after back-transformation.

<table>
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<tr>
<th>Mineral</th>
<th>Pre-Harvest</th>
<th>1 Year Post-Harvest</th>
<th>3 Years Post-Harvest</th>
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<td></td>
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