Université du Québec en Abitibi-Témiscamingue

GROWTH, THINNING SHOCK, CARBON SEQUESTRATION, AND MORTALITY FOLLOWING PARTIAL CUTS IN ESKER FORESTS

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PRÉSENTATION DU JURY

Cette thèse a été évaluée par le jury composé des membres suivants :

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ÉPIGRAPHE

In the end, everything will be okay. If it's not okay, it's not the end.

AVANT-PROPOS

This thesis is divided into five chapters. Chapter I provides a general introduction, including a literature review aimed at establishing the scientific context of the study and highlighting its relevance. Chapters II to IV constitute the core of the thesis and address the research hypotheses formulated in this work. These chapters are written in English and follow the structure of scientific manuscripts intended for publication in international peer-reviewed journals. Chapter II has been submitted to *Forestry: An International Journal of Forest Research*. Chapter III will be published in *Forest Ecology and Management* in 2026, and Chapter IV was published in *Trees: Structure and Function* in April 2025. Chapter V presents the general conclusions of the thesis and is based on the findings reported in the preceding chapters. In this final chapter, the main results of the thesis are discussed, the limitations of the study are indicated, and perspectives for future research are proposed.

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GENERAL INTRODUCTION

The boreal forest. The boreal forest represents the second largest biome on Earth, accounting for 27 % of the world's forest surface (UNECE, 2024). This biome is primarily located between 45° and 70° N, mainly in Russia (63 %), Canada (28 %), Scandinavia (4 %), and Alaska (3 %) (Fig. 1) (Burton et al., 2010). Climatologically, the boreal forest is marked by long, cold winters, and a short growing season (50–130 days with mean temperatures > 10 °C) (Burton et al., 2010; UNECE, 2024; Engle et al., 2025). Floristically, the dominant tree genera are represented by softwoods of *Abies*, *Picea*, *Larix,* and *Pinus spp*, in addition to hardwoods of *Betula* and *Populus spp.* (McLaren and Turkington, 2013). However, the proportions of these species in the boreal forest vary by region. For example, in Canada, black spruce (*Picea mariana* (Mill.) BSP) is the dominant tree species across much of its boreal forest, whereas in many regions of Russia, larch species (*Larix spp.)* dominate the landscape (Hytteborn and Maslov, 2005; Hermosilla et al., 2024).

The boreal forest provides a wide array of ecosystem services (Reid et al., 2005; Hof et al., 2023). Cultural services are particularly significant, encompassing recreational activities such as hiking, skiing, or hunting (Himes, 2025), or holding spiritual and cultural value, especially for Indigenous communities, including the Yupik in Alaska, the Sámi in Fennoscandia, the Evenk in Russia, or the Cree in Canada (UNECE, 2024). Among the provision services, the boreal biome contains the greatest amount of surface freshwater in the world and helps regulate its quality and quantity (Gauthier et al., 2015; Grosbois et al., 2023; Luke et al., 2007; UNECE, 2024). Moreover, the boreal forest provides non-woody products (e.g., mushrooms, berries, or game meat), and wood products, with two-thirds of its surface producing 17% of the global roundwood harvest (Gauthier et al., 2015; Gundersen et al., 2019; Himes, 2025; Hof et al., 2023; UNECE, 2024).

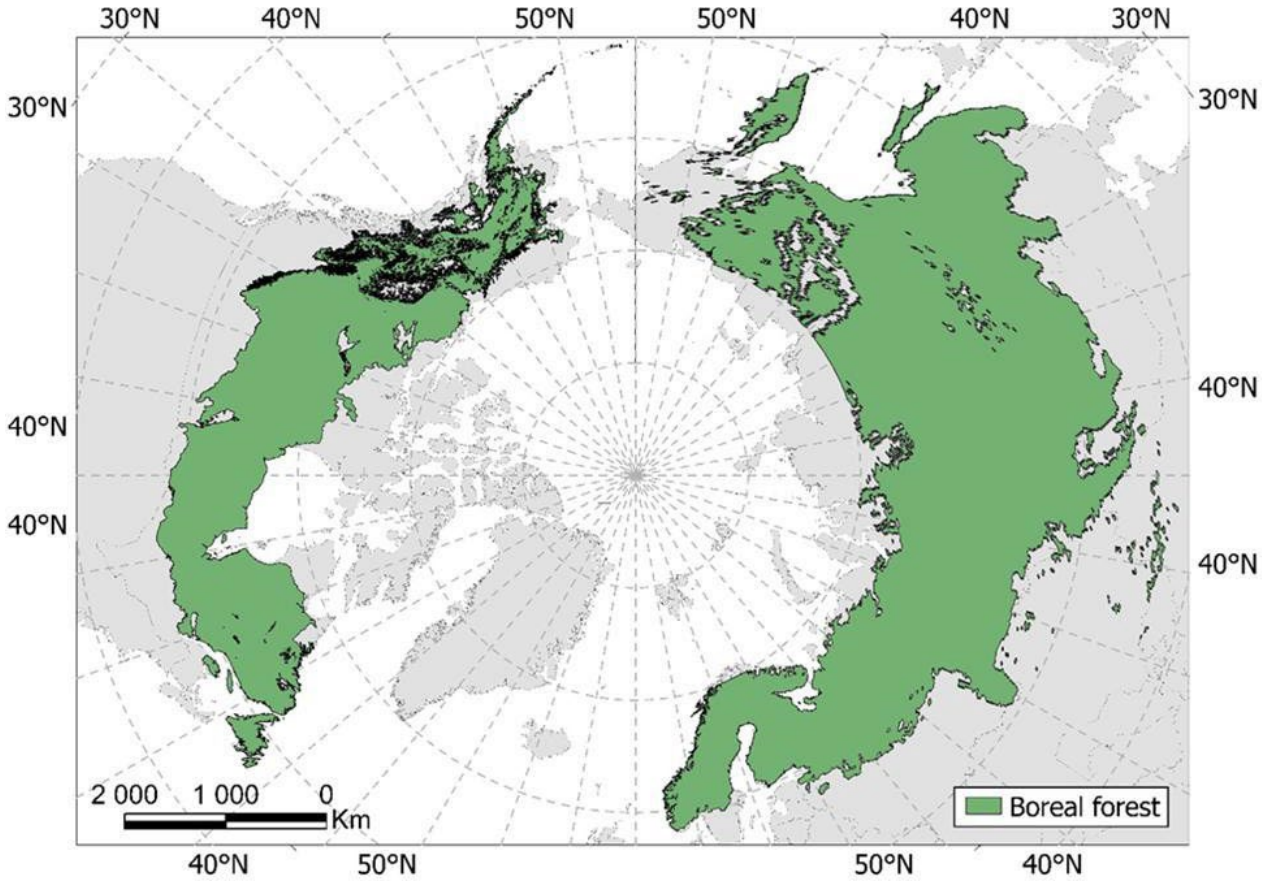

Figure 1
World distribution of the boreal forest.
Coordinate system: North Pole Azimuthal Equidistant. Map created using ArcGIS Pro
3.3.0 (ESRI, Redlands, United States).
Source: Brandt, 2009; University of Maryland, 2015.

The forests located in this biome also provide key regulating services, such as climate regulation through the warming effect of its albedo, the condensation through the emission of organic vapours (Spracklen et al., 2008; Kuusinen et al., 2012; Lintunen et al., 2022; Hasler et al., 2024), and cloud formation due to the formation of secondary organic aerosols (Šimpraga et al., 2019). The photosynthesis-driven carbon storage also contributes to climate regulation, as atmospheric CO_2 is directly linked to the absorption of solar radiation and the increase in global mean surface temperatures (Mitchell, 1989; Hao et al., 2025).

Natural disturbances, such as fire, insect outbreaks, beaver or windthrow, naturally shape the boreal forest (Shorohova et al., 2023), altering key forest attributes, such as species composition, forest structure, and successional pathways (Thom and Seidl, 2016; Kulha et al., 2019; Anyomi et al., 2022). Fire is a dominant natural disturbance in most of the boreal forest (Gauthier et al.,

2023), while other natural disturbances, such as insect outbreaks and windthrow, have a major role in forest landscapes with low fire frequencies (De Grandpré et al., 2018). Windthrows, or blowdowns, lead to tree uprooting or stem breakage when the wind forces exceed the tree anchorage strength or stem resistance (Quine and Gardiner, 2007). Windthrows vary in scale, with partial windthrows affecting several hectares under strong winds (Fischer et al., 2013; Girard et al., 2014), while large-scale or stand-replacing windthrows, often driven by extreme winds from convective storms or low-pressure systems, can impact much larger areas (Bouchard et al., 2009; Fischer et al., 2013; Girard et al., 2014). Climate change is currently altering the natural disturbance regimes and thus affecting the ecosystem services that the boreal forest provides (Seidl et al., 2023). For instance, in the case of windthrows, mean wind speeds are generally projected to decrease across most regions of the boreal forest (IPCC, 2021), which would alter the dynamics of partial windthrows. In addition, extra-tropical cyclones, such as Storm Sandy in Canada or Ophelia in Norway, are expected to become less frequent but more intense (Montoro Girona et al., 2023; Saad et al., 2017), thereby increasing the likelihood and severity of large-scale windthrows.

Sustainable forest management. Forest management for commercial supply started in Canada in the 19th century and was performed through selective cutting, targeting pine (*Pinus spp.*) and spruce (*Abies spp.*) trees (Burton et al., 2003; Boucher et al., 2009; Labrecque-Foy and Montoro Girona, 2023). During the early decades of the 20th century, the timber demand rose, leading to an increase in the production of the pulp and paper industries (Rotherham and Armson, 2016). During these decades, selective practices were replaced by clear cuts targeting all conifer species (Boucher et al., 2009). Clear cuts are a group of silvicultural treatments that harvest most of the trees in the stand at once, followed by artificial regeneration, or seeds from adjacent

stands or harvested trees (Keenan and Kimmins, 1993). The dominance of clear cuts as a major harvesting technique was based on its better cost-efficiency and the greater after-harvest soil exposure that provided suitable conditions for the regeneration of conifer species of commercial interest (Rosenvald and Lõhmus, 2008; Burton et al., 2010).

During the 1970s, forest management in Canada evolved from a focus on clear cuts and timber production toward integrating non-timber values (Boucher et al., 2009; Rotherham and Armson, 2016). By 1995, the principles of Sustainable Forest Management and the ecosystem approach were adopted, emphasizing ecological integrity, complexity, and uncertainty (Convention on Biological Diversity, 2004; Rotherham and Armson, 2016; Kayes and Mallik, 2020). This shift led to the emergence of Forest Ecosystem Management (Gauthier et al., 2009), promoting silvicultural practices that emulate natural disturbances to sustain biodiversity and ecosystem services while reducing the differences between managed and natural forests (Aakala et al., 2023).

Under this context, several proposals were made to achieve the Forest Ecosystem Management goals, with the three-cohort model being an example of a proposal for the Canadian forests (Bergeron et al., 2001; Bergeron & Harvey, 1997; Gauthier et al., 2009). This model proposed different management alternatives based on the stand's development stage following a fire. Clear cuts and other low-retention cuts are recommended for stands where the canopy consists of pioneer species established after the fire. Partial cuts are suggested when shade-intolerant succession species are replacing pioneer species, while selection cutting is advised for stands without pioneer species. Partial cuts are a group of low-retention silvicultural treatments in which only a part of the stand is harvested to emulate tree succession or intermediate disturbance dynamics, such as insect outbreaks or windthrows (Fig. 2) (Bose et al., 2014; Thorpe and Thomas, 2007). Selection cutting represents the lowest-impact treatment, removing single trees or small groups of trees from the stand while mimicking small-

scale disturbances such as tree collapse due to senescence (Qi et al., 2016; Latterini et al., 2023).

Figure 2
Aerial view of a shelterwood cut in a jack pine-dominated stand over esker soil. Drone pilot: Cristiano Vieira. GREMA drone model: DJI Mini 3 PRO. Saint-Dominique-du-Rosaire, Quebec, Canada. August 17, 2024.

Impacts of clear cuts on forest ecosystems. Despite the growing interest in the use of partial cuts during the last 30 years, clear cuts remain the predominant silvicultural practice across all Canadian provinces and territories, accounting for an average of 86% of the harvested area (2002 – 2022 period) (Fig. 3) (National Forestry Database, 2020). However, the use of clear cuts as a way of mimicking fire has been questioned due to significant differences between clear cut and fire-affected stands in soil properties, including humus layer thickness, pH, moisture, nutrient fluxes, and solar radiation levels (Simard et al., 2001; Nybakken et al., 2012; Dymov, 2017). Regeneration patterns, understorey composition, and the diversity of both vertebrate species (e.g., mammals) and invertebrate species (e.g., insects, mollusks, and soil microbes) also differ markedly from those in unharvested or fire-disturbed forests in the middle term (Fisher and Wilkinson, 2005; Ilisson and Chen, 2009; Johansson et al., 2010; Hylander, 2011; Smenderovac et al., 2017; Jean et al., 2019).

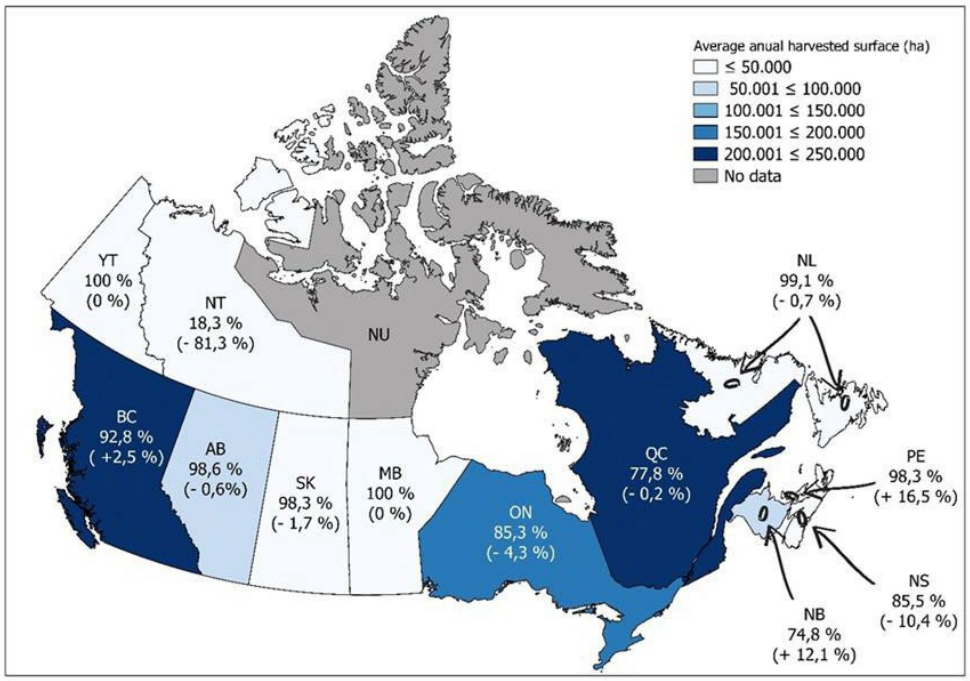

Figure 3
Average annual harvested surface in each Canadian province, proportion of managed area harvested through clear cuts, and increase or decrease in the forest surface managed through partial cuts
(2000 – 2020 period).

Coordinate system: Canada Albers Equal Area Conic.
Source: Natural Resources Canada (NRCan). Harvest data: National Forestry Database (NFD). Map created using QGIS Pro 3.38.1.

Clear cuts can reduce deadwood abundance, old-tree and hardwood representation, and structural diversity (Gauthier et al., 2009; Gustafsson et al., 2010; Krankina & Harmon, 1994; Pedlar et al., 2002). These silvicultural treatments also alter stand age distribution, even with rotation lengths similar to natural fire intervals, and in some areas can promote paludification (i.e., accumulation of organic matter over time driven by elevated soil moisture and increased *Sphagnum spp.* cover) (Bergeron et al., 2002; Lavoie et al., 2005; McRae et al., 2001). At the landscape scale, wildfires create a complex mosaic of patches that enhances biodiversity, unlike the more uniform structure of clear cut landscapes, which increases patch isolation and impairs species dispersal and gene flow (Gauthier et al., 2009; McRae et al., 2001). Clear cuts also impact hydrological systems by altering food web health, surface runoff, water temperature, and chemistry (Carignan et al., 2000; Sørensen et al., 2009; Bahuguna et al., 2010; Myrstener et al., 2025), prompting the preservation of residual unharvested strips (i.e., riparian buffers) to mitigate these effects (Fig. 4) (Richardson et al., 2012). All these impacts have further contributed to focus research on potentially more sustainable alternatives for forest management, such as partial cuts.

Figure 4
Riparian buffer strip located between a clear cut stand and a lake in La Motte, Quebec, Canada.
Drone pilot: Ruben Jo M. Leroy.

The thinning shock. Improved tree growth has been observed following different partial cut treatments, such as diameter-limit cuts (Thorpe et al., 2007; Pamerleau-Couture et al., 2015; Valkonen et al., 2017), commercial thinning (Moulinier et al., 2015; Bose et al., 2018; Saarinen et al., 2020), shelterwood cuts (Barna et al., 2010; Prévost and DeBlois, 2014; Montoro Girona et al., 2016), and variable retention cuts (Powers et al., 2010; Montgomery et al., 2013; Xing et al., 2018). However, residual trees often experience a period of growth decline or stagnation following harvest, commonly referred to as "*thinning shock*" or "*growth shock*," which can last from 1 to 7 years before they show any sign of enhanced growth rates (Fig. 5) (Bose et al., 2020; DeBell et al., 2002; Emmingham and Elwood, 1983; French et al., 2023; Kneeshaw et al., 2002; Montoro Girona et al., 2016; Picchio et al., 2018). Thinning shocks have been observed following diameter-limit cuttings (Bevilacqua et al., 2005; Thorpe et al., 2007; Gendreau-Berthiaume et al., 2012), commercial thinning cuts (Pukkala et al., 2002; Bebber et al., 2004; Vincent et al., 2009; Picchio et al., 2018; Nicoll et al., 2019; French et al., 2023), and uniform shelterwood cuts (Youngblood, 1991; Montoro Girona et al., 2016).

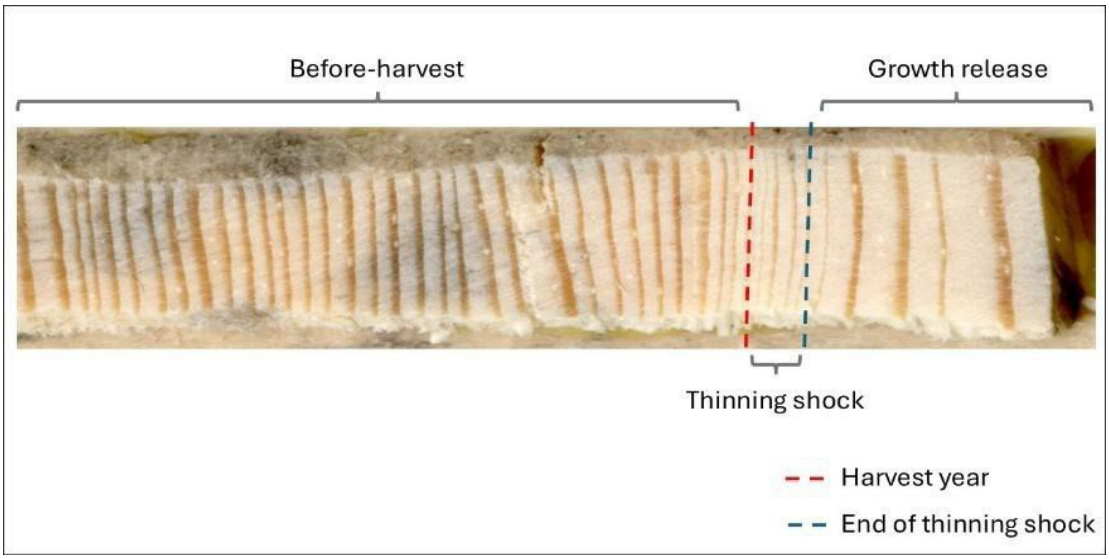

Figure 5
Schematic representation of a 6-year thinning shock in a cross-dated jack pine increment core.

Differences in non-photosynthetic biomass proportion (Kneeshaw et al., 2002), an increase in resource investment in cone production or post-harvest root growth to increase tree stability and nutrient assimilation have been hypothesized to be the origin of the growth shock (Youngblood, 1991; Price et al., 1996; Thorpe et al., 2007; Montoro Girona et al., 2016). An after-harvest acclimatization process (Bevilacqua et al., 2005; Jones and Thomas, 2007; Thorpe et al., 2008; Montoro Girona et al., 2016; Bose et al., 2020), due to the changes in the stand relative humidity, solar radiation light penetration, air temperature, soil temperature, wind speed, and evapotranspiration following harvest (Bourgeois et al., 2004; Vesala et al., 2005; Weng et al., 2007; Goudiaby et al., 2011; Zhang et al., 2018a) has also been hypothesized to be behind the thinning shock. Other authors have recently suggested that the observed decline in midday water potential following thinning and the rises in temperature and vapour pressure deficit could induce stomatal closure and, at the same time, reduce photosynthesis and cause thinning shock (French et al., 2023). However, this hypothesis is primarily supported by indirect evidence, as stomatal conductance during thinning shock has not yet been directly measured, and thus the origin and driver factors of thinning shock remain unknown.

Impacts of forest management on forest carbon. Forest management alters the forest carbon in several ways. The increase in soil exposure due to alterations in canopy openness alters carbon sequestration by increasing soil organic matter decomposition rates, which increases soil temperature and moisture content, and thus reduces the carbon content in soil pools (Ameray et al., 2021). In addition, carbon sequestration in managed stands is also altered due to stem removal and the subsequent reduction in litterfall (Jandl et al., 2007). It seems that forest carbon stocks remain lower in managed stands than in unharvested forests (Lee et al., 2002; Borys et al., 2016). However, the degree to which forest management alters forest carbon stocks varies according to the silvicultural treatments applied. Lee et al. (2002) compared the carbon stocks of unharvested, partially cut, and clear cut boreal trembling aspen (*Populus tremuloides* Michx.) - balsam fir (*Abies balsamea* (L.) Mill.) in Ontario, Canada. Their work revealed that stands managed by partial cuts showed intermediate values in terms of carbon contained in forest floor, litter, and in terms of carbon sequestered during the 3 years following harvest. Moreover, simulation models for red spruce (*Picea rubens* Sarg.) stands of Nova Scotia, Canada, followed this trend by exposing greater total ecosystem carbon stocks in the partially cut stands (Taylor et al., 2008).

Soil carbon stocks remain relatively stable with increasing partial cut intensity (Nilsen and Strand, 2008; Ruiz-Peinado et al., 2016; Zhang et al., 2018a). In contrast, aboveground carbon stocks

are directly affected by stem removal and thus generally decline after harvest (D'Amato et al., 2011). In low-intensity treatments that selectively remove smaller-diameter trees, however, aboveground stocks can be maintained because of the greater amount of carbon stored in residual trees and the enhanced post-harvest radial growth rates, which can help compensate for part of the initial carbon loss (Hoover and Stout, 2007; D'Amato et al., 2011). Nevertheless, the increase in windthrow mortality that is often observed in residual stands (Montoro Girona et al., 2019; Ruel and Gardiner, 2019), in addition to the projected increase in wind-related extreme events due to climate change (Saad et al., 2017; Aakala et al., 2023; Montoro Girona et al., 2023a), could further reduce the aboveground carbon stocks and call into question the

viability of partial cut treatments, not just from a biodiversity or economic perspective (Hallinger et al., 2016; Shorohova et al., 2023), but also as silvicultural tools to achieve carbon-oriented objectives.

Windthrow mortality and root grafting. Windthrows are driven by a complex interaction of biotic, abiotic, and anthropogenic factors, including topography (Baker et al., 2002; Waldron et al., 2013; Guimond et al., 2024), local wind conditions (Ruel, 1995; Montoro Girona et al., 2019; Guimond et al., 2024), in addition to stand-level (Dobbertin, 2002; Bouchard et al., 2009; Griess and Knoke, 2011; Valinger and Fridman, 2011; Hlásny et al., 2021; Polinko et al., 2022), and tree-level variables (Hämäläinen et al., 2016; Lavoie et al., 2012; Montoro Girona et al., 2019; Rich et al., 2007; Scott et al., 2005; Valinger et al., 2011).

Among the tree-level variables, root architecture and root traits likely condition the impacts of windthrow events. For example, root systems with greater root plate width, longer and more horizontal branches, and root angles from the taproot closer to 90° confer better uprooting resistance (Stokes et al., 1996; Danjon et al., 2005; Štofko and Kodrík, 2008; Krause et al., 2014). Root grafts, where neighbouring trees fuse their roots until reaching vascular continuity (Graham & Bormann, 1966), have been suggested as a factor contributing to the greater resistance of European beech (*Fagus sylvatica* L.) trees during a rockfall simulation in the French Alps (Stokes et al., 2005) and Tabonuco trees (*Dacryodes excelsa* Vahl.) following a tropical hurricane (Basnet et al., 1993). While root grafting has been proven to affect growth, resource sharing, and disease transmission (Bloomberg and Reynolds, 1982; Hessburg and Hansen, 1986; Fraser et al., 2006; Tarroux et al., 2010), its role in windthrow mortality remains unexplored.

Soil characteristics (moisture, depth, texture, frost frequency, or paludification) have also been related to windthrow mortality (Peltola et al., 1999, 2000; Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Taylor et al., 2019). Sandy soils have been found to enhance resistance to

uprooting in tap-root species like jack pine (*Pinus banksiana* Lamb.) (Elie and Ruel,

2005; Dupuy et al., 2007). However, greater windthrow mortality rates have been observed in riparian buffers located on the sandy soils of the eskers following clear cuts, compared to edges on clay-rich substrates (Guimond et al., 2024). This apparent contradiction suggests that partial cuts may increase vulnerability to windthrow in esker forests. Nevertheless, the windthrow susceptibility of forest stands located on these soils has never been assessed.

Eskers. Eskers are straight or sinuous ridges with glacier origins made up of sand and gravel that can extend from ten to thousands of kilometres and can exceed 50 meters in height (Livingstone et al., 2015). Eskers form beneath glaciers when the interface between the ice and its bed reaches the melting point, allowing liquid water to flow subglacially (Boulton et al., 2009). This meltwater, driven by gravity, carves subglacial drainage channels within active ice (i.e., ice that is moving forward), transporting water and leading to the deposition of sediments (Clark and Walder, 1994). Eskers are sandy deposits commonly found in areas previously covered by major ice sheets, such as the Innuitian, Cordilleran, and Laurentide ice sheets in Canada (Dalton et al., 2023). These sandy deposits are found throughout much of Canada (Fig. 6), as the country was extensively glaciated during the Last Glacial Maximum, with ice sheets reaching elevations of up to 3,000 meters above sea level (Dyke et al., 2002). The Laurentide ice sheet was the last one to melt around 8,000 years ago, leaving more than 20,000 eskers spread across the different Canadian regions (Storrar et al., 2014; Dalton et al., 2023), such as the Abitibi-Témiscamingue region, in western Quebec (Fig. 6).

The low water retention capacity of eskers facilitates the formation and the quality of underground aquifers, which serve as important freshwater sources that are currently being exploited for human consumption (Nadeau et al., 2015). Furthermore, the presence of several vertebrate and invertebrate species has been strongly associated with esker lakes (Hasan et al., 2023; Grosbois et al., 2025). Beyond their hydrological and biodiversity value, eskers are subject to recreation, gravel extraction, and forest harvesting activities, further intensifying pressure on these types of forests (Smerdon et al., 2012; Grosbois et al., 2025). The dry, sandy soils of the eskers are classified as

Arenosols according to the FAO-UNESCO soil classification system, presenting poor water and nutrient retention, to which jack pine is well adapted and often forms pure stands (Liu, 1990; Tubridy and Meehan, 2006; Sileshi et al., 2022).

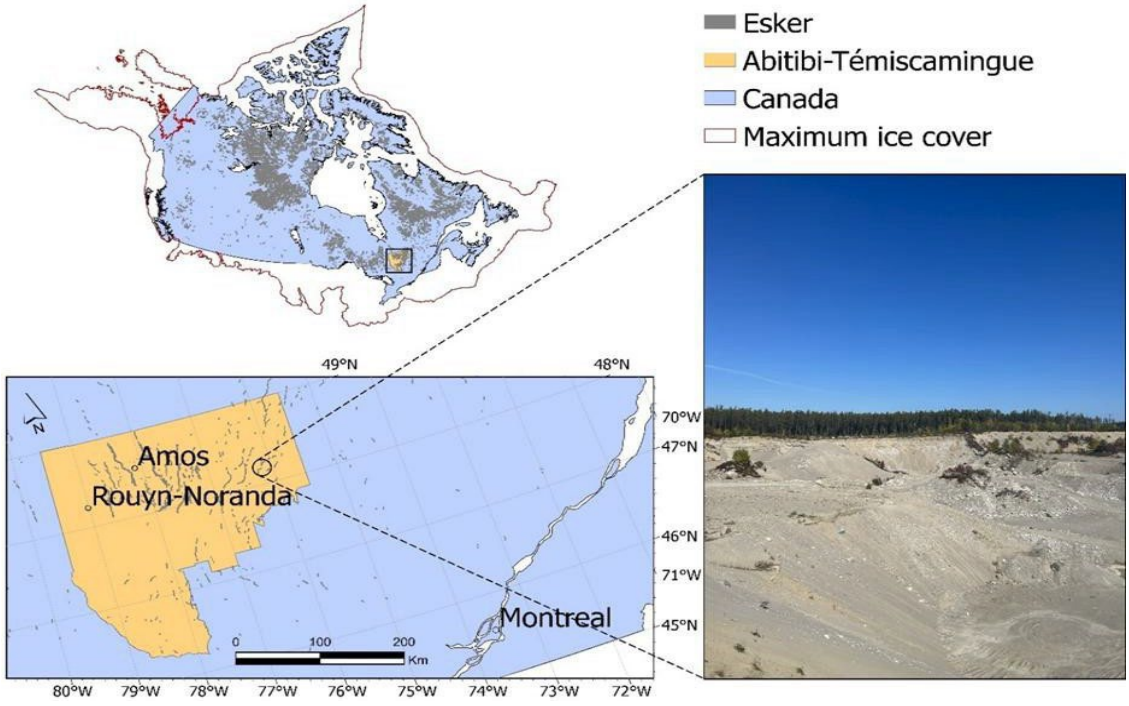

Figure 6
Mapped eskers in Canada and in the Abitibi-Témiscamingue region. Coordinate system: Canada Albers Equal Area Conic.
Maximum ice cover corresponds to 22.000 years ago as estimated by Dalton et al. (2023). Ice cover: Dalton et al. (2023). Eskers in Canada: Storrar et al. (2014), Eskers in Abitibi-Témiscamingue: Nadeau et al. (2015), Administrative boundaries: open.canada.ca.
Picture was taken in a former aggregates plant for gravel extraction. Saint-Mathieu-Berry esker, Abitibi-Témiscamingue, Quebec, Canada. Map created using ArcGIS Pro 3.3.0 (ESRI, Redlands, United States).

Jack pine is a common species in the esker forests (Hasan et al., 2023). This pine species is shade-intolerant and reproduces effectively through serotinous cones, which contain resin beneath their scales that only volatilizes under the high temperatures generated by wildfires (Greene et al., 2013). The success of jack pine in successfully colonizing sun-exposed sandy soils can be attributed to its water-related physiological adaptations, such as the regulation of stomatal opening to water demand or the capacity of revealing low water deficits under moderate drought conditions (Olugbadieye et al., 2025; Thivierge-Lampron et al., 2025). Jack pine is one of the major boreal conifer species of Canada in terms of its distribution range, expanding

from some of the easternmost locations of Nova Scotia to the Mackenzie River, in the Northwest Territories (Payette et al., 2017). Economically, jack pine is also one of the most important commercial tree species in Canada due to its adequate strength for structural building and the

fiber length for quality paper (Deighton et al., 2021). The commercial interest in jack pine has led to increased harvesting in jack pine-dominated stands growing on esker substrates. However, despite the commercial interest of jack pine esker forests, there is no current information regarding how these forests react to the partial cuts that are being performed.

General objective. This thesis aims to evaluate the effects of partial cut treatments in jack pine-dominated esker forests by analyzing tree growth responses, aboveground carbon stocks, and windthrow-related mortality.

Thinning Shock and Tree Growth Analysis Following Partial Cuts in Boreal Forests

Objectives: to examine how partial cuts influence growth release and thinning shock in residual jack pine trees growing in esker forests, and if thinning shocks are observed, to identify the main factors that govern their occurrence, intensity, and duration.

Hypotheses: thinning shock will occur in residual jack pines and will be longer and more intense with increasing harvest intensity, since the degree of stand-level environmental alteration rises with harvest intensity. We also expected thinning shock to be linked to a temporary reduction in stomatal conductance, which will be reflected by a temporary decrease in ^{13}C discrimination (i.e., less negative $\delta^{13}C$). Finally, we hypothesized that growth release would be more pronounced as harvest intensity increases and in trees located closer to skidding trails, due to the reduction in tree competition.

Impacts of Partial Cuts on Aboveground Carbon Stocks

Objectives: to verify if tree removal and subsequent carbon loss due to windthrow will

result in decreased aboveground carbon stocks in partially cut stands.

Hypotheses: stand live aboveground carbon stocks are expected to decrease as partial cut intensity increases, because the loss of trees will outweigh the growth of the remaining ones. In contrast, we hypothesized that stand deadwood carbon stocks will increase with harvest intensity, due to increased windthrow mortality. Windthrow mortality will be influenced by tree size and stand exposure, particularly in vulnerable areas such as skidding trail edges, heavily harvested zones, sites with low interspecific competition, topographically exposed locations, and areas with high wind incidence.

Windthrow Mortality Influenced by Natural Root Grafting in Boreal Jack Pine Forests

Objective: Determine if there is a relationship between natural root grafting and windthrow mortality in jack pine trees.

Hypotheses: it is expected that grafted trees would be less susceptible to uprooting than non-grafted trees, due to the greater anchorage provided by root grafts. In contrast, a higher proportion of stem breakage was anticipated among grafted trees compared to uprooting. Additionally, trees located closer to one another are expected to exhibit a greater frequency of root grafts.

Study sites and sampling protocol. The present thesis was conducted in the Abitibi-Témiscamingue region, Quebec, Canada. All the study sites are located in the boreal biome, within the balsam fir - white birch (*Betula papyrifera* Marsh.) bioclimatic domain (MRNF, 2023) (Fig. 5). The climate is classified as cold and humid, with a mean annual temperature of 1.5 °C (1981–2010, Amos station) and an average of 97 frost-free days per year. The growing season typically lasts between 81 and 100 days (Government of Canada, 2024). Mean annual precipitation totals 929 mm, of which 27 % falls as snow. Average monthly wind speeds range from 37 to 50 km/h over the same period (1981–2010) (Government of Canada, 2024).

The first (thinning shock and growth release) and the second (carbon stocks and windthrow mortality) chapters share the same site selection criteria and sampling

protocol, which was established in 2020 (Fig. 7). Three silvicultural treatments were chosen: control, thinning (30-35

% of basal area removal), and shelterwood (40-50 % of basal area removal), each replicated eight times. Thinning is oriented at reducing stand density to stimulate tree growth and improve timber yields, whereas shelterwood cuts are intended to facilitate regeneration, particularly of shade-tolerant species. Stands were selected based on the following criteria: location on esker-derived soils of fluvioglacial origin or on comparable sandy soils of glaciolacustrine origin, and a jack pine composition exceeding 60% of total stand basal area. On harvested stands (i.e., thinning and shelterwood), we attempted to select study sites with the same harvest year. However, due to the limited availability of suitable sites, we ultimately included stands in which harvesting occurred between 9 and 14 years before sampling. We also attempted to select stands with the same management approach. Nevertheless, in the study region, thinning seemed to be performed following a harvest from below, while shelterwood stands were showing signs of harvest from above. Control stands were chosen within natural forests with no documented history of silvicultural interventions. The stand selection process was guided by forest inventory data.

provided by the Quebec Ministry of Natural Resources and Forests (Government of Quebec, 2019). The thinning treatment was conducted in a strip pattern, where a 5-meter-wide skidding trail was completely cleared of trees. Using the articulated arm of a forest harvester, an additional 30–35 % of trees (with DBH > 9 cm) were selectively removed within a 5-meter zone on either side of each trail, with harvested trees preferentially belonging to the smaller DBH classes. Between these harvested zones, 6 to 8-meter-wide residual strips were left intact. The shelterwood treatment used the same equipment and a comparable layout but involved the removal of 40–50 % of all merchantable trees along the same lateral zones, with priority given to larger-diameter individuals.

The sampling protocol of the third chapter (natural root grafting) consisted of four sites (referred to as Excavation sites, Fig. 7) located within riparian buffer strips that were

selected in 2022. Riparian buffers were chosen due to their proximity to water bodies, which ensured a continuous water supply during the hydraulic excavation of root systems. Preference was given to forest strips adjacent to recent clear cuts to increase the likelihood of windthrow mortality and to obtain a greater number of well-preserved cross-sectional disks from dead trees. Sites with sandy and sloped soils were also prioritized, as these conditions facilitate both excavation and effective water drainage. Moreover, sites were considered as candidates for sampling if they presented all mortality types: snag, broken, and uprooted trees.

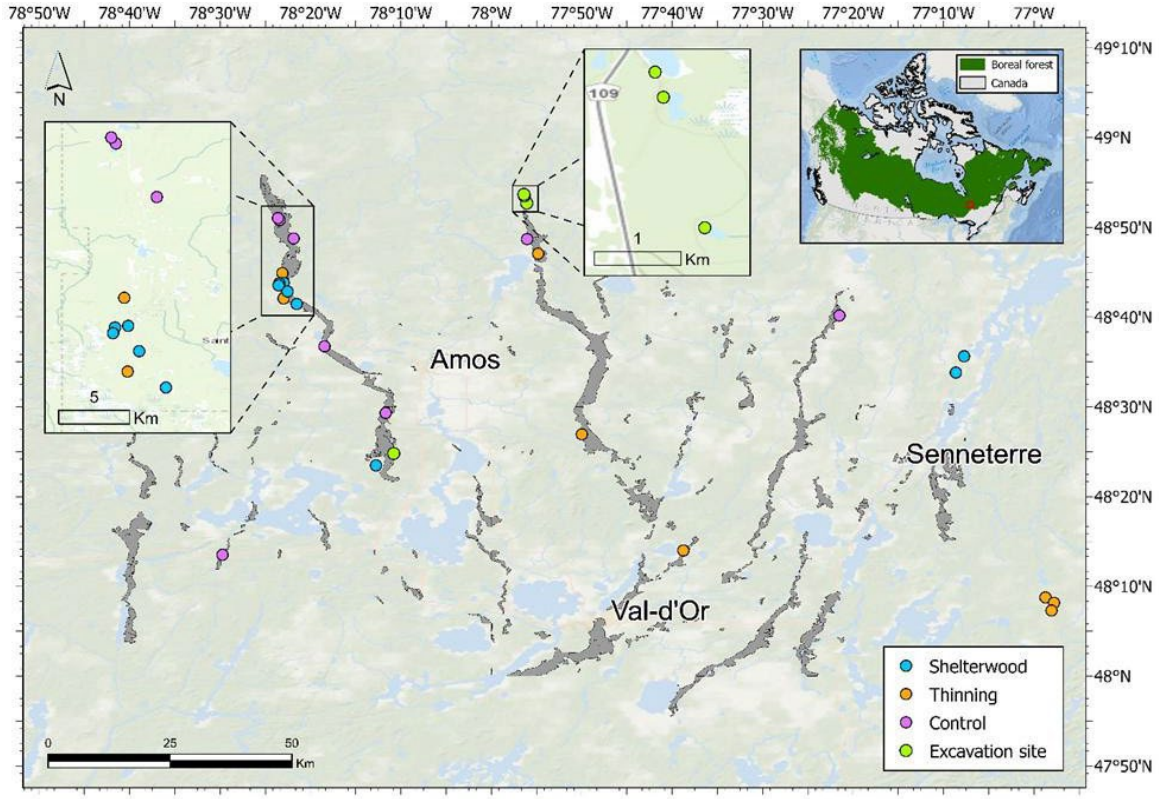

Figure 7
Location of all the study sites sampled in this thesis. Coordinate system: WGS 1984 North Pole LAEA Canada.
Sources: Eskers in Canada: Storrar et al (2014), Administrative boundaries: open.canada.ca, Basemap: ESRI basemaps. Map created using ArcGIS Pro 3.3.0 (ESRI, Redlands, United States).

Thesis outline. This PhD thesis started in January 2022. This research was performed within the GREMA (Groupe de recherche en écologie de la MRC Abitibi) research group at the Université du Québec en Abitibi-Témiscamingue (UQAT), with the support of the Centre d'étude de la forêt (CEF-CFR). It was conducted as part of a tailor-made PhD program in Forestry and Ecosystem Management.

This work is organized into three chapters. These chapters are formatted as individual articles intended for submission to peer-reviewed international journals.

Chapter I analyzes the growth release in residual jack pines following partial cuts of different harvest intensities. In addition, this chapter also determines if there is the presence of thinning

shock in jack pine esker forests, assesses if the thinning shock is related to a temporary alteration in stomatal behavior during the first years following harvest, through an analysis of alpha-cellulose $\delta^{13}C$. Lastly, this chapter analyzes the driving factors of the thinning shock presence, length, and intensity to better understand this tree growth phenomenon. A first internship was performed at the GEOTOP laboratory of the Université du Québec à Montréal (UQAM) under the supervision of Étienne Boucher to complete the necessary laboratory work for the alpha-cellulose extraction and the measurement of its $\delta^{13}C$. The interpretation of the tree growth $\delta^{13}C$ was developed during a second internship at the Swiss Federal Research Institute (WSL) under the supervision of Arun

K. Bose. This chapter has been submitted to Forestry: An International Journal of Forest Research, from Oxford Academic.

Chapter II assesses the impacts of partial cuts of different harvest intensities on the live aboveground carbon stocks and on the carbon stocks located in deadwood of the jack pine esker forests. In addition, this chapter analyzes the driver factors of the carbon gains experienced by residual trees 8 years following harvest and the driving factors of snag, broken, and stem breakage mortality on each treatment. This chapter has been published online in *Forest Ecology and Management*. Reference: Alcalá-Pajares, M., DesRochers, A., & Girona, M. M. (2026). *Impacts of partial cuts on aboveground carbon stocks in esker forests. Forest Ecology and Management*, 601, 123355. (Alcalá-Pajares et al., 2026)

Chapter III explores the influence of natural root grafting in jack pine residual stands in windthrow mortality, focusing on the effect of natural root grafting in tree uprooting and stem breakage likelihood. In addition, a complementary analysis of the relationship between root grafting frequency and distance among trees is also included in this chapter. This work was published in the journal *Trees: Structure and Function, from*

Springer. Reference: *Alcalá-Pajares, M., Montoro Girona, M., & DesRochers, A. (2025). Windthrow mortality influenced by natural root grafting in boreal jack pine forests. Trees, 39(3), 1-9.* (Alcalá-Pajares et al., 2025)

A general conclusion synthesizing the main findings, highlights the primary contributions of the research, discusses methodological limitations, and offers recommendations for future research.

1. THINNING SHOCK AND TREE GROWTH ANALYSIS FOLLOWING PARTIAL CUTS IN BOREAL FORESTS

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Résumé

Les coupes partielles sont considérées comme une alternative durable à la gestion traditionnelle dans la forêt boréale en raison de leur impact moindre sur la biodiversité, la structure et la régénération forestières. Cependant, la croissance des arbres stagne souvent pendant plusieurs années après les coupes partielles, un phénomène appelé « *choc de croissance* ». Cette étude a évalué les facteurs à l'origine du choc de croissance et de la reprise de croissance qui s'ensuit dans les peuplements dominés par le pin gris de l'ouest du Québec, au Canada. Notre plan expérimental comprenait trois traitements d'intensité de récolte (% d'enlèvement de la surface terrière): témoin (0 %), éclaircie (30 à 35 %) et coupe progressive (40 à 50 %). La croissance annuelle, la durée (c'est-à-dire le temps de retard) et l'intensité du choc de croissance sur la croissance et la composition isotopique $\delta^{13}C$ des cernes des arbres ont été analysées à l'aide d'approches dendrochronologiques. Le choc de croissance était 30 % plus fréquent chez les arbres situés à proximité des pistes de débardage (c'est-à-dire les chemins créés pour le transit des machines forestières servant à l'extraction du bois) et 10 % plus intense dans les peuplements de coupe progressive. Dans le traitement d'éclaircie et de la coupe progressive, la durée de la période de choc était respectivement de 7 % et de 25 % plus longue dans les 5 premiers mètres à partir des sentiers de débardage, comparativement aux arbres situés à l'intérieur des coupes. Huit ans après la récolte, la croissance radiale des arbres résiduels avait augmenté de 54 % dans les traitements d'éclaircie et de 29 % dans les traitements de coupe progressive par rapport au témoin, ce qui reflète probablement l'élimination des arbres plus grands et se traduit par une proportion plus élevée d'arbres résiduels plus petits, à croissance initialement plus lente, dans le traitement de coupe progressive. Pendant la période de choc de croissance, les valeurs $\delta^{13}C$ sont devenues plus négatives par rapport aux niveaux pré-récolte dans les deux traitements et ont continué à baisser par la suite, indiquant que la réduction de la croissance causée par le choc n'était pas due à une fermeture stomatique temporaire immédiatement après la récolte. Nos recherches remettent en question la relation suggérée entre le choc et la fermeture stomatique et soulignent l'importance de ce phénomène dans la compréhension et la prévision de la dynamique de croissance après la récolte.

Mots-clés : Forêt boréale, isotopes de carbone, dendrochronologie, gestion forestière, pin gris, récolte partielle.

Abstract

Partial cuts are considered a sustainable alternative to traditional management in the boreal forest because of their lower impact on forest biodiversity, structure, and regeneration. However, tree growth often stagnates for some years after partial cuts, a phenomenon labelled as "*thinning shock*". This study evaluated the factors behind thinning shock and the subsequent growth release in jack pine-dominated stands of western Quebec, Canada. Our sampling protocol included three harvest intensity (% basal area removal) treatments: control (0 %), thinning (30 – 35 %), and shelterwood harvesting (40 – 50 %). Annual growth, duration (i.e., delay-time), and intensity of thinning shock on growth and the $\delta^{13}C$ isotopic composition of tree rings were analyzed using dendrochronological approaches. Thinning shock was 30 % more frequent in trees closer to skidding trails (i.e., paths created for the transit of forest machinery extracting wood) and 10 % more intense in shelterwood stands. In the thinning treatment, the duration of the thinning shock period was 7 % longer within the first 5 meters from the trail, whereas in shelterwood treatments, it was 25 % when trees were growing at the same distances. Eight years post-harvest, residual tree growth increased by 54 % in thinning and 29 % in shelterwood treatments relative to the control, likely reflecting the removal of larger trees and resulting in higher proportions of smaller, initially slower-growing residual trees in the shelterwood treatment. During the thinning shock period, $\delta^{13}C$ values became more negative compared to pre-harvest levels in both treatments and continued to decline thereafter, indicating that the growth reduction caused by thinning shock was likely not due to a temporary stomatal closure immediately following harvest. Our research puts into question the suggested relationship between thinning shock and stomatal closure and highlights the importance of this phenomenon in the understanding and prediction of after-harvest growth dynamics.

Keywords: Boreal forest, carbon isotopes, dendrochronology, forest management, jack pine, partial harvest

1.1 Introduction

Partial cuts are a group of silvicultural treatments that harvest a proportion of the stems within a stand and are considered promising alternatives to clear cuts for the sustainable management of boreal forests (Thorpe and Thomas, 2007). Following harvest, residual trees experience an improvement in radial growth rates because of the reduction in tree competition for resources (Pamerleau-Couture et al., 2015; Barrette et al., 2018; Lemay et al., 2018). Consequently, greater improvements in tree growth rates have been registered with increasing harvest intensity (Mäkinen and Isomäki, 2004; Moulinier et al., 2015), and localized in trees growing near trails opened for forest machinery transit (i.e., skidding trails) (Genet and Pothier, 2013; Montoro Girona et al., 2017). Moreover, post-harvest growth trends have also been related to the harvest approach, with harvests selectively removing large-diameter trees (i.e., harvest from above) resulting in lower mean post-harvest tree growth rates when compared to those performed from below (Saarinen et al., 2020). In addition, the presence of a shared vascular connectivity throughout their roots (i.e., natural root grafts) has also been reported to reduce the magnitude of the growth response (Tarroux et al., 2010).

The tree growth response can be delayed, revealing a period of time, labelled by some authors as “thinning shock”, during which radial growth rates remain stable or decline for 1 to 7 years before any noticeable growth release occurs (Emmingham and Elwood, 1983; DeBell et al., 2002; Kneeshaw et al., 2002; Picchio et al., 2018). Thinning shocks have been observed after canopy openings created by road construction (Urban et al., 1994), following seed-tree cuts (Montoro Girona et al., 2016), thinning (Pukkala et al., 2002; Bebber et al., 2004; Vincent et al., 2009; Bose et al., 2014; Picchio et al., 2018; Nicoll et al., 2019), diameter-limit cutting (Bevilacqua et al., 2005; Thorpe et al., 2007; Gendreau-Berthiaume et al., 2012), or shelterwood cuts (Youngblood, 1991; Montoro Girona et al., 2016). Previous results have linked the thinning shock to a temporary shift in resource allocation toward root development, as evidenced by the observed increase in root growth during this period (Urban et al., 1994; Vincent et al., 2009; Nicoll et al., 2019). This shift would enhance tree anchorage under increased wind exposure and compensate for higher transpiration rates resulting from greater wind

penetration after stem removal (Urban et al., 1994; Vincent et al., 2009; Nicoll et al., 2019).

In addition, recent work has related the thinning shock to a stomatal closure triggered by increased temperature and vapour pressure deficit in the canopy microenvironment following harvesting (French et al., 2023). However, this hypothesis has largely been based on indirect evidence, and stomatal conductance during the delay in growth response has not been measured (French et al., 2023). Changes in stomatal conductance can be inferred from stable carbon isotope ratios ($\delta^{13}C$) recorded in annual tree rings (Dietrich et al., 2016). In C_3 plants, the enzyme Rubisco discriminates against the heavier carbon isotope (^{13}C) during CO_2 fixation (Farquhar et al., 1989; McDowell et al., 2003). When stomata close, internal CO_2 concentration decreases, leading to reduced ^{13}C discrimination and thus more positive $\delta^{13}C$ values in plant biomass (Siegwolf et al., 2023). Therefore, $\delta^{13}C$ provides an integrated proxy to evaluate whether stomatal closure occurred during thinning shock.

Our study assessed the thinning shock following partial cuts in boreal esker forests dominated by jack pine (Rudolph and Laidly, 1990). Eskers are sandy substrates created by subglacial streams (Boulton et al., 2009). Sandy soils act as natural filters, maintaining adequate surface and freshwater quality, which is of vital interest for local communities (Nadeau et al., 2015). In addition, freshwater ecosystems located next to eskers are characterized by distinct invertebrate and vertebrate communities (Hasan et al., 2023). Jack pine forests growing on eskers have historically been managed through clear cuts. However, concerns about the impacts of such silvicultural treatments on water chemistry (Jerabkova et al., 2011; Grosbois et al., 2023) and biodiversity (Lunde et al. 2025) have led to an increasing adoption of partial cutting practices in these forests. Despite this shift, the effects of partial cuts on the radial growth of jack pine trees established on esker soils have never been assessed. Understanding these effects is crucial for developing silvicultural prescriptions adapted to these sensitive environments.

This work aimed to assess the impact of partial cuts on growth release in residual jack

pine trees, to evaluate the occurrence of thinning shocks previously observed in jack pine trees (Moulinier et al., 2015), and to investigate the underlying causes and key drivers influencing the occurrence, intensity, and duration of these delays. We expected to find (1) longer and more intense thinning shocks with increasing harvest intensity as the stand environmental alterations are greater with greater density reductions, (2) thinning shocks in residual trees being related to a temporary reduction in stomatal conductance reflected by a temporary decrease in ^{13}C discrimination (i.e. less negative $\delta^{13}C$), and (3) more pronounced tree growth releases during the 8 yeas following harvest with increasing harvest intensity and in trees closer to the skidding trail due to the reduction in tree competition.

1.2 Materials and methods

1.2.1 Study area

The study area is located in the Abitibi-Témiscamingue region, Quebec, Canada (Fig. 8). This region is situated in the balsam fir - white birch bioclimatic domain, dominated by the previously mentioned species and by black spruce, trembling aspen, and jack pine (MFFP, 2021; MRNF, 2023). The climate is classified as cold and humid continental according to the Köppen-Geiger classification (Government of Quebec, 2012). The average annual temperature is 1.5 °C (1981–2010, Amos station), with 929 mm of average annual precipitation which 27 % falls in the form of snow (Government of Canada, 2024). The region experiences 97 frost-free days per year, and the growing season lasts between 81 and 100 days (Government of Canada, 2024). During the Wisconsinan glacial period, the Laurentide ice sheet covered much of eastern Canada (Dyke et al., 2002). As the ice sheet retreated, it left behind glacial features, including eskers, which are elongated, linear to curved sand and gravel deposits formed by glacial meltwaters (Storrar et al., 2014). These sandy and xeric soils are included in the arenosol category of the FAO-UNESCO soil classification system and are often dominated by jack pine (Starr and Lindroos, 2006; Hoffer and Tardif, 2009).

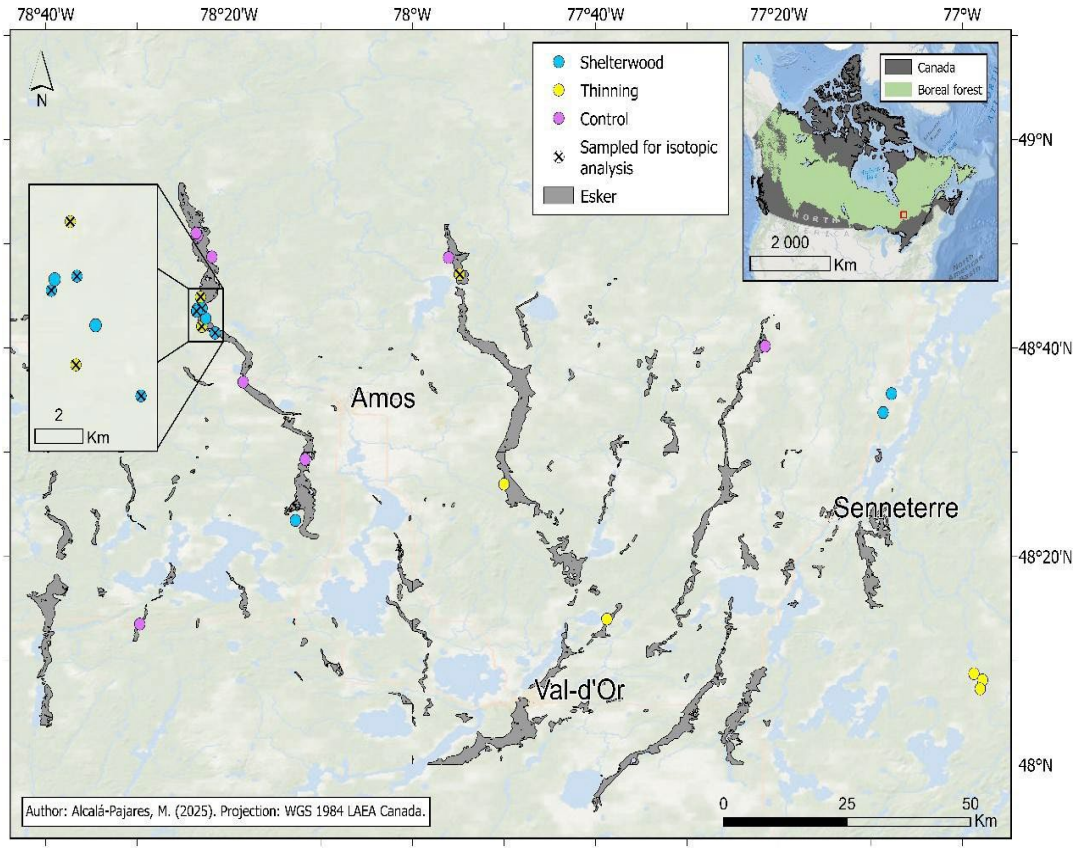

Figure 8
Locations of the study sites of the thinning shock chapter by silvicultural treatment and sampling in western Quebec, Canada.
The map was created using ArcGIS Pro 3.3.0 (ESRI, Redlands, United States).

1.2.2 Site selection and sampling protocol

In 2022, a sampling protocol involving 24 sites was established to assess the effects of different partial cut treatments. Site selection was based on substrate type, focusing on esker ecosystems characterized by glaciolacustrine and fluvioglacial soils, and on species composition, selecting jack pine-dominated (> 60 %) stands. The treatments were: thinning, shelterwood, and an untreated control, with eight replicate sites per treatment. The selection procedure was based on the data provided by forest inventories from the Ministry of Natural Resources and Forests of Quebec (Government of Quebec, 2019). During the site selection phase, we encountered challenges in identifying a sufficient number of sites for each partial cut treatment (i.e., thinning or shelterwood) sharing the same harvest year. Despite our efforts, the limited

availability of suitable sites led us to select sites with differing harvest years for each treatment from 2008 to 2013.

1.2.3 Silvicultural treatments

Two partial cut treatments were used in this study: commercial thinning and an irregular shelterwood system (Table 1). Thinnings are conducted to reduce stand density and enhance the growth and wood quality of residual trees, whereas shelterwood cuts aim at maintaining partial canopy cover to support and protect natural regeneration. Thinning operations were carried out in a strip layout. Entire tree removal (100 %) occurred along 5-meter-wide skidding trails, from which the articulated arm of a forest harvester reached an additional 5 meters on each side to selectively remove approximately 30–35% of trees with a diameter at breast height (DBH) greater than 9 cm, and thus leaving a partially cut strip (Fig. 9). Furthermore, 6–8-meter-wide uncut residual bands were left following the 5 meters of the partially cut strip (Fig. 9). The shelterwood treatment employed the same harvesting equipment and followed a comparable layout but involved the removal of 40–50% of all merchantable trees on both sides of the skidding trails. The greater proportion of codominant trees in the partially cut strip in the thinning treatment and the greater proportion of suppressed trees in the partially cut strip of shelterwood treatment suggest that thinning was performed from below, harvesting small-diameter trees, while the shelterwood treatment followed a from-above harvest, targeting trees from the greater DBH classes (Annexe A). In both treatments, logs were transported with forest forwarders, and no post-harvest treatment was performed.

Table 1
Description of study sites for the thinning shock chapter.
ID: Site ID, Elev. = Elevation, MAT = mean annual temperature, MAP = mean annual precipitation, DBH = diameter at breast height, JP = jack pine.

ID	Treatment	arvest year	Elev. (m)	MAT (°C)	MAP (mm)	Stand age (years)	Density (trees/ha)	DBH (cm)	H (m)	Species (%)	
										JP	Rest
C1	Control	-	337	0.5	882	100-111	900	18.4	17.2	93	7
C2	Control	-	330	0.9	891	47-56	800	16.8	15.5	77	23
C3	Control	-	326	0.9	891	54-57	883	20.3	20.1	84	16
C4	Control	-	342	0.5	876	56-71	1333	15.7	19.4	61	39
C5	Control	-	333	0.5	876	57-73	683	19.9	17.8	92	8
C6	Control	-	339	1.1	900	85-91	1300	19.0	18.4	80	20
C7	Control	-	354	1.3	887	70-75	1350	16.6	21.0	61	39
C8	Control	-	333	0.8	897	68-83	800	16.8	14.9	91	9
E1	Thinning	2011	337	0.7	891	96-105	633	18.3	16.3	95	5
E2	Thinning	2011	356	1.3	929	59-63	667	18.8	18.5	96	4
E3	Thinning	2009	337	0.5	882	63-79	933	17.7	17.1	97	3
E4	Thinning	2010	351	1.3	929	58-61	1033	17.2	17.6	76	24
E5	Thinning	2013	327	0.7	891	53-64	1133	12.0	10.9	97	3
E6	Thinning	2010	376	1.3	929	57-66	833	20.8	19.9	73	27
E7	Thinning	2009	362	1.1	911	61-64	1017	15.7	14.3	92	8
E8	Thinning	2008	328	1.4	903	51-58	533	19.1	18.3	83	17
S1	Shelterwood	2011	336	0.5	882	72-79	633	16.5	16.7	100	0
S2	Shelterwood	2011	341	0.5	882	84-99	633	22.5	18.9	96	4

S3	Shelterwood	2011	339	0.7	891	66-78	650	15.6	13.3	100	0
S4	Shelterwood	2011	338	0.5	882	74-98	867	15.3	15.3	89	11
S5	Shelterwood	2011	345	1.3	885	91-97	550	17.9	18.6	74	26
S6	Shelterwood	2010	320	1.0	939	99-104	917	16.5	15.7	78	22
S7	Shelterwood	2011	334	0.5	882	68-79	750	16.1	16.3	89	11
S8	Shelterwood	2010	318	1.0	939	100-103	833	15.9	16.4	72	28

Figure 9
Sampling protocol for the thinning shock chapter
(A) corresponds to a drone view of partial cut site and (B) a schematic representation of the spatial harvest pattern and the plot location in a partial cut site.

1.2.4 Sampling protocol

One 600 m² (10 × 60 m) plot was established per site, perpendicularly oriented to the skidding trail. For all commercial trees (DBH > 9 cm) in the plot, we noted the species, DBH, spatial position as the distance to the skidding trails, and tree social status (suppressed, co-dominant, or dominant). To measure competition, a subsample of 8 trees per plot was randomly selected, half in the first 5 meters from the skidding trail (forest edge) and the other half in the 6-8 m wide forest interior section (Fig. 9). This subsample was selected to reduce the time invested in forest

inventories due to the even-aged structure of our stands. Additionally, tree height (Vertex IV, Haglöf Sweden AB, Långsele, Sweden / Suunto Clinometer, Suunto Oy, Vantaa, Finland), distance to the closest skidding trail, and competition measurements were taken from the mentioned subsampled trees. Competition was estimated by the Hegyi Index (CI_i, Equation 1), so that greater values reveal greater inter-specific competition (Biging and Dobbertin, 1995). A 4-meter radius was established around each tree to estimate competition, noting the diameter of the study tree (DBH_i), the diameter of all the trees included in the radius (DBH_j) with a height above breast height (1.3 m), and the distance from each tree to the study tree ($Distance_{ij}$).

$$CCCC_{ii} = \sum_{jj=1}^{mm} \frac{DDBBBB_{jj}}{DDiiDDDDDDmmDDDDiijj} \times \frac{1}{DDBBBB_{ii}} \quad (1)$$

The Hegyi index was chosen because it strikes a good balance between simplicity and accuracy, providing results comparable to those obtained with more complex indices (Holmes and Reed 1991). The radius length was chosen to be included within the maximum distance at which the strongest correlations between growth and competition have been reported for pine stands (Pukkala and Kolström 1987), and because a similar radius has been selected in previous work focused on harvested stands with similar ranges in post-harvest tree density (Montoro Girona et al. 2019).

1.2.5 Dendroecological data collection and preparation

To assess radial growth, one increment core was extracted at breast height (1.3 m) from 36 trees per plot during the summers of 2022 and 2023, making a total of 864 cores from 24 sites. As all trees within each plot originated from the same fire event, a subsample of trees was cored near the root collar to estimate stand age. Specifically, 8 trees per plot were selected for age determination (n = 192), following sample sizes for age estimation in even-aged jack pine stands registered in the literature (Howard et al., 2004). All cores were extracted using either a manual increment borer or a cordless drill equipped with a specialized attachment compatible with a 5.15 mm diameter increment borer (Haglöf Sweden AB, Långsele, Sweden), which enhanced both the speed of extraction and the quality of the cores obtained (Gärtner et al., 2023; Fonti et al., 2025). The cores were air-dried, mounted on wooden laths, sanded using progressively finer grits of sandpaper (600-1000 grain), and then scanned with an EPSON Expression 12000XL scanner (SEIKO EPSON CORP., Owa, Japan). Tree rings were measured and analyzed using CooRecorder (Version 9.8.0, Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Cross-dating

and tree-ring measurements were verified using Past5 (Version 5.0.620, SCIEM). Raw ring-width series were analyzed with the dplR R package (Bunn, 2008).

A third set of increment cores was collected at breast height in October 2023 using a wider 12 mm increment borer (Haglöf Sweden AB, Långsele, Sweden) to obtain sufficient biomass for cellulose extraction and subsequent isotopic analysis. A subsample of 6 sites was selected, with 3 sites belonging to the thinning treatment and

the other 3 to the shelterwood treatment. At each site, two trees were randomly selected within the forest edge (i.e., the first 5 meters from the skidding trail), and two additional trees were randomly selected from the forest interior. One core was extracted from each tree (n = 24). Cores were stored individually in plastic holders inside a freezer to prevent fungal growth. The frozen samples were dried for 72 hours at 65 °C before performing the dendrochronological analysis. The surface of the dried samples was cut with a core-microtome for better tree-ring visualization (Bladon et al., 2007; Gärtner and Nievergelt, 2010). The wood cores were then scanned (EPSON Expression 12000XL, SEIKO EPSON CORP., Owa, Japan), cross-dated using CooRecorder (Version 9.8.0, Cybis Elektronik & Data AB, Saltsjöbaden, Sweden), and verified using Past5 (Version 5.0.620, SCIEM).

Due to extremely narrow tree rings for some post-harvest years (e.g., thinning shock years), we decided to work with tree-ring blocks (Loader et al., 2007). A before-harvest period, thinning shock period, and the period following the thinning shock (i.e., the long-term gain period) were delimited for each increment core. The limits of each period were determined according to the results of the cross-dating step. Tree-ring blocks were visualized with a binocular microscope and extracted with a razor blade. The before-harvest period comprised the 10 years preceding harvest. Thinning shocks of varying durations (1 to 7 years) were observed. This resulted in different numbers of tree rings being included in the tree-ring blocks for the thinning shock and long-term gain periods. No pointer years (i.e., abrupt growth increases or declines due to biotic or abiotic disturbances) were detected during this period. The wood contained in each block was stored in 2 mL Eppendorf capsules and then ground with an ultra-centrifugal mill (Mixer Mill MM400, Retsch GmbH, Haan, Germany). Alpha-cellulose was extracted following the procedure of the GEOTOP-UQAM laboratory (Gibson et al., 2022), and 0.4 mg samples were packed into tin capsules for $\delta^{13}C$ measurements. Alpha-cellulose samples were analyzed with an isotope ratio mass spectrometer (IsoPrime100, Elementar UK Ltd., Cheadle, UK) coupled with an elemental analyzer (Vario MicroCube, Elementar UK Ltd., Cheadle, UK). All isotope measurements were conducted at the GEOTOP-UQAM facilities at a precision (standard deviation) of ± 0.3

‰ and were referenced to Vienna Pee Dee Belemnite (VPDB).

1.2.6 Data analyses

To ensure clarity, the statistical analysis section is organized into three subsections, each corresponding to a specific research objective. The first subsection investigates the main drivers of the thinning shocks. The second subsection focuses on the analysis of the $\delta^{13}C$. Lastly, the third subsection examines radial growth over the eight years following harvest.

All models included in the following subsections were fitted using the lme4 package (R Development Core Team, 2022), with *p*-values added using the lmerTest package (Kuznetsova et al., 2015). Normality and homogeneity of residuals were checked, and square root transformations were applied when needed. Model selection was based on Akaike's Information Criterion (AIC) using the AICcmodavg package (Mazerolle, 2006), R^2 values were estimated with the MuMIn package (Barton and Barton, 2015), and the most influential variables of each model were estimated through a standardization of the model coefficients using the effectsize package (Ben-Shachar et al., 2020).

1.2.7 Drivers of the thinning shock

All thinning shock metrics were derived from raw radial growth measurements from increment cores. The thinning shock was characterized using three indicators: presence, intensity, and delay time (i.e., duration, in years, of the thinning shock). A tree ring will be considered as part of the thinning shock if it shows a lower or similar width relative to the average width of the 10 tree rings (i.e., years) preceding harvest. Any annual growth exceeding the pre-harvest mean was considered an improvement and therefore not part of the thinning shock, with no additional thresholds applied to account for interannual variability. For trees exhibiting a thinning shock, the start of the thinning shock period was the earlywood of the year after the harvest. The end of the thinning shock was identified as the first post-harvest year in which radial growth exceeded the 10-year pre-harvest average.

The variable thinning shock presence was a binary variable indicating whether each tree

exhibited at least one year of thinning shock (0 = absence, 1 = presence). Chi-squared tests were used to detect significant ($p < 0.05$) differences among treatments in the proportion of trees exhibiting a thinning shock, with the test chosen because the response variable is binary and categorical comparisons were being made (Tallarida and Murray, 1987). Expected frequencies in each category were checked to ensure that all cells met the minimum threshold (≥ 5) required for the Chi-squared test, and all observations were independent. To assess the variables explaining the presence of thinning shock, we fitted a generalized linear mixed model with the thinning shock presence as a binary response. The model included distance, the mean radial growth of the 10 years before harvest, the treatment, and their interaction as fixed effects. In addition, the site was included as a random effect to account for the hierarchical structure of the data.

The variable delay time was defined as the number of years considered as part of the detected thinning shock. The variable intensity represents the severity of radial growth reduction during the thinning shock. It was calculated by dividing the average radial growth during the 10 years before harvest by the average growth during the thinning shock. Therefore, this variable is dimensionless, and higher values represent more intense reductions in radial growth during the thinning shock. The long-term gain period began with the first ring exceeding the average of the 10 years before harvest and lasted until the last complete ring. This implied that the number of years included in the long-term gain period varied depending on the number of years included in the thinning shock.

One-way ANOVA was used to compare the mean intensity and delay time among treatments. Linear mixed models were also used to evaluate the variables behind the intensity and delay time of the thinning shock. The distance to the skidding trail, average growth before harvest, treatment, and the interaction between distance and treatment were considered as fixed effects, while site accounted for a random effect. A Wilcoxon paired test was performed to detect differences in the delay-time of the thinning shock among partial cut treatments.

1.2.8 $\delta^{13}C$ during the thinning shock

Values of alpha-cellulose $\delta^{13}C$ were corrected for Suess effect (i.e., changes in atmospheric abundance of ^{13}C isotopes due to anthropogenic activities) (Keeling, 1979) using the public access data of monthly $^{13}C/^{12}C$ concentrations from the Mauna Loa Observatory, USA. The corrections of the $\delta^{13}C$ of each tree-ring ($\delta^{13}C_{alpha\text{-}cellulose}$) were performed using Equation 2 (McCarroll et al., 2009), in which $\delta^{13}C_{atm}$ is the isotopic atmospheric composition for the year in which a tree ring was formed, and $\delta^{13}C_{pre}$ is the pre-industrial $\delta^{13}C$ value of -6.4 ‰. Therefore, the values analyzed in this manuscript correspond to corrected $\delta^{13}C$ ($\delta^{13}C_{corr}$).

$$\delta^{13}C_{corr} = \delta^{13}C_{alpha\text{-}cellulose} - (\delta^{13}C_{atm} - \delta^{13}C_{pre}) \quad (2)$$

The model assessing the explanatory variables behind $\delta^{13}C_{corr}$ included tree height, distance to the skidding trail, social status, period (before harvest, thinning shock, long-term gain), and treatment as fixed effects. Given the hierarchical structure of our data, we included random effects to account for variability at different levels. Specifically, we included Tree nested within Site (1 | Site/Tree). This structure accounts for potential site-level effects, allowing us to separate variation among trees from variation among sites. In addition, the described random factor accounts for repeated measurements of $\delta^{13}C$ for the same tree across the three periods: before-harvest, thinning shock, and growth release periods.

A set of 34 LMMs, including global and null models, was considered, grounded in ecological theory (Anderson and Burnham, 2002). The models differed in the combination and complexity of fixed effects considered: some tested single predictors (e.g., tree height, DBH, age, competition, social status, treatment, period or distance to skidding trails), others included additive effects of multiple variables, and several incorporated biologically justified interactions (e.g., competition and distance to trails) (Annexe A). When constructing models with multiple additive predictors or interaction terms, we avoided including variables that are theoretically or empirically correlated

(e.g., DBH and height) to prevent multicollinearity and ensure more reliable interpretation of model parameters.

Radial growth 8 years following harvest

We analyzed and modelled post-harvest differences in radial growth and basal area increment (BAI) using data from the 8 years following harvest. This 8-year period encompassed both the thinning shock and long-term-gain phases described above. For each site, the harvest year was designated as year 0. Each harvested site was paired with a control site, using the harvest year as the reference point for assigning year 0 to the corresponding control. Random pairing was justified by the lack of significant differences in environmental variables between sites. To evaluate the impacts of treatments on tree growth, linear mixed-effect models were used, including the treatment, year, and their interaction as fixed effects, while random effects were the paired control site, site, and tree, with the tree nested within the site and site within the pair (1|Pair/Site/Tree). Growth differences between edge and interior trees were assessed using Wilcoxon paired tests or t-tests, depending on normality (Zimmerman, 1996). Wilcoxon paired tests were also used to analyze the differences in competition levels between edge and interior trees per treatment and between treatments.

1.3 Results

1.3.1 Thinning shock parameters

Thinning shocks were 182.4 % and 329.9 % more frequent in the thinning and shelterwood treatments, respectively, when compared to their paired controls (Table 2).

Table 2
Mean proportion of trees showing thinning shocks per treatment compared to the control paired to each treatment.

Treatment	Proportion (%)	Std. Dev	Std. Error	Lower 95% CI	Upper 95% CI
Controls paired to Thinning	13.5	10.2	3.6	5.0	22.0
Thinning	38.12	12.1	4.3	28.0	48.2
Controls paired to Shelterwood	12.8	10.6	3.8	4.0	21.7
Shelterwood	54.9 44.5	12.4 65.3	4.4		

The thinning shock was 30 % more frequent in the shelterwood than in the thinning treatment ($\chi^2(1) = 11.15$, $p < 0.01$, Fig. 3 A). Following the treatment, the distance to skidding trails was one of the most influential variables, with the thinning shock being more likely to occur in trees located closer to the skidding trail ($p < 0.05$, Table 3, Annexe A), with 49 % of edge trees (0 to 5 meters) experiencing shocks, compared to 44 % for interior trees (> 5 meters) ($p < 0.05$, Fig. 3 B). The shortest delay time was 1 year, while the longest lasted for 7 years (Fig. 3 C). Thinning shocks were similar ($p > 0.05$) among treatments, lasting on average 2.46 and 2.88 years in the thinning and shelterwood treatments, respectively (Fig. 3 D).

The interaction between treatment and distance to skidding trails was the predictor that had the greatest influence on the delay time, followed by treatment alone. In the thinning treatment, edge trees exhibited thinning shocks that lasted 2.5 years in the

edge (0 to 5 meters) and 2.4 years in the interior (> 5 meters), which implies that in the thinning treatment, edge trees showed 7 % longer shocks in the edge compared to the forest interior trees (p > 0.05, Figure 3 E, Table 3, Annexe A). Conversely, in the shelterwood treatment, edge trees revealed thinning shocks that lasted from 2.6 years in the edge and 3.3 years in the interior (p > 0.05, Figure 3 E, Table 3, Annexe A). This implied that in the shelterwood treatment, edge trees presented 25 % shorter thinning shocks compared to those from interior trees (p > 0.05, Fig. 3 E, Table 3).

The treatment was the most influential predictor of the intensity of the thinning shock, with the thinning shocks being 10 % more intense in the shelterwood compared to the thinning treatment (p_{RG}< 0.05, p_{BAI} < 0.01, Fig. 3 F, Table 3, Annexe A).

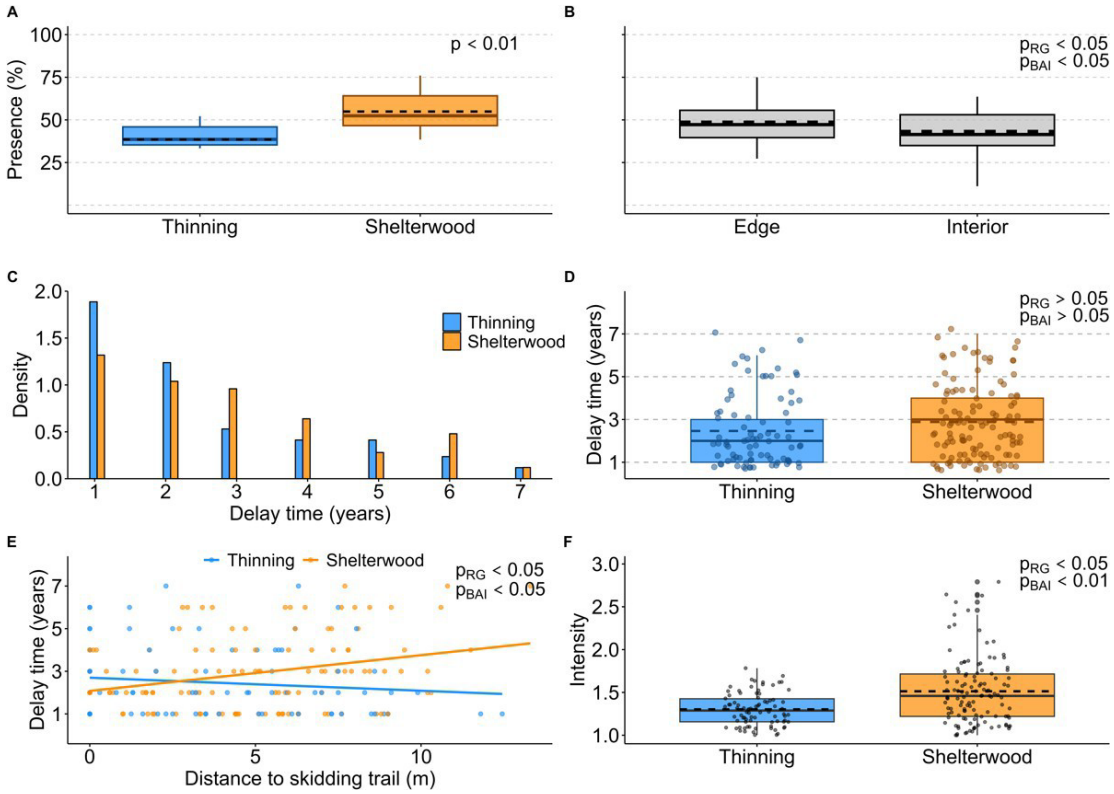

Figure 10
Average proportion of trees showing thinning shocks per treatment (A). Factors influencing the thinning shock presence (B), delay time (E), and intensity (F). Distribution of thinning shocks across treatments, showing the density of observations for each treatment (C). Average delay time per treatment (D).

Dashed lines in the boxplots represent the group means. Significant influences found when including radial growth in the models are represented by "p_{RG}", while those obtained when basal area increment was included are represented by "p_{BAI}".

Table 3
Summary table showing the *p*-values for the models analyzing thinning shock presence, delay time, and intensity.
Statistics, coefficients, confidence intervals, and R-squared values are included in Annexe A.

Response variable	Growth metric	Parameter		*p*-value
Presence	Radial growth	Intercept		0.49
		RG_{BH}		0.53
		Treatment: Shelterwood		0.41
		Distance Shelterwood	*	0.14
		Distance		**< 0.05**
	BAI	Intercept		0.44
		BAI_{BH}		0.43
		Treatment: Shelterwood		0.40
		Distance Shelterwood	*	0.15
		Distance		**< 0.05**

Delay time	Radial growth	Intercept		**< 0.01**
		Distance	0.54	
		RG_{BH}	0.33	
		Treatment: Shelterwood	0.41	
Distance * Shelterwood			**< 0.05**	
BAI		Intercept		**< 0.01**
Distance				0.56
BAI_{BH}				0.28
Treatment: Shelterwood			0.35	
Distance * Shelterwood			**< 0.01**	

Intensity	Radial growth	Intercept	**< 0.01**	
Distance				0.55
RG_{BH}				0.18
Treatment: Shelterwood			**< 0.05**	
Distance * Shelterwood			0.78	
BAI		Intercept		**< 0.01**
Distance				0.48
BAI_{BH}				0.17
Treatment: Shelterwood			**< 0.01**	
Distance * Shelterwood			0.80	

1.3.2 $\delta^{13}C$ during the thinning shock

The values of $\delta^{13}C_{corr}$ revealed a decreasing trend in both treatments, being more negative in the thinning shock period compared to the before harvest period, and more negative in the long-term gain period compared to the thinning shock period ($p < 0.01$, Fig. 4 C, D, Table 4). The $\delta^{13}C_{corr}$ signal in the thinning treatment revealed that average $\delta^{13}C_{corr}$ values were 0.11 ‰ (0.45 %) lower in the thinning shock compared to the before-harvest period, while average $\delta^{13}C$ values were 0.18 ‰ (0.75 %) lower in the long-term gain period compared to those from the thinning shock (Fig. 4 C). Moreover, the $\delta^{13}C_{corr}$ signal in the shelterwood treatment revealed that average $\delta^{13}C_{corr}$ values were 0.34 ‰ (1.40 %) lower in the thinning shock compared to the before-harvest period, while average $\delta^{13}C$ values were 0.15 ‰ (0.62 %) lower in the long-term gain period compared to those from the thinning shock period (Fig. 4 D). The selected model also exposed that values of $\delta^{13}C$ increased with increasing tree height ($p < 0.01$, Table 4, Fig. 5). Tree height was the most influential predictor with 71 % of total importance compared to the period (29 %).

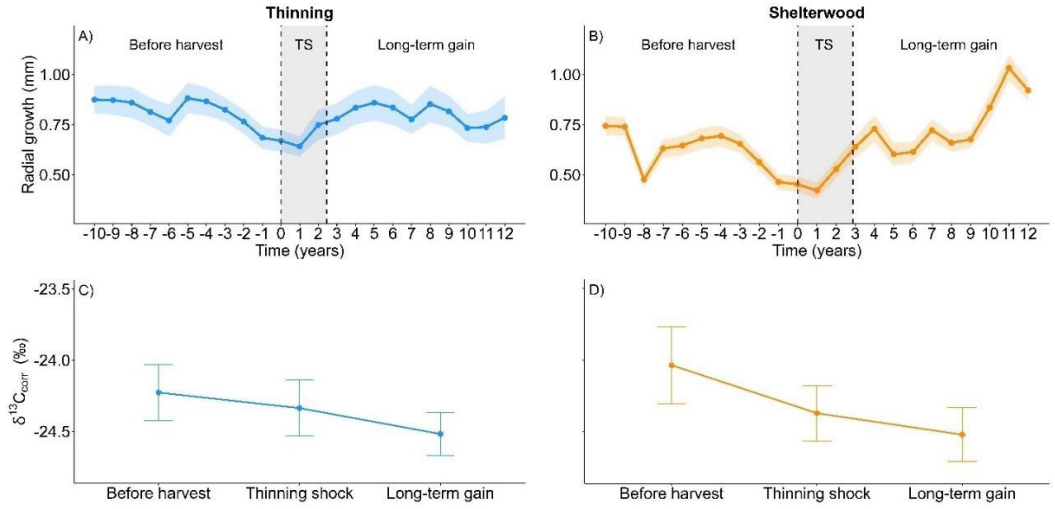

Figure 11
Raw radial growth (A and B), and mean $\delta^{13}C_{corr}$ (‰) values with standard error of subsample trees per period (C and D).
Vertical dashed lines represent the harvest year (t = 0) and the average last thinning shock year (TS) of subsample trees of each treatment. Shaded areas surrounding each growth curve represent the standard error (SE).

Table 4
Parameters, coefficients, and confidence intervals (CI) for the chosen linear mixed model for assessing the differences in $\delta^{13}C$.
σ1: standard deviation of the random intercept for trees nested within sites. σ2: standard deviation of the random intercept for site. σ3: residual standard deviation. Variance explained by the fixed effects alone (R^2_m): 44.1 %. Variance explained by both fixed and random effects (R^2_c): 80.2 %.

Parameter	Coefficient (β)	Std. Dev	Std. Error	*p*-value	Lower 95% CI	Upper 95% CI
σ_1		0.44	-	-	0.31	0.62
σ_2		0.00	-	-	0.00	0.36
σ3		0.33	-	-	0.28	0.41
Intercept	-29.32	-	0.71	**< 0.01**	-30.76	-27.82
Height	0.22	-	0.04	**< 0.01**	0.12	0.31
Period: thinning shock	-0.38	-	0.09	**< 0.01**	-0.92	-0.55
Period: long-term gain	-0.73	-	0.09	**< 0.01**	-0.57	-0.19

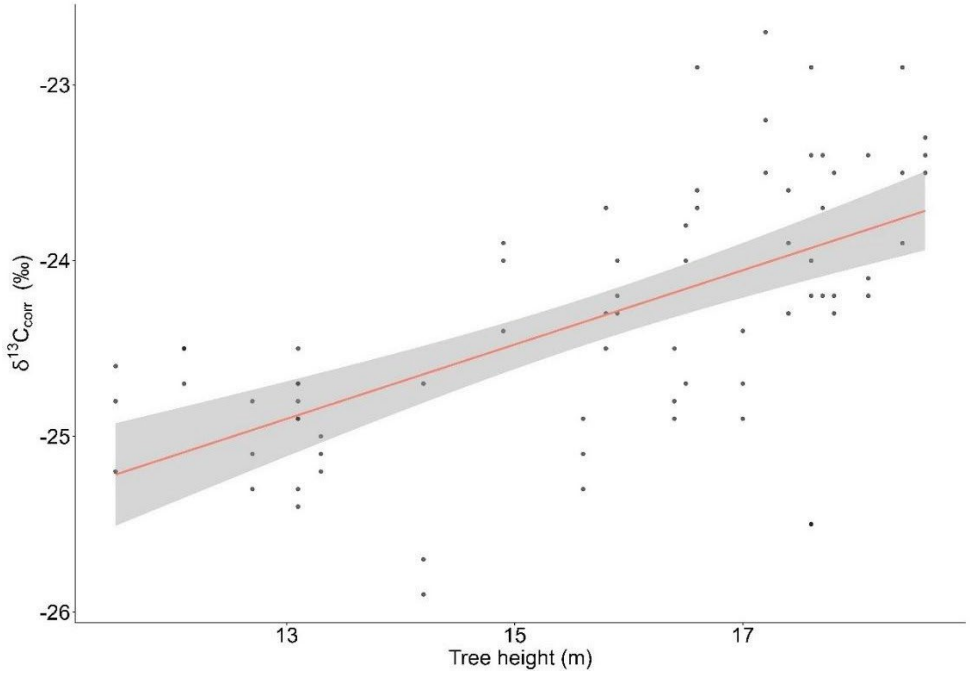

Figure 12
Relationship between tree height and alpha-cellulose δ¹³Ccorr values with a fitted linear trend and 95 % confidence interval.

1.3.3 Growth response of residual trees

In the first year after harvest (year 1), trees in thinning sites exhibited higher radial growth rates and similar basal area increment compared to control trees. In contrast, trees in shelterwood stands revealed lower growth rates compared to control trees (year 1, Fig. 13, Table 4). Over the entire 8-year post-harvest period, however, trees from the thinning and shelterwood treatments registered greater average radial growth rates than those from control stands. On average, trees in thinning and shelterwood sites showed 54 % and 29 % greater ring-width growth, respectively, compared to control trees during the 8 years following harvest ($p < 0.05$, Fig. 13 B, Table 4). Likewise, mean BAI was 30 % higher in thinning and 9 % higher in shelterwood treatments relative to the control ($p < 0.01$, Fig. 13 B).

Table 5
Parameter estimates, coefficients, and 95% confidence intervals (CI) from the linear mixed-effects model of radial growth and BAI.

….. β: coefficient; σ_1: standard deviation of random intercept for Tree nested within Site and Pair; σ_2: standard deviation of random intercept for Site/Pair; σ_3: standard deviation of random intercept for Pair; σ_4: residual standard deviation. R^2_m: marginal R^2 (variance explained by fixed effects); R^2_c: conditional R^2 (variance explained by fixed and random effects).

Parameter	β	Std. Dev	Std. Error	p-value	Lower 95% CI	Upper 95% CI
Radial growth: R^2_m : 7.31 %, R^2_c : 79.74%						
σ_1	-	0.221	-	-	0.21	0.23
σ_2	-	0.075	-	-	0.05	0.10
σ_3	-	9.1e-06	-	-	0.000	0.06
σ_4	-	0.123	-	-	0.12	0.13
Intercept	0.708	-	0.022	**< 0.01**	0.67	0.75
Shelterwood	-0.083	-	0.037	**< 0.05**	-0.13	0.000
Thinning	0.107	-	0.038	**< 0.01**	0.03	0.18
Year	-0.012	-	9.0e-04	**< 0.01**	-0.02	-0.01
Year * Shelterwood	0.037	-	0.002	**< 0.01**	0.03	0.04
Year *	0.011	-	0.002	**< 0.01**	0.00	0.01

Thinning

Basal area increment (BAI): R^2_m = 3.22 %, R^2_c = 83.84 %

σ_1	-	5.856	-	-	5.58	6.15
σ_2	-	1.695	-	-	1.06	2.26
σ_3	-	0.000	-	-	0.00	0.96
σ_4	-	2.729	-	-	2.68	2.77
Intercept	16.002	-	0.517	**< 0.01**	15.01	17.00
Shelterwood	-3.259	-	0.883	**< 0.01**	-4.96	-1.56
Thinning	0.843	-	0.898	0.358	-0.89	2.57
Year	-0.226	-	0.020	**< 0.01**	-0.27	-0.19
Year * Shelterwood	0.828	-	0.035	**< 0.01**	0.76	0.90
Year * Thinning	0.318		0.035	**< 0.01**	0.25	0.39

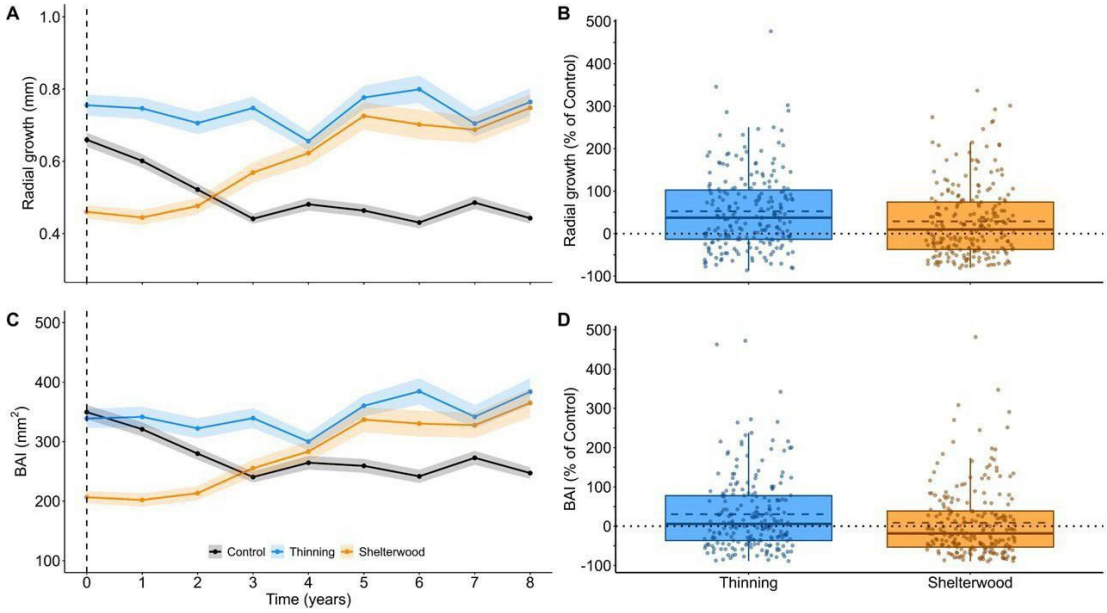

Figure 13
Mean radial growth (A, B) and basal area increment (C, D) following harvest. Vertical dashed lines represent the harvest year (t = 0), and shaded areas correspond to the standard error (SE). Radial growth (B) and BAI (D) as a proportion of the mean of the control 8 years following harvest, represented by the horizontal dashed line at 0. Dashed lines inside the boxplots represent the group mean.

When assessing the differences in tree growth between edge and interior trees 8 years following harvest, we found that in the thinning treatment, edge trees grew 0.16 mm/year (24 %) and 101,01 mm^2/year (35 %) more than interior trees (Fig. 7 A, B). Furthermore, in the shelterwood treatment edge trees grew 0.17 mm/year (30 %) and 96,86 mm^2/year (38 %) more than interior trees during the 8 years after harvest (Fig. 7 C, D). Differences in radial growth rates between edge and interior trees were detected starting in the fourth year after harvest for both the thinning and shelterwood treatments (Fig. 7 A, C). Furthermore, differences in basal area increment (BAI) were observed from the third post-harvest year in both treatments (Fig. 7 B, D).

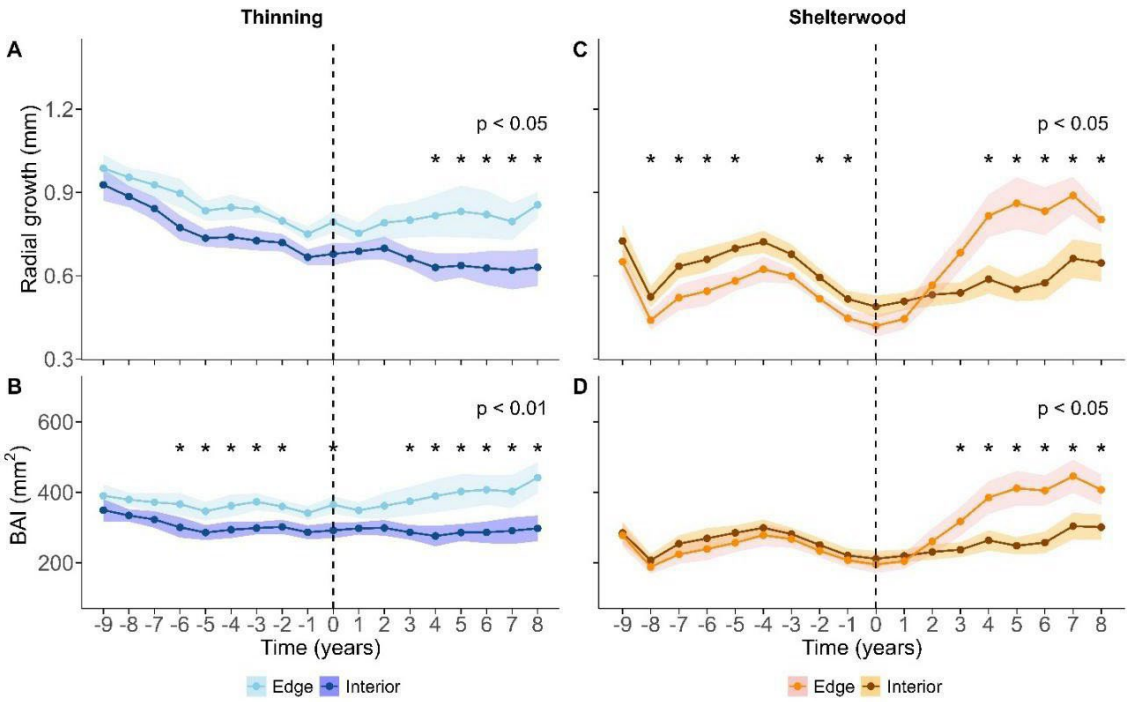

Figure 14
Radial growth and basal area increment (BAI) for the tree position (edge and interior trees) before and after thinning (A, C) and shelterwood (B, D). Vertical dashed lines represent the harvest year (t = 0). Shaded areas represent the standard error (SE). Lighter lines correspond to edge trees (i.e., trees located ≤ 5 meters from the skidding trails) while darker lines represent interior trees (i.e., trees located > 5m from the skidding trails. Asterisks (*) represent annual differences found among edge and interior trees.

1.4 Discussion

1.4.1 Thinning shock

Our results revealed lower $\delta^{13}C$ values during the thinning shock period compared to pre-harvest years. This trend toward more negative $\delta^{13}C$ values suggests that stomatal closure was unlikely behind the thinning shock and points toward a maintained or even enhanced CO_2 assimilation following harvest. Since $\delta^{13}C$ reflects the balance between stomatal conductance and net photosynthesis, more negative values may indicate either increased stomatal conductance with no change in net photosynthesis or a constant stomatal conductance with a decrease in net photosynthesis (Cernusak et al., 2013; Siegwolf et al., 2023). While we did not measure $\delta^{18}O$ in tree rings, nor source water and atmospheric $\delta^{18}O$, or ambient humidity, which would help distinguish

between these mechanisms (Roden and Siegwolf, 2012), the observed $\delta^{13}C$ patterns do not suggest a reduction in stomatal conductance. This interpretation is supported by previous findings in jack pine stands managed with similar harvest intensities (30–50%), which reported stable photosynthetic efficiency following harvest (Goudiaby et al., 2011).

We defined the thinning shock period as the years following harvest during which radial growth remained at or below the average of the 10 years prior to harvest, allowing us to distinguish between pre-harvest, thinning shock, and long-term gain phases. Radial growth declined notably in the first post-harvest year and remained lower than the pre-harvest average throughout the thinning shock period. This decline in stem growth during the thinning shock period overlaps with the more negative $\delta^{13}C$ values during the same years, suggesting an increase in stomatal conductance. This apparent mismatch may indicate that trees were not water-stressed following harvest, and that fixed carbon was likely allocated to sinks other than the stem. This contradicts our hypothesized relationship between the thinning shock and a temporary stomatal closure and challenges previous assumptions (French et al., 2023).

One possible explanation is a reduction in the photosynthetic-to-non-photosynthetic tissue ratio following harvest, potentially associated with root grafting. In such cases, assimilates may have been redirected to support the root system biomass of removedbut previously grafted neighbouring trees. This explanation is substantiated by consistent findings of reduced post-thinning growth in grafted jack pines due to carbon being diverted to maintain the root systems or stumps of harvested trees (Tarroux et al., 2010). Alternatively, in the absence of root grafts, a temporary reduction in stem growth could be related to resource allocation to the root systems to increase stem anchorage and improve nutrient uptake. While root growth was not directly measured in this study, previous research has shown increases in coarse root development overlapping with the period showing a delay in the growth response (Urban et al., 1994; Kneeshaw et al., 2002; Vincent et al., 2009). Additionally, increases in fine root biomass have also been observed following thinning (López et al., 2003; Shen et al., 2017), which further contributes to supporting this hypothesis.

Furthermore, immediate post-harvest growth responses may be expressed at other stem heights. Nicoll et al. (2019) showed that while radial growth measured at 0.1 m and at breast height exhibited a delayed growth response following harvest, the same trees displayed an immediate growth increase when measurements were taken at 3 and 4.5 m above the ground, which supports this hypothesis.

This physiological explanation goes in line with our spatial and treatment-level results. Thinning shocks were more intense in the shelterwood treatment, where a higher proportion of trees was removed, and more frequent in trees located closer to skidding trails (i.e., the areas where harvesting operations were concentrated). These findings suggest that the thinning shock is not only influenced by overall harvest intensity but also by the spatial distribution of harvest within the stand. Trees exposed to more pronounced alterations in local stand conditions, such as those near skidding trails or in heavily harvested areas, may have experienced more frequent and greater shifts in belowground carbon allocation.

Our results also revealed that in thinning stands, trees located closer to skidding trails experienced longer thinning shocks, while in shelterwood stands, longer shocks were observed in trees located further away from skidding trails. The higher harvest intensity in the shelterwood treatment likely increased wind exposure for the residual trees, which may have contributed to the elevated windthrow mortality observed among these stems (Annexe A). In addition, the greater mean age of shelterwood stands (86 ±13 years) compared to thinning stands (66 ±14 years) may have also contributed to a greater windthrow mortality following harvest. Windthrow mortality might have created new canopy gaps further from the skidding trails and later in time, potentially prolonging the period during which trees prioritized belowground carbon allocation and promoting the delay in their radial growth recovery. Consistent with this interpretation, greater windthrow mortalities have been reported with increasing harvest intensity in a wide variety of boreal forest types (Bose et al., 2014; Montoro Girona et al., 2023c). In addition, increasing windthrow and standing dead mortality in partially cut jack pine stands have been observed over time, with mortality rising from 0 % in the first year to approximately 31 % fifteen years after harvest (Gauthier and Tremblay, 2019). We

thus encourage future research to investigate how the timing and extent of post-harvest mortality influence the duration and intensity of the thinning shock in residual trees.

We also observed that $\delta^{13}C$ values increased with tree height. This trend may reflect greater crown light exposure in taller trees, as enhanced irradiance can lead to lower stomatal conductance and higher $\delta^{13}C$ values (Berry et al., 1997; Graham et al., 2014).

1.4.2 Residual tree growth

Residual tree growth increased in both partial cut treatments during the 8 years following harvest. Yet, the response differed in magnitude. Growth was initially lower in the shelterwood treatment (40–50 % removal) compared to the thinning treatment (30–35 % removal). However, the average growth rates between treatments converged by the fourth year. One likely explanation for the initially lower growth in trees from the shelterwood treatment could be the result of a from-above harvesting approach, which typically removes larger-diameter trees and leaves behind a stand dominated by smaller, slower-growing individuals. The initially lower pre-harvest growth observed in trees from the shelterwood treatment likely contributed to the reduced growth performance observed early in the 8 years following harvest. The eventual convergence of growth rates may reflect a delayed but stronger response of these smaller trees. This interpretation is consistent with observations by Moulinier et al. (2015), who found that jack pine trees in smaller DBH classes showed lower volume increments initially but experienced greater relative growth increases following partial cuts.

In both partial cut treatments, trees located near skidding trails exhibited higher growth rates than interior trees. This is likely the result of the observed reduction in inter-specific competition in the edges of the skidding trails (Fig. S2, Annexe A), which would have increased resource availability, such as light and soil moisture. Strong evidence supports this explanation, including observations of edge-driven growth enhancements which have also been observed for other boreal species, including black spruce and balsam fir following clear cuts (Genet and Pothier, 2013), black

spruce under shelterwood systems (Montoro Girona et al., 2016), and lodgepole pine (*Pinus contorta* Dougl.) near roads (Bowering et al., 2006), in addition to the increased light penetration registered in closer locations to the skidding trail and the higher soil moisture levels with increased canopy openings (McDowell et al., 2003; Bladon et al., 2006; Delgado et al., 2007).

In our study, the difference in tree competition between the edge and the interior was unexpectedly greater in the thinning treatment (45%) than in the shelterwood treatment (32%) (Fig. S2, Annexe A). This suggests that additional factors beyond initial harvest intensity influenced post-treatment stand structure. One possible explanation is that windthrow mortality was more pronounced in the shelterwood treatment due to the greater harvest intensity or the advanced age. Such mortality would reduce the number of live stems recorded during forest inventories, lowering competition indices.

1.5 Implications for forest management

The thinning shock, defined as a delayed growth response following harvest, is an important consideration for forest managers aiming to optimize stand productivity. Thinning shocks were more frequent in trees located near skidding trails, and their duration and intensity varied depending on both the silvicultural treatment applied and tree proximity to those trails. We found that in the thinning treatment, trees closer to skidding trails experienced longer growth shocks, whereas in shelterwood treatment,

trees farther from trails showed more prolonged shocks, likely due to increased windthrow exposure over time. Our findings reveal a delay in growth enhancement following harvest and suggest that future growth models should explicitly incorporate response delay dynamics (Thorpe and Thomas, 2007). Factors such as skidding trail density, strip width, treatment type, and mortality must be considered to avoid overestimation of stand growth in early post-harvest years.

Although residual tree growth improved following the period of growth response delay across both partial cut treatments, the shelterwood treatments resulted in lower tree

growth rates than the thinning treatment. This outcome is likely due to the removal of dominant trees with initially higher growth rates, compounded by the more intense and prolonged thinning shocks observed in shelterwood-treated trees. These findings emphasize the importance of tree size selection when designing silvicultural interventions.

Thinning aims to reduce stand density, promote growth, and enhance timber revenues (Kerr and Haufe, 2011), while shelterwood systems are designed to mimic natural disturbances and support regeneration, especially of shade-tolerant species such as black spruce (Gauthier et al., 2023; Kim et al., 2025). Larger trees, preferentially removed in the shelterwood treatment, are more susceptible to windthrow (Rich et al., 2007), which can compromise both regeneration and timber yield. Given the goal of shelterwood treatments to enhance regeneration, along with the reported windthrow risk in esker forests (Guimond et al., 2024), we recommend a from-above harvesting approach, prioritizing the removal of larger-diameter trees, such as the one described in this study. This method may enhance regeneration success, reduce windthrow mortality, and increase timber revenue due to the removal of large-diameter trees.

1.6 Conclusion

Our findings suggest that the thinning shock is not caused by stomatal closure, as indicated by the observed more negative $\delta^{13}C$ values during the shock period compared to the before-harvest period. Instead, the thinning shock is more likely driven by shifts in resource allocation to either increased root growth, biomass demands of the root systems of formerly grafted trees that were harvested, or to higher parts of the stem that were not analyzed in this study. The presence, intensity, and duration of thinning shocks were influenced by both the silvicultural treatment applied and the proximity of trees to skidding trails. Over the eight years following harvest, residual trees exhibited enhanced growth compared with control trees, with growth rates being higher in the thinning treatment than in the shelterwood treatment. This was likely due to the removal of larger DBH trees in the shelterwood treatment, which initially present greater growth rates, as well as the more prolonged and intense thinning shocks observed in trees from the shelterwood treatment. These results add

valuable insights into tree growth dynamics following partial cuts and highlight the need to incorporate this phenomenon into growth models aiming for high predictive accuracy.

Author contribution statement

MAP, MMG, and AD conceived and designed the experiment. MAP conducted the field and laboratory work, performed the data curation, analyzed and interpreted the data, and wrote the first draft of this manuscript. MMG and AD provided funding, supervision, fieldwork coordination, resources, validation, methodological validation, and project administration for this research, as well as reviewed and edited the manuscript. AKB provided internship supervision and administrative support for this research, as well as reviewed and edited the manuscript. EB provided funding, internship supervision, and administrative support for the alpha-cellulose extraction, as well as reviewed and edited the manuscript. MML reviewed and edited the manuscript.

2. IMPACTS OF PARTIAL CUTS ON ABOVEGROUND CARBON STOCKSIN ESKER FORESTS

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Résumé

Les impacts des coupes partielles sur les stocks de carbone restent incertains en raison de la mortalité élevée due au vent après la récolte, qui peut contrecarrer les effets positifs de la coupe sur la croissance des peuplements. Cette étude a évalué les effets des coupes partielles et de la mortalité des arbres sur les stocks de carbone aériens huit ans après la coupe dans les forêts de pins gris. Le protocole d'échantillonnage comprenait 24 sites présentant différentes intensités de récolte (%): témoin non récolté, éclaircie commerciale (30-35 %) et coupe progressive (40-50 %). Des analyses dendrochronologiques et des équations allométriques ont été utilisées pour quantifier le carbone dans la biomasse vivante et morte (arbres morts sur pied, cassés et déracinés). Les augmentations des stocks de carbone individuels des arbres entre l'année précédant la récolte et la huitième année après la récolte étaient plus faibles dans les contrôles et similaires dans les traitements de coupe partielle. Huit ans après la récolte, les stocks de carbone vivant par hectare étaient 41 % plus faibles dans le traitement de coupe progressive que dans les peuplements non récoltés, mais restaient similaires entre les traitements d'éclaircie et les témoins. Les arbres plus grands et ceux poussant plus près des pistes de débardage ont affiché une augmentation plus élevée des stocks de carbone, ces derniers présentant une augmentation moyenne supérieure de 33 %. Les stocks moyens totaux de carbone dans le bois mort étaient 55 % plus élevés dans le traitement témoin que dans les coupes partielles en raison de la réduction du carbone dans les chicots dans les peuplements récoltés. Le déracinement a été influencé par le traitement de récolte et la proximité des pistes de débardage, tandis que la rupture des tiges a été déterminée par les caractéristiques des arbres (hauteur, âge et concurrence) et la distance par rapport aux pistes. La proportion de chicots était liée à la vitesse moyenne annuelle du vent. Ces résultats suggèrent que l'éclaircie pourrait maintenir les stocks de carbone forestier grâce à des prescriptions visant à préserver les stocks de carbone des chicots.

Mots clés : équations allométriques, chablis, dendrochronologie, écologie des perturbations, gestion forestière, mortalité des arbres, sylviculture

Abstract

The impacts of partial cuts on carbon stocks remain uncertain due to elevated post-harvest windthrow mortality that may counteract the positive effects of thinning on stand growth. This study evaluated the effects of partial cuts and tree mortality on aboveground carbon stocks eight years after harvest in jack pine forests. The sampling protocol included 24 sites with varying harvest intensities (%): unharvested control, thinning (30–35 %), and shelterwood (40–50 %) treatments. Dendrochronological analyses and allometric equations were used to quantify carbon in live and dead biomass (snags, broken, and uprooted trees). Increases in individual tree carbon stocks between the pre-harvest year and the eighth year post-harvest were lower in controls and similar among partial cut treatments. Eight years after harvest, live carbon stocks per hectare were 41 % lower in the shelterwood treatment than in unharvested stands but remained similar between the thinning and control treatments. Larger trees and those growing closer to skidding trails showed greater increases in carbon stock, with the latter exhibiting a 33 % higher increase on average. Mean total deadwood carbon stocks were 55 % higher in the control than in the partial cuts due to reduced snag carbon in harvested stands. Uprooting was influenced by harvest treatment and proximity to skidding trails, while stem breakage was driven by tree characteristics (height, age, and competition) and distance to trails. The proportion of snags was explained by mean annual wind speed. These findings suggest that thinning could sustain forest carbon stocks with prescriptions aiming at maintaining snag carbon stocks.

Keywords: allometric equations, dendrochronology, disturbance ecology, forest management, silviculture, tree mortality, windthrow

2.1 Introduction

The boreal forest represents a globally significant carbon reservoir, holding nearly one-third of the planet's terrestrial carbon stocks (Gauthier et al., 2015). Approximately 25

% of the carbon in Canadian boreal forests is found in aboveground biomass, with the remainder distributed between soils (40 %) and dead organic matter such as litter and deadwood (35 %) (Kurz et al., 2013). Traditionally, the Canadian boreal forest has been harvested through clear cuts due to their economic and operational advantages and their similarity to wildfires in terms of disturbance scale (Rosenvald and Lõhmus, 2008; Fenton et al., 2009; Montoro Girona et al., 2023c). Over the past two decades, growing recognition of the multiple values and functions of forest ecosystems, coupled with increasing interest in management approaches that balance productivity and conservation, has led to a diversification of silvicultural practices, including the implementation of partial cuts (Rotherham and Armson, 2016; Kayes and Mallik, 2020; Montoro Girona et al., 2023c), which currently account for 25 % of the harvested area in Quebec (CCPM, 2023). Partial cuts are a group of silvicultural treatments that harvest only a proportion of the trees in the stand, reducing the impacts of forest management on biodiversity, regeneration, or soil properties when compared to clear cuts (Bose et al., 2014; Zhou et al., 2015; Kim et al., 2025). Moreover, similar soil carbon stocks have been observed following partial cuts compared to unharvested stands (Nilsen and Strand, 2008; Ruiz-Peinado et al., 2013, 2016; Bravo-Oviedo et al., 2015; Zhang et al., 2018b; Cachinero-Vivar et al., 2021). However, partial cuts reduce stand density and enhance individual tree growth (Montoro Girona et al., 2023c), therefore altering the live aboveground carbon stocks. Trees with lower pre-harvest growth rates, higher crown class, and younger age tend to exhibit greater growth following harvest (Moulinier et al., 2015; Montoro Girona et al., 2016). In addition, tree growth increases with higher harvest intensity, lower interspecific competition, and proximity to skidding trails (Goudiaby et al., 2012; Pamerleau-Couture et al., 2015; Montoro Girona et al., 2017).

In young stands approaching canopy closure, tree mortality is primarily driven by self-thinning of suppressed individuals resulting from both intra- and interspecific

competition, which in turn leads to the formation of snags (i.e., standing dead trees) (Vospernik and Sterba, 2015; Wallraf and Wagner, 2019). In mature boreal stands, tree mortality is also driven by natural disturbances, such as windthrows (Shorohova et al., 2011). Windthrow mortality is observed when wind forces exceed the tree anchorage strength or stem resistance, leading to uprooting or stem breakage (Klaus et al., 2011; Quine et al., 2021). Partial cuts alter snag abundance through the removal of suppressed or lower-crown-class trees, as in commercial thinning from below (Graves et al., 2000; Wisdom and Bate, 2008), but create canopy openings that increase windthrow mortality by reducing the wind dissipation effect of the stems and increasing wind penetration (Achim et al., 2005; Thorpe et al., 2008). The observed increase in post-harvest mortality may compromise the capacity of these forests to maintain their carbon stocks, raising doubts about the long-term sustainability of partial cuts from a carbon storage perspective.

Our study focused on jack pine–dominated esker forests, which typically develop on sandy substrates characterized by poor water and nutrient retention (Tubridy and Meehan, 2006; Sileshi et al., 2022; Hasan et al., 2023). This substrate acts as a natural filter, thereby improving the quality of surface and groundwater, which is used for human consumption (Nadeau et al., 2015). Since clear cuts have been reported to alter the water chemistry of nearby lakes (Jerabkova et al., 2011; Grosbois et al., 2023), local governments are now promoting partial cuts in even-aged jack pine stands to provide continuous forest cover over the eskers and minimize the harvest impacts. Sandy substrates also improve tree resistance to windthrow in species with taproot systems, such as jack pine (Elie and Ruel, 2005; Dupuy et al., 2007). Yet, windthrow mortality rates have been reported to be greater in esker forest edges left after clear cuts compared to those located on clayey substrates (Guimond et al., 2024). Understanding post-harvest mortality and assessing the impacts of partial cuts on deadwood carbon dynamics is crucial for adapting silvicultural approaches to the specific conditions of jack pine-dominated forests and to align them with broader strategies aimed at reducing atmospheric CO_2 emissions (Lee et al., 2002).

This study assessed the impact of partial cuts on aboveground carbon stocks of live trees and deadwood biomass. We expected live aboveground carbon stocks per hectare to decline 8 years following harvest, with increasing harvest intensity due to stem removal and an insufficient post-harvest tree growth to offset the tree loss from harvesting. Snag abundance typically declines with decreasing stand density (Russell et al., 2012), and snags consist mostly of smaller-diameter trees (Greif & Archibold, 2000). Windthrow mortality, which increases with harvest intensity, stand exposure, and tree size (Rich et al., 2007; Valinger and Fridman, 2011; Montoro Girona et al., 2019; Beese et al., 2019; Guimond et al., 2024), tends to result in the death of larger trees, thereby contributing to greater individual deadwood biomass. Therefore, we expected total deadwood carbon stocks to increase with harvest intensity, primarily due to the input from these windthrown large trees. We also anticipated higher windthrow rates in more exposed stand areas, such as along skidding trail edges, in stands with lower interspecific competition, in topographically exposed sites, and in locations with greater wind incidence.

2.2 Materials and methods

2.2.1 Study area

The study was conducted in the Abitibi-Témiscamingue region, Quebec, Canada (Fig. 16). The study area is located in the jack pine-dominated esker forests of the balsam fir-white birch bioclimatic domain (MRNF, 2023). During the Wisconsinan glacial period, the Laurentide Ice Sheet covered large parts of eastern Canada (Dyke et al., 2002; Storrar et al., 2014). As the ice retreated, it left behind elongated and curved ridges of sand and gravel deposited by meltwater streams beneath the glacier, labelled as eskers (Storrar et al., 2014), which provide suitable conditions for jack pine growth (Starr and Lindroos, 2006; Hoffer and Tardif, 2009). The climate is classified as cold and humid, with a mean annual temperature is 1.5 °C and 97 frost-free days per year (1981–2010, Amos station). The growing season lasts between 81 and 100 days (Government of Canada, 2024). The study area has a mean annual precipitation of 929 mm, 27% of which falls as snow (Government of Canada, 2024). Average monthly wind speeds range from 37 to 50 Km/h (1981–2010) (Government of Canada, 2024).

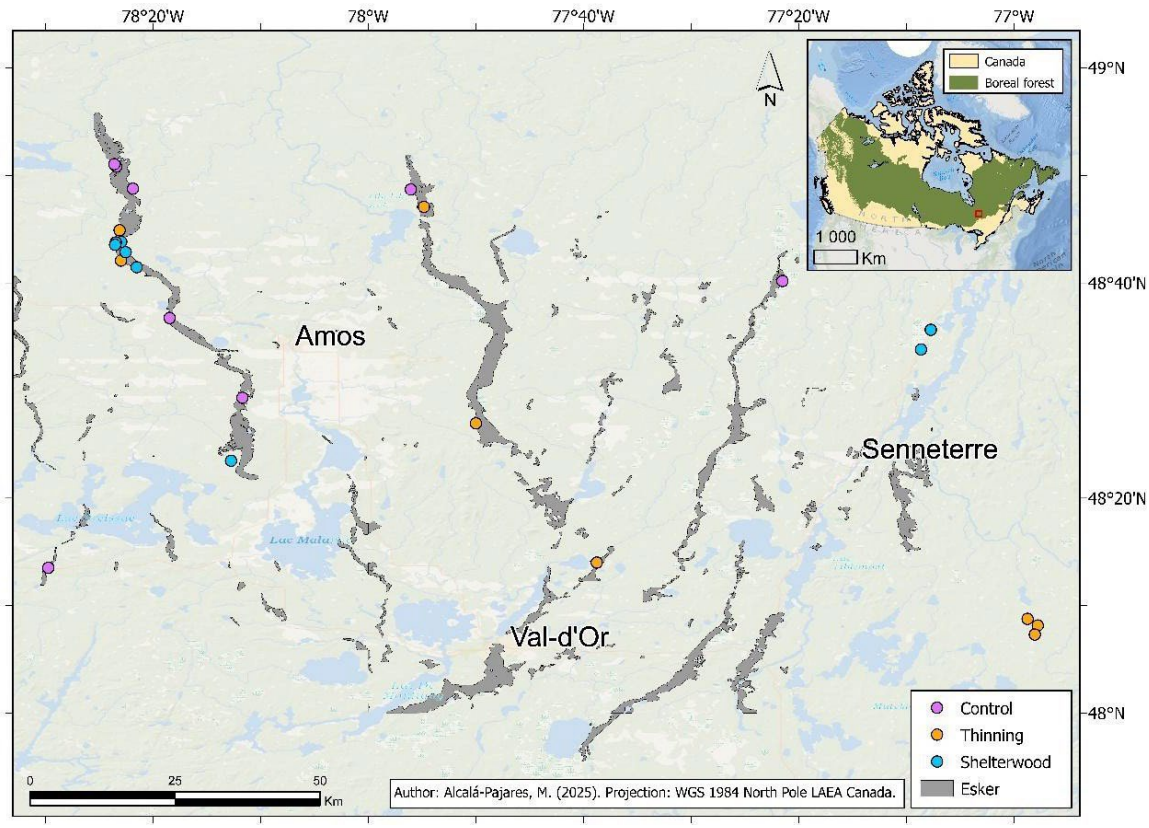

Figure 15
Study area and study site locations by treatment.

2.2.2 Site selection and sampling protocol

The harvest treatments were operationally implemented by forest companies (between 2008 and 2013), and suitable study blocks were subsequently selected in 2020. Three silvicultural treatments (control, moderate, and heavy thinning) were each replicated 8 times (Table 5). Stands were selected on well-drained sandy soils, which originated from fluvio-glacial deposits (eskers) or from glaciolacustrine deposits of similar texture adjacent to them. In these stands, jack pine accounted for more than 60% of the total basal area. Control stands were selected in natural forests with no recorded history of silvicultural interventions. The stand selection process relied on information from the forest inventories provided by the Ministry of Natural Resources and Forests of Quebec (Government of Quebec, 2019). We acknowledge that some plots assigned to the same treatment are spatially clustered, which may partially

confound observed treatment effects due to site-specific environmental heterogeneity. This limitation is addressed in the statistical analyses by incorporating the site as a fixed effect in our analysis.

2.2.3 Silvicultural treatments

Two commercial thinning treatments were chosen: a commercial thinning, which removed 30–35 % of the basal area, and a shelterwood treatment, which removed 40–50 % of the basal area. Thinnings followed a strip pattern, with trees completely removed along 5-meter-wide strips (i.e. skidding trails). From these trails, a mechanized forest harvester with a maximum boom reach of 5 m extracted all trees with DBH > 9 cm within 5 m on either side of the trail (Fig. 17). Forest harvesters with maximum boom reaches of 5 meters were selected to reduce the impact of machinery transit on soil and understory vegetation. Skidding trails were executed every 11-13 meters. Logs were subsequently transported using forest forwarders, and no post-harvest treatment was performed. A 6–8-meter-wide intact residual strip was left in the stand beyond each partially harvested strip.

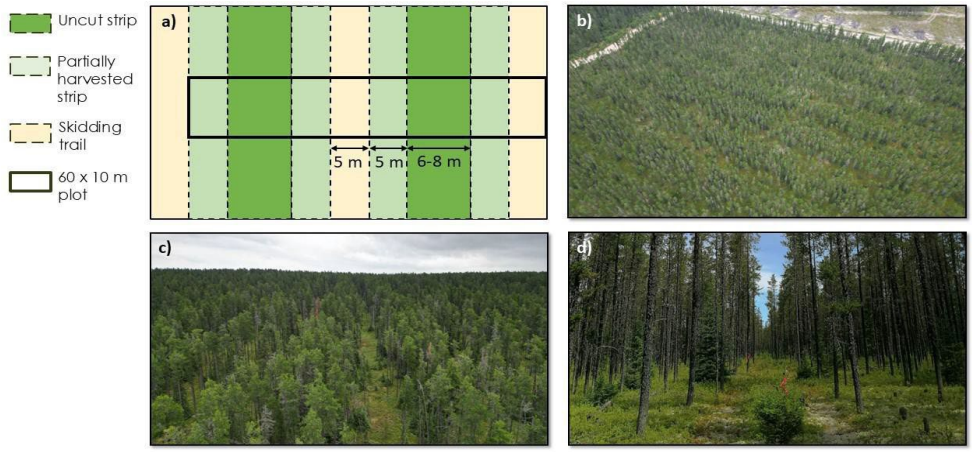

Figure 16
Schematic representation of the spatial pattern of silvicultural treatment and the plot location (a).
Aerial view of a shelterwood cut (b). Aerial view of a skidding trail (c). Ground view of a skidding trail and residual strip (d).

2.2.4 Data collection

A forest inventory was conducted during the summer of 2022. One 60 × 10 m (600 m^2) plot was established at each study site perpendicularly to the skidding trail (Fig. 17 b). Tree species and diameter at breast height (DBH, measured at 1.3 m) were recorded for all live and dead trees with DBH > 9 cm. A DBH threshold of 9 cm was used to align with the minimum merchantable tree diameter in Quebec (Barrette et al., 2018; Duchateau et al., 2020; MRNF, 2022). Each live tree was classified according to its crown class. Crown class was determined by visually assessing relative crown size and light exposure among neighbouring trees, ensuring representation of dominant, co-dominant, and suppressed individuals. Dominant trees had large, fully exposed crowns; co-dominant trees had moderately sized crowns partially shaded by dominants; and suppressed trees had small, heavily shaded crowns. Dead trees were also classified into three categories: snag, broken, or uprooted, according to previous literature (Montoro Girona, 2019; Ruel and Gardiner, 2019; Guimond et al., 2024). Dead trees were classified as snags if they were standing and showed no signs of stem breakage. Dead trees exhibiting stem breakage were considered broken, while dead trees that had fallen with partially or fully exposed root systems were classified as uprooted. All live and dead trees were classified as forest edge (≤5 m from the skidding trail) or forest interior (>5 m) trees.

A subset of eight jack pines was selected to measure tree height and interspecific competition. The subsample trees included individuals from all three crown classes (dominant, co-dominant, and suppressed) to capture structural diversity within the stand. At least one tree from each crown class was selected per plot, and the remaining five trees were chosen randomly. To ensure that sample trees were representative of the full range of competitive conditions within each plot, half of the subsample trees were located in the forest interior (>5 m) and half in the edge (≤5 m). Heights were estimated with a clinometer (Suunto Oy, Vantaa, Finland) or a Vertex (Haglöf Sweden AB, Långsele, Sweden). Competition was estimated by adapting the Hegyi Index formula (CI_i, Equation 3) (Biging and Dobbertin, 1995), defined as:

$$CCCC = \sum_{jj=1}^{mm} \frac{DBHBHBH_{jj}}{DBHBHBH_{ii}} \times \frac{1}{Distance_{ijij}^{nn}} \quad (3)$$

Where CI_i is the competition index for the focal tree i, DBH_i is the DBH of the focal tree i, in cm, DBH_j is the diameter of the neighbouring tree j, in cm, $Distance_{ij}$ is the distance between the focal tree i and the neighbouring tree j, in m, and n is the number of neighbouring trees located within the radius. A 4-meter radius was defined around each of the 8 selected focal trees (i.e., subsample trees), based on distances where strong correlations between growth and competition have been reported for other pine species (Pukkala and Kolström, 1987). Within this radius, we measured the DBH of the focal tree (DBH_i) and all surrounding trees (DBH_j) taller than 1.3 m, as well as the distance from each neighbouring tree to the focal tree ($Distance_{ij}$).

Plot-level metrics for tree height and interspecific competition were calculated as the mean of the eight subsample jack pines from each plot. DBH was measured for all live jack pines in the plot, and the plot-level DBH metric was calculated as the mean of these measurements. No height–diameter (H–DBH) model was applied because the DBH range of the sampled trees used to measure height was higher than that of the full inventory. Applying a regression under these conditions would have required extrapolation beyond the calibration range, potentially biasing height estimates. However, because some trees in edge plots were harvested, the number of available trees was occasionally lower than in interior plots. We therefore acknowledge that the sample size for DBH measurements was not fully balanced among zones.

Table 6
Mean stand characteristics by silvicultural treatment for each study site.

ID	Treatment	tand age (years)	Density (trees/ha)	DBH (cm)	eight (m)	Species proportion (%)	
						Jack pine	Others
C1	Control	100-111	900	18.4	17.2	93	7
C2	Control	47-56	800	16.8	15.5	77	23
C3	Control	54-57	883	20.3	20.1	84	16
C4	Control	56-71	1333	15.7	19.4	61	39
C5	Control	57-73	683	19.9	17.8	92	8

C6	Control	85-91	1300	19.0	18.4	80	20
C7	Control	70-75	1350	16.6	21.0	61	39
C8	Control	68-83	800	16.8	14.9	91	9
E1	Thinning	96-105	633	18.3	16.3	95	5
E2	Thinning	59-63	667	18.8	18.5	96	4
E3	Thinning	63-79	933	17.7	17.1	97	3
E4	Thinning	58-61	1033	17.2	17.6	76	24
E5	Thinning	53-64	1133	12.0	10.9	97	3
E6	Thinning	57-66	833	20.8	19.9	73	27
E7	Thinning	61-64	1017	15.7	14.3	92	8
E8	Thinning	51-58	533	19.1	18.3	83	17
S1	Shelterwood	72-79	633	16.5	16.7	100	0
S2	Shelterwood	84-99	633	22.5	18.9	96	4
S3	Shelterwood	66-78	650	15.6	13.3	100	0
S4	Shelterwood	74-98	867	15.3	15.3	89	11
S5	Shelterwood	91-97	550	17.9	18.6	74	26
S6	Shelterwood	99-104	917	16.5	15.7	78	22
S7	Shelterwood	68-79	750	16.1	16.3	89	11
S8	Shelterwood	100-103	833	15.9	16.4	72	28

2.2.5 Dendrochronological analysis

For growth analysis, one core at breast height was collected from 36 live jack pines per plot (n = 864). Breast height was chosen because allometric equations for estimating tree biomass and carbon stocks are typically based on diameter measurements at this height (Lee et al., 2002; Nilsen and Strand, 2008; Ruiz-Peinado et al., 2013, 2016; Bravo-Oviedo et al., 2015). Extracting cores at a standardized height and analyzing them using dendrochronology allowed us to reconstruct past DBH values from radial growth data and estimate pre-harvest DBH (DBH_{bh}) and DBH eight years after harvest. This approach also facilitates comparisons with existing studies based on DBH-derived carbon estimates. Estimates of DBH were only reconstructed for the cored trees. In addition, the distance of each cored tree to the skidding trails was measured with a measuring tape. Cores were extracted using a cordless drill with a 5.15 mm increment borer (Haglöf Sweden AB, Långsele, Sweden) to fasten the core extraction and to improve core quality (Gärtner et al., 2023; Fonti et al., 2025).

Tree age was estimated from the same subsample of eight trees per plot (n = 192) selected for measuring height and interspecific competition. These trees were chosen from the set of 36 cored trees per plot. Given the even-aged structure of the stands, we consider that sampling eight trees per plot is sufficient, as trees within each plot are relatively uniform in growth stage, ensuring representative age estimates. Due to the absence of adventitious roots in mature pines, which can otherwise lead to an underestimation of tree age (Desrochers and Gagnon, 1997; Plourde et al., 2009), we estimated tree age by extracting a second set of increment cores at ground level. This approach was taken to avoid underestimating age caused by the time required for a tree to reach breast height (Palik and Pregitzer, 1995). Mean stand age was calculated as the mean of the eight sampled jack pines per plot.

All cores were air-dried, glued to wood boards, sanded with progressively finer grits of sandpaper (600-1000 grain), and scanned (Expression 12000XL, SEIKO EPSON CORP., Suwa, Japan). Tree rings were measured and analyzed with CooRecorder (Version 9.8.0, Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Cross-dating and

tree-ring measurements were subsequently verified with Past5 (Version 5.0.620, SCIEM). The DBH at the moment of harvest (DBH_{bh}) and 8 years following were estimated using the dplR package of RStudio (Bunn, 2008).

2.2.6 Aboveground and deadwood carbon estimation

Aboveground carbon stocks were based on allometric equations. We selected the DBH-based equations developed in Lambert et al. (2005), as they were based on mature jack pine populations of nearby locations, a criterion previously followed in the literature (Park, 2015). These equations were used to estimate the aboveground biomass of live trees, including wood, bark, branches, and needles, as well as the total biomass combining all components. Root biomass fraction was not estimated due to the current lack of mature jack pine-based allometric equations, including this fraction (Alban and Laidly, 1982; Gower et al., 1997; Lambert et al., 2005; Hunt et al., 2010; Fradette et al., 2021).

The product of the total aboveground tree dry biomass and the estimated species-specific carbon concentration was used to calculate tree aboveground carbon stocks. The estimated carbon concentration for black spruce followed the value provided by (Larocque et al., 2014), while the values from (Lamlom & Savidge, 2003) were used for the other tree species inventoried. Tree aboveground carbon content was estimated at the year before harvest and at the 8th year following harvest using allometric equations based on DBH_{bh} and DBH of the 8th year post-harvest, respectively.

Deadwood biomass was estimated for all trees measured in 2022 using DBH-based allometric equations from Lambert et al. (2005). Deadwood biomass estimates were based on snags, broken, and uprooted trees. Biomass estimates were based on the DBH at the time of measurement, 11–14 years post-harvest, rather than after 8 years. For uprooted and broken trees, bark was still present at breast height when DBH was measured, supporting the use of the selected allometric equations. For some snags, bark was partially missing at breast height; in these cases, the equations may slightly underestimate total aboveground deadwood due to the smaller measured DBH.

Branches and broken portions of the bole were not calculated separately, but all dead tree material was assumed to remain on-site, so these components are included in the total aboveground biomass estimates. In this study, we assumed that tree mortality occurred after harvest, as previous studies have reported peaks in tree mortality during the first years following partial cuts (Thorpe et al., 2008). Therefore, we assumed that the 2022 measurements reasonably represented conditions eight years post-harvest. We also assumed that all material from trees that died remains on-site and contributed to aboveground biomass, so no correction for material lost via breakage or removal was applied. Finally, we assumed that DBH measurements represented total aboveground biomass for snag, broken and uprooted dead trees according to other previous studies (Bravo-Oviedo et al., 2015).

2.2.7 Climatic, topographic and exposure variables

Climatic and topographic variables were compiled to study the factors influencing windthrows (Annexe B). Data on wind speed 30 m above the ground were obtained from the Wind Atlas public database from the Government of Canada, whose data is based on a 2 km grid and a 10-minute time resolution (Government of Canada, 2016). Elevation and slope were obtained for each study site from the Forêt Ouverte public database provided by the Ministère des Forêts, de la Faune et des Parcs (MFFP) of Quebec (Government of Quebec, 2019). Slope data had a resolution of 10 meters, and elevation data had a resolution of 1 meter. Two slope types were identified in our study: null (0-3 %) and gentle (4-8 %). We calculated a topographical exposure index (Topex) based on a simplification of the Topex index developed by Ruel and Dornier (2002). This simplification was justified by the gentle topography of the region. To calculate our simplified Topex index, 1000-meter transects were oriented along the North-South, East-West, Northeast-Southwest, and Northwest-Southeast directions using the centroid of each plot as the start point for each transect. The transect length was selected following the one used in the literature (Ruel and Dornier, 2002). We considered the chosen length as sufficient, as longer transects did not yield additional precision (Ruel and Dornier, 2002). For each transect, the highest (Z_{max}) and lowest (Z_{min}) points were determined, the corresponding angle ($\theta_{transect}$), was extracted, and

all corresponding angles for each of the four transects at each location were summed to obtain the final value (Equation 4).

ZZZZDDZ Z – ZZZZiimm (4)

180

$D\theta\theta DDmnDDDDDDDD = DD\theta\theta DDDDDDnn$ (

) × 1000

ππ

The Fetch index is another measure of site exposure, which represents the uninterrupted distance that wind travels across an open area before encountering a barrier (Scott and Mitchell, 2005). This index was estimated using two sets of 8 transects following the eight cardinal directions with a maximum distance of 600 meters with ArcMap (version 10.8.1, ESRI 2020, United States) (Annexe B). We used a longer transect length than previous studies (e.g., 300 m, Scott and Mitchell, 2005) because the flat terrain at our study sites allows wind to travel greater distances before encountering barriers. The 600 m distance was based on previous studies utilizing longer transects (Montoro Girona et al., 2019). The first set of transects measured the uninterrupted distance from the plot until it encountered a natural or anthropogenic barrier that defines an open area, such as lakes, paths, or clear cut neighbouring stands. The second set of transects extended this measurement by assessing the distance from the plot to the opposite edge of the open area. Finally, the Fetch index for each site was calculated as the product of the average transect length from both the first and second sets of transects.

2.2.8 Data Analysis

Live aboveground carbon stocks

One-way ANOVAs were conducted to assess significant differences ($p < 0.05$) in stand-level mean live aboveground carbon stocks per hectare among treatments in the year before harvest and in the 8th year following harvest. Repeated-measures ANOVAs were performed to detect significant differences in carbon stocks per tree across periods within each treatment. Post-hoc pairwise comparisons among treatments were conducted using Tukey HSD tests.

Linear mixed models were used to identify variables influencing changes in individual tree carbon stock between the year before harvest and the 8th year following harvest. The response variable was the difference in carbon stocks for each tree between the pre-harvest year and the 8th year post-harvest. Fixed effects included DBH_{bh}, competition, age, distance to the skidding trail, tree crown class, and treatment (Annexe B), while the site was treated as a random effect. A set of 37 models was constructed based on ecological theory (Anderson and Burnham, 2002), along with a global and a null model to test the hypothesis that no variables affect tree radial growth.

Deadwood carbon stocks

To evaluate differences among treatments in terms of mean deadwood carbon stocks per hectare (stand-level metric), data were first assessed for normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test). When assumptions of normality and homoscedasticity were met, a one-way ANOVA was performed, followed by a Tukey HSD post hoc test to identify pairwise differences among treatments. When these assumptions were not satisfied, the non-parametric Kruskal–Wallis test was used instead, followed by Dunn's post hoc test.

To assess the factors driving the proportion of dead trees at the stand level, we constructed a series of generalized linear mixed models for each of the three categories of dead trees: snag, broken, and uprooted trees. For each dead tree type, the response variable was the proportion of affected trees per plot, calculated as the

number of trees in each dead tree category divided by the total number of trees in the plot. Models were fitted with a binomial error distribution and a logit link function, using the total number of trees per plot as the binomial denominator to account for differences in sample size among sites. Fixed effects included forest structural attributes (mean DBH, mean height, slenderness ratio, mean competition, mean age), topographic variables (altitude, slope, topex, fetch index), wind exposure (mean annual wind speed at 30 m above ground), and treatment (Annexe B). Site was included as a random intercept to account for potential site-level variability. In total, 29 candidate models were developed based on ecological hypotheses, ranging from a null model containing only the intercept to a full model including all fixed effects. When significant differences in stand-level proportions of dead trees were detected among treatments, post hoc pairwise comparisons were conducted using Tukey's HSD tests.

A separate analysis was conducted to examine the effect of tree position relative to the skidding trail on the presence of each dead tree type. For this, we used a set of generalized linear models with a binary response variable indicating whether each tree died (1) or survived (0) during the study period. Predictor variables included the distance of each tree to the skidding trail, the treatment type, and their interaction. Tree position was categorized as either stand edge or stand interior. These models, therefore, estimate the probability of dead tree occurrence at the individual-tree level.

Post-hoc pairwise comparisons were performed using Tukey HSD tests with the agricolae package (de Mendiburu, 2025) and Dunn tests were performed using the FSA package (Ogle and Ogle, 2017). Levene tests were performed using the car package (Fox et al., 2012). Generalized linear mixed models with a binary response variable were created with the lme4 package (Bates et al., 2015). Model selection was guided by Akaike's Information Criterion (AIC) (Wagenmakers and Farrell, 2004), with preference given to the model with the lowest AIC. Multicollinearity was assessed in all models by calculating different Variance Inflation Factors (VIF). Standard Variance Inflation Factor or the adjusted Generalized Variance Inflation Factor (car package) were employed, depending on the presence or absence, respectively, of categorical variables in the selected model (Fox and Monette, 1992; Fox et al., 2012). Correlations

among variables, in addition to the verification of the normality and random distribution of the residuals, were analyzed for all models. Marginal R-squared (R^2_m) and Conditional R-squared (R^2_c) were estimated with the MuMIn package (Barton and Barton, 2024).

2.3 Results

2.3.1 Live aboveground carbon stocks

In both the year before harvest and the 8th year following harvest, the only difference in mean stand live aboveground carbon was found between the control and shelterwood treatments (Table 6). In the year before harvest, stands subjected to the shelterwood treatment had 43 % (30.97 Mg ha^{-1}) lower carbon stocks compared to the control (54.10 Mg ha^{-1}), while thinning and control stands showed similar mean aboveground carbon stocks (Table 6). In the 8th year following harvest, stands subjected to the shelterwood treatment had 41 % (33.12 Mg ha^{-1}) lower carbon stocks compared to the control (56.54 Mg ha^{-1}). Similar mean aboveground carbon stocks were found among the control and the thinning treatment (Table 6), although the thinning tended to have lower (-25 %) live carbon stocks compared to the control treatments. Mean carbon stocks per hectare increased across all treatments between the before- and after-harvest periods (Table 6, Annexe B). However, trees in partially cut stands exhibited a greater carbon stock increase among periods compared to the controls. Specifically, carbon stocks increased by 4.5 % (3.42 Kg Tree^{-1}) in control sites, while larger increases were observed in thinning (+ 7.4 %, 4.14 Kg Tree^{-1}) and shelterwood (+ 6.9 %, 3.65 Kg Tree^{-1}) sites in the 8th year after harvest compared to the pre-harvest period (Table 6).

Table 7
Mean live aboveground carbon stocks per hectare (Mg ha^{-1}) on each treatment in the before-harvest year and in the 8th year following harvest, and mean per-tree carbon stock change across periods.

SD = Standard deviation, SE = Standard error, and CI = 95% confidence intervals. Letters indicate statistically significant differences between treatments within each dead tree type; treatments sharing a letter are not significantly different at α = 0.05. Carbon stocks calculated from the DBH-based allometric equations of Lambert et al. (2005).

Treatment	Mean carbon (Mg ha^{-1})	Post-hoc group	SD	SE	Lower 95 % CI	Upper 95 % CI	Mean tree carbon stock change (%)	Post-hoc group
Before-harvest year								
Control	54.10	a	15.73	5.56	40.95	67.25	-	-
Thinning	39.23	ab	11.10	3.93	29.95	48.51	-	-
Shelterwood	30.97	**b**	12.31	4.35	20.68	41.27	-	-
8th year following harvest								
Control	56.54	a	16.10	5.69	43.08	70.00	+ 4.5	a
Thinning	42.14	ab	11.36	4.02	32.64	51.63	+ 7.4	**b**
Shelterwood	33.12	**b**	12.97	5.59	20.27	43.96	+ 6.9	**b**

The most parsimonious model assessing the variables behind the difference in mean individual tree carbon stocks (Annexe B) between the year before harvest and at the 8th year following harvest was dependent on stand mean inter-specific competition, DBH_{bh}, and the distance to the skidding trail (Table 7). However, the only variables that influenced the change in tree carbon stocks among periods were the latter two. Trees with larger pre-harvest DBH (DBH_{bh}) showed greater increases in carbon stocks per tree (Table 7; Figs. S6–S7 Annexe B). Additionally, trees located closer to skidding trails exhibited the highest per-tree carbon stock increases (Table 7; Figs. S8–S9 Annexe B), with those within 5 meters of the trails showing 33 % higher carbon stocks compared to trees in the forest interior. The selected model explained 61.8 % of the variance (R^2_c) of the biomass change, with 53.7 % of the variance accounted for by the fixed effects alone (R^2_m).

Table 8
Parameter estimates and 95% confidence intervals (CI) from the selected linear mixed-effects model explaining tree-level changes in carbon stocks between the year before harvest and the 8th year following harvest and the 8th year following harvest.
σ_1: standard deviation of the random intercept for the site grouping factor. σ_2: standard deviation of the residual errors.

Parameter	Coefficient (β)	Std. Dev	Std. Error	*p*-value	Lower 95% CI	Upper 95% CI	VIF
σ_1	-	1.00	-	-	0.00	1.73	-
σ_2	-	2.20	-	-	1.88	2.54	-
Intercept	-4.89	-	1.48	< 0.01	-7.93	-1.78	-
Competition	0.05	-	0.22	0.82	-0.39	0.47	1.52
DBH_{bh}	0.54	-	0.08	**< 0.01**	0.40	0.68	1.35
Distance	-0.26	-	0.08	**< 0.01**	-0.41	-0.12	1.15

2.3.2 Deadwood carbon stocks

Mean total deadwood carbon stocks were 55 % higher in the Control (4.83 Mg ha^{-1}) compared to the partial cut treatments (3.11 Mg ha^{-1} on average) (Table 8). When the type of dead tree was examined separately, stand uprooted and broken tree carbon stocks did not differ significantly among treatments. In contrast, stand snag carbon stocks were 104 % higher in the Control (2.84 Mg ha^{-1}) than in the partial cut treatments (1.39 Mg ha^{-1} on average).

Table 9
Deadwood carbon stocks per hectare (Mg ha^{-1}) per treatment and dead tree type (stand-level values).
SD = Standard deviation, SE = Standard error, and CI = 95% confidence intervals. The term "Total" stands for the calculations made considering all the dead tree types (snag, broken, uprooted) together. Letters indicate statistically significant differences between treatments within each dead tree type; treatments sharing a letter are not significantly different at α = 0.05. Carbon stocks calculated from the DBH-based equations of Lambert et al. (2005).

Dead tree type	Treatment	Mean carbon (Mg ha^{-1})	Post-hoc group	SD	SE	Lower 95% CI	Upper 95% CI

	Control	4.83	a	4.76	0.97	2.82	6.85
Total	Thinning	2.62	**b**	2.40	0.49	1.61	3.64
	Shelterwood	3.60	**b**	2.30	0.47	2.63	4.58
	Control	0.11	a	0.32	0.07	-0.03	0.24
Uprooted	Thinning	0.31	a	0.98	0.2	-0.10	0.73
	Shelterwood	0.61	a	1.35	0.28	0.03	1.18
	Control	1.89	a	3.59	0.73	0.38	3.40
Broken	Thinning	1.19	a	2.21	0.45	0.26	2.13
	Shelterwood	1.35	a	2.21	0.45	0.42	2.28
	Control	2.84	a	4.69	0.96	0.86	4.82
Snag	Thinning	1.12	**b**	2.06	0.42	0.25	1.99
	Shelterwood	1.65	**b**	2.66	0.54	0.52	2.77

2.3.3 Drivers of the proportion of dead trees

Similar stand proportions of dead trees were detected among the control and shelterwood treatments, with these proportions being lower in the thinning treatment (Fig. 18 A). Windthrow accounted for the largest proportion of dead trees compared to snags in both the thinning (58 %) and shelterwood (61 %) treatments. In contrast, control stands showed a lower proportion of windthrow (47 %) relative to snags (Fig. 18 A).

The selected logistic regression model used to assess factors driving the stand proportion of uprooted trees included treatment, mean stand height, competition, and

tree age as predictors (Table 9, Annexe B). Our results showed that the proportion of uprooted trees was similar between the control and thinning treatments (Fig. 18 B),while it was six times higher in the shelterwood treatment compared to the control and 2.5 times higher than in the thinning treatment (Table 9, Fig. 19 A). The model assessing uprooting proportions exhibited a null deviation of 69.86 and a residual deviation of 40.15, indicating that the model fit was significantly better than the null model.

The logistic regression model identified as best explaining the stand-level proportion of broken trees included mean stand height, mean stand age, and mean interspecific competition as predictors (Table 9, Annexe B). The proportion of broken trees per stand increased significantly with both stand mean height and stand mean age, with each one standard deviation increase in height and age associated with approximately 37 % and 25 % higher odds of breakage, respectively (Table 9, Fig. 19 C-E). In contrast, higher mean interspecific competition was linked to a 14 % reduction in the odds of tree breakage. The proportion of broken trees did not differ significantly among treatments (Figure 18 C). The selected model for assessing the proportions of broken trees revealed a null and residual deviance of 49.36 and 25.08, respectively, which shows a good model fit when compared to the null model.

In the most parsimonious logistic regression model explaining the stand-level proportion of uprooted trees, the only predictor was the mean annual wind speed 30 m above the ground (Table 5, Annexe B). This model revealed that snag proportions per stand increased with wind speed measured 30 m above the ground (Table 9, Fig. 19 B). According to the model, for each standard deviation increase in mean annual wind speed, the odds of trees being snags increase by approximately 11.8 times. Similar stand-level proportions of snags were observed in the shelterwood treatment compared to the control. In contrast, lower proportions were found in the thinning treatment (Fig. 18 D). The model assessing snag stand proportions revealed a null deviance of 76.91 and a residual deviance of 58.93, which shows an adequate model fit.

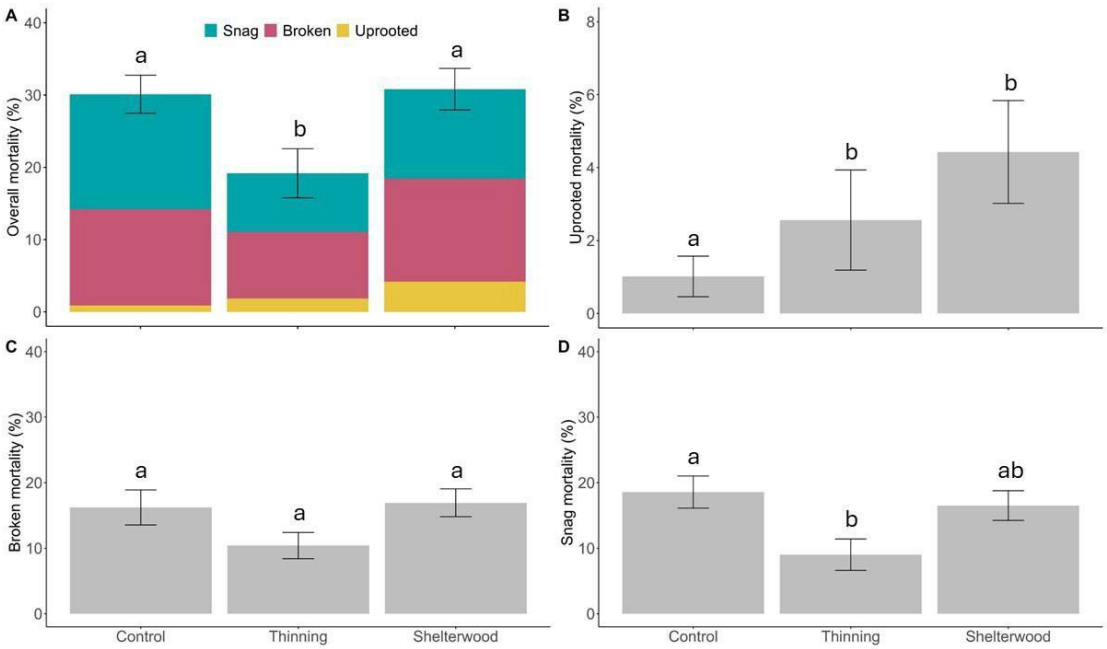

Figure 17
Mean stand proportion of overall (A), uprooted (B), broken (C), and snag (D) mortality per treatment.
Vertical bars represent the standard error (SE). Letters indicate significant (p < 0.05) differences among treatments.

Table 10
Parameters, coefficients, and confidence intervals (CI) for the selected generalized linear models assessing variables influencing stand-level proportions of dead trees for each dead tree type.
VIF: Variance Inflation Factor. σ1: standard deviation of the random intercept for the site grouping factor.

Uprooted							
R^2_m = 31.1 %. R^2_c = 70.5 %. AICc = 91.08							
Parameter	**Coefficient (β)**	**St. Dev**	**Std. Error**	***p*-value**	**Lower 95% CI**	**Upper 95% CI**	**VIF**
σ1	-	0.86	-	-	0.31	0.60	-
Intercept	-5.21	-	0.60	< 0.01	-6.68	-4.19	-
Thinning	0.91	-	0.73	0.21	-0.62	2.46	-
Shelterwood	1.84	-	0.68	**< 0.01**	0.51	3.42	-
Broken							
R^2_m = 59.19 %. R^2_c = 59.19 %. AICc = 130.37							
σ1	-	0.0	-	-	0.00	0.31	-
Intercept	-2.01	-	0.07	< 0.01	-2.17	-1.87	-
Mean height	0.32	-	0.09	**< 0.01**	0.15	0.49	1.09
Mean age	-0.15	-	0.07	**< 0.01**	-0.30	-0.01	1.06

Mean competition	0.22	-	0.07	**< 0.05**	0.07	0.37	1.03
Snag							
R^2_m = 20.7 %. R^2_c = 60.2 %. AICc = 145.02							
σ1	-	0.40	-	-	0.2	0.67	-
Intercept	-2.06	-	2.31	< 0.01	-2.31	-1.84	-
Wind speed	2.47	-	0.55	**< 0.01**	0.06	0.49	-

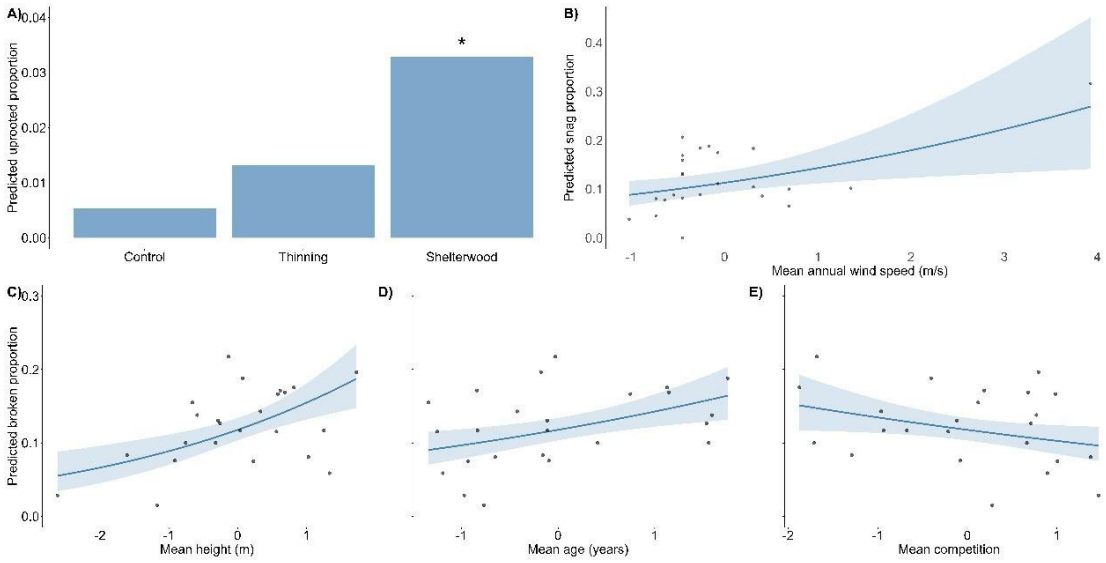

Figure 18
Predicted proportions of each dead tree type based on the models assessing the proportions of each dead tree type.
Variables in the horizontal axis are scaled to standardize them due to their different units. Asterisk (*) indicates the significant ($p < 0.05$) differences detected among treatments. The shaded area around the regression line represents the 95% confidence interval of the regression, indicating the range where the true mean response is likely to fall.

Greater proportions of uprooted and broken trees were found in trees located in the first 5 meters from the skidding trail compared to distances beyond that limit. Generally, snag proportions did not differ significantly with distance to the skidding trail (Table 10).

Table 11
Parameters, coefficients, confidence intervals (CI), and McFadden's pseudo-R-squared for the models assessing the influence of the distance to the skidding trail on each dead tree type.
Position: I = stands for the position referring to distances beyond 5 meters from the skidding trail.

Response variable	Coefficient (β)	Std. Error	*p*-value	Lower 95% CI	Upper 95% CI	$R^2_{McFadden}$
Uprooted						
Intercept	-3.37	0.34	< 0.01	-4.11	-2.77	21.22 %
Position: I	-1.57	0.79	**< 0.05**	-3.45	-0.20	
Shelterwood	0.47	0.42	0.26	-0.33	1.33	
Position: I * Shelterwood	1.02	0.89	0.25	-0.61	3.04	
Broken						
Intercept	-2.01	0.19	< 0.01	-2.40	-1.66	41.2 %
Position: I	-0.61	0.30	**< 0.05**	-1.22	-0.03	
Shelterwood	0.46	0.24	0.06	0.00	0.93	
Position: I * Shelterwood	-0.01	0.39	0.99	-0.76	0.76	
Snag						

Intercept	-2.70	0.25<	0.01	-3.23	-2.24	44.2 %
Position: I	0.50	0.32	0.12	-0.11	1.15	
Shelterwood	0.77	0.30	**< 0.05**	0.19	1.38	
Position: I * Shelterwood	-0.50	0.40	0.22	-1.30	0.28	

2.4 Discussion

2.3.4 Live aboveground carbon stocks

Our results showed that partial cuts increased individual tree carbon stocks but had contrasting effects on stand-level live aboveground carbon. While similar live aboveground carbon stocks were found among the moderate thinning treatment (30–35% stem removal) and the controls, a 41% decline was found in the shelterwood treatment (40–50% stem removal). Although mean live carbon in thinning stands was approximately 25% lower than in controls, this difference was not statistically significant, reflecting the high variability in the impacts of harvest on the carbon stocks across our study sites. Standing live volume immediately declines following harvest by an amount proportional to the stems removed. Subsequent growth trajectories may be parallel if residual trees compensate for the increment lost from harvested trees through crown expansion, or divergent if canopy openings are too large to permit full compensation, thereby reducing stand productivity (McKinnon and Kayahara, 2006). In our study, trees in thinning stands grew faster than those in controls, yet total stand carbon remained similar 8 years post-harvest, consistent with a parallel yield trajectory. In contrast, the shelterwood stands exhibited a decline in stand-level carbon, reflecting a divergent trajectory due to insufficient compensation by the improved radial growth of residual trees. However, because our assessment spans only 8 years post-harvest, and previous studies have shown that jack pine stands subjected to heavy thinnings of comparable intensity can achieve parallel trajectories after 10 years (Barrette et al., 2018), our timeframe may be too short to fully assess the yield trajectory of the shelterwood treatment. Due to the low number of thinned sites in our study area, our study sites were heterogeneous in terms of stand density, tree DBH, and forest age. This within-treatment variability could have influenced the observed responses, such as carbon stocks and growth trajectories and should be taken into account when interpreting our results.

Our model determined that trees with greater DBH at the time of harvest (DBH_{bh}) exhibited the greatest biomass increase after harvest. The increase in tree biomass with increasing initial DBH may be attributed to the larger crowns, which enhance light

interception and support higher growth potential (Dronova et al., 2011; Mensah et al., 2020). Furthermore, our model indicated greater biomass change in trees located closer to skidding trails. This was likely due to reduced competition near trail edges, where partial harvesting was primarily conducted (Fig. S10 Annexe B). Trees growing in these areas likely benefited from increased light availability, which in turn improved tree growth and individual tree carbon stocks. This conclusion aligns with previous findings reporting reduced tree competition and increased light availability following canopy openings (Chase et al., 2016), as well as with studies documenting higher light intensities and enhanced tree growth rates near road or trail edges in other conifer species (Bowering et al., 2006; Delgado et al., 2007; Genet and Pothier, 2013; Montoro Girona et al., 2016).

2.3.5 Deadwood carbons stocks

The proportion of uprooted trees increased in partial cut stands. This increase in uprooting can be explained by the loss of tree-to-tree mechanical support following stem removal. These effects were particularly pronounced in the shelterwood treatment, which had the highest harvest intensity and therefore the greatest reduction in mechanical support. Supporting this explanation, previous studies have shown that reducing neighbour tree support lowers the critical wind speed (i.e. the threshold at which wind induces structural failure in trees), making them more vulnerable to wind damage (Peterson and Cannon, 2021). In addition, the proportion of trees showing stem breakage was higher with decreasing stand competition and near the skidding trails, consistent with reduced tree-to-tree contact and mechanical support in these locations. Although the proportion of uprooted trees was higher in shelterwood stands, the mean carbon per hectare of uprooted trees remained similar across treatments. This likely reflects the lower proportion of codominant trees and higher proportion of suppressed trees in shelterwood stands (Annexe B), which likely implied that many of the additional uprooted trees were smaller and contributed relatively less to mean total carbon per hectare.

The increase in stem breakage with greater stand mean height may be attributed to lower stem taper (i.e., stem diameter decreases more gradually with tree height) in

taller trees. Such morphological characteristics may have compromised mechanical stability, making trees more susceptible to structural failure after harvest. Similar findings have been reported in Monterey pine (*Pinus radiata* D. Don) stands, where lower taper was associated with reduced resistive bending moments (Moore, 2000), indicating a diminished capacity to withstand wind stress. Another possible explanation is that taller trees experience higher bending moments (i.e., greater torque). Since the bending moment is defined as the product of force applied (e.g. wind) and lever arm distance (Peltola, 2006), an increase in height extends the lever arm through which wind acts. As a result, for a given wind force, the torque at the base increases with tree height (Peltola, 1996), leading to greater mechanical stress. In addition, stem breakage increased with stand age, likely due to the existing positive correlation between stand age and mean height (Béland and Bergeron, 1996). Moreover, the increasing stem breakage with tree age could also be related to the greater presence of wood decay, as wood decay increases with age and its presence reduces the wind speed needed to induce stem breakage (Honkaniemi et al., 2017; Aishan et al., 2024). Overall, these results demonstrate that morphological and age-related stand attributes are key determinants of structural stability and wind damage susceptibility.

The application of partial cuts altered both the snag proportions and their contribution to carbon stocks. A reduction in snag abundance was found in the thinning treatment when compared to shelterwood and control stands, whereas snag proportions in shelterwood and control stands remained similar. Differences in snag carbon stocks across treatments may reflect a combination of stand age and harvest patterns. Shelterwood stands were older on average (86 ± 13 years) than control (76 ± 19 years) and thinning stands (66 ± 14 years), likely resulting in higher pre-harvest snag abundance, as snag numbers generally increase with stand age (Lee, 1998). In shelterwood stands, a lower proportion of codominant trees and a higher proportion of suppressed trees suggest harvesting was conducted from above (Annexe B), selectively removing larger codominant while retaining smaller and mid-diameter trees, including suppressed individuals and potential future snags. Consequently,

snag abundance remained similar to controls, but mean snag carbon stocks per hectare were lower because retained trees were smaller and contained less carbon. In thinning stands, a larger fraction of small- and mid-diameter trees, including both existing and potential snags, was removed, reducing snag abundance and mean carbon stocks per hectare. These patterns explain why total deadwood carbon stocks were lower in both shelterwood and thinning treatments compared to controls, despite similar amounts of uprooted and broken trees, highlighting the influence of stand structure and harvest strategy on snag carbon and deadwood stocks.

Our models revealed that snag abundance increased with increasing wind speed 30 m above the ground. It is difficult to explain this relationship, and a before-harvest forest inventory may have allowed us to further explain the driving factors behind the proportions of snags in our study. Therefore, we recommend future studies assessing the driver factors of snag mortality to include pre-harvest data.

2.4 Implications for forest management

The jack pine-dominated, even-aged forests on esker substrates in Quebec are currently transitioning from a clear cut-dominated management approach to one emphasizing greater tree retention (i.e., partial cuts). This shift, promoted by the local administrations, aims to reduce the impacts of forestry on both surface and groundwater, which are of vital interest for local communities and biodiversity conservation (Nadeau et al., 2015; Hasan et al., 2023). Therefore, although partial cuts fall outside the traditional even-aged management of jack pine stands, these treatments are being tested as potential alternatives to clear cuts for the esker forests. Our study addresses how two partial cut treatments impact the aboveground carbon stocks of jack pine-dominated esker forests. The selected partial cuts included a commercial thinning with 30–35% basal area removal using a from-below approach, and a shelterwood treatment with 40–50% basal area removal using a from-above approach.

Live aboveground carbon stocks were similar in the thinning treatment compared to those of unharvested stands 8 years after harvest. In contrast, lower live aboveground

carbon stocks were found in shelterwood stands. Given that trees with wider pre-harvest DBH accumulated more carbon during the 8 years following harvest, retaining large-diameter trees appears advisable when forest management aims to sustain carbon storage through tree growth and may be advised when performing the shelterwood treatment.

In our study, trees located closer to skidding trails exhibited greater radial growth and therefore greater aboveground biomass increases, likely because of improved growth conditions near the trail edges (Bowering et al., 2006; Genet and Pothier, 2013; Montoro Girona et al., 2016). Future research should incorporate distance to skidding trails and trail density when modelling the carbon impacts of partial cuts or retention forestry in boreal forests. Our findings also highlight that the distance from trees to skidding trails significantly influenced the type of post-harvest mortality, with increased uprooting and stem breakage near trail edges, in accordance with previous work (Thorpe et al., 2008; Montoro Girona et al., 2019). Therefore, forest managers should carefully design skidding trail density, especially in windthrow-prone areas, to mitigate ecological impacts and reduce economic losses as, to the best of our knowledge, skidding trail density is not currently included among the criteria guiding harvest design in this region. One practical approach to reduce trail density while maintaining harvest intensity may be to fell trees using chainsaws and extract logs with cable skidders to existing trails, which can maintain harvest intensity while reducing skidding trail density. In addition, the shelterwood treatment, which removed 40–50% of the basal area, resulted in greater tree uprooting compared to the other treatments. Consequently, this level of harvest intensity may be inadvisable for managing jack pine stands on esker soils, whereas thinnings with a lower intensity of 30–35% could be more suitable to minimize windthrow mortality. Furthermore, stem breakage was found to increase with stand age, mean stand height, and in areas with lower competition. These factors should therefore be carefully considered when planning silvicultural interventions to reduce mechanical damage and maintain stand stability.

Deadwood carbon stocks were lower in both thinning and shelterwood treatments than in control stands, primarily due to reduced snag carbon in the partially cut stands, while

the carbon stocks in uprooted and stem-broken trees remained relatively unchanged. To mitigate these reductions, forest managers should prioritize snag retention during harvest operations, thereby maintaining deadwood carbon closer to control levels. Furthermore, the proportion of snags decreased in the thinning treatment when compared to the rest of the treatments. This decline could compromise biodiversity goals since snags play a crucial role in forest biodiversity, as snags are necessary for a wide variety of organisms for habitat, nesting or foraging (Nilsson et al., 2001; Aakala et al., 2007; Michel and Winter, 2009; Weiss et al., 2018). Therefore, besides the impacts of carbon stocks, thinning might also conflict with objectives related to habitat conservation. Thus, the retention of snags may be advised from both a carbon and biodiversity perspective. Given that live carbon stocks under thinning are already comparable to controls, achieving similar total deadwood carbon stocks through the retention of snags would make this treatment a strong candidate for carbon-oriented forest management.

The results indicate that partial cuts and canopy openings influence both uprooting and stem breakage through reductions in tree-to-tree mechanical support. Forest managers should carefully consider how harvesting intensity and pattern affect stand structure, particularly the density and spatial arrangement of residual trees. Retaining clusters of codominant trees or maintaining higher stand competition in strategic areas could reduce the risk of wind-induced uprooting and stem breakage, and thus should be assessed in future silvicultural trials, as has been done in other regions (Urgenson et al., 2013; Hämäläinen et al., 2016). Furthermore, the greater susceptibility of older trees to mechanical failure highlights the need to carefully consider stand age in management decisions, as studies in nearby regions suggest an optimal rotation period of approximately 73 years for jack pine when accounting for wood resistance (Duchesne, 2006), and several of our harvested sites exceeded that threshold.

Author contribution statement

MAP: Conceptualization, Methodology, Software, Data curation, Investigation, Formal analysis, Validation, Visualization, Writing – original draft. MMG and AD: Conceptualization, Funding acquisition, Resources, Project administration, Supervision, Validation, Writing – review & editing.

3. WINDTHROW MORTALITY INFLUENCED BY NATURAL ROOT GRAFTING IN BOREAL JACK PINE FORESTS

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Résumé

Le chablis est une perturbation naturelle qui affecte la dynamique forestière et se caractérise par le déracinement ou la rupture des troncs lorsque la force du vent dépasse la résistance des ancrages ou des troncs. La mortalité due au chablis a été associée à plusieurs facteurs écologiques biotiques et abiotiques. Cependant, l'influence du greffage naturel des racines sur la mortalité due au vent reste inconnue. Cette recherche a évalué l'influence du greffage des racines sur la mortalité due au vent en excavant les systèmes racinaires du pin gris (*Pinus banksiana*) dans quatre zones tampons riveraines touchées par le vent et en analysant les greffes de racines à l'aide d'une approche dendrochronologique. Nos résultats ont révélé que le greffage naturel des racines diminuait la probabilité de déracinement, mais augmentait la propension à la rupture des tiges. De plus, le greffage des racines était plus fréquent chez les arbres plus proches les uns des autres. Ces résultats suggèrent que le greffage des racines influence le type de mortalité due au vent, la proximité des arbres étant un bon indicateur du greffage des racines. Cette étude fournit des informations précieuses sur la dynamique du vent, particulièrement utiles pour gérer la mortalité due au vent après une récolte partielle et dans les zones tampons riveraines, pour conserver les sols et pour atténuer les impacts des événements liés au vent dans le contexte du changement climatique.

Mots clés : dendrochronologie pin gris greffage racinaire mortalité des arbres chablis

Abstract

Windthrow is a natural disturbance affecting forest dynamics, characterized by tree uprooting or stem breakage when wind forces surpass tree anchorage strength or stem resistance. Windthrow mortality has been related to several ecological biotic and abiotic factors. However, the influence of natural root grafting on windthrow mortality remains unknown. This research evaluated the influence of root grafting on windthrow mortality by excavating root systems of jack pine (Pinus banksiana) in four windthrow-affected riparian buffers and analyzing root grafts using a dendrochronological approach. Our results revealed that natural root grafting decreased the uprooting likelihood but increased the propensity for stem breakage. In addition, root grafting occurred more frequently in trees closer to one another. These results suggest that root grafting influences the windthrow mortality type, with tree proximity being a good predictor for root grafting. This study provides valuable insights into windthrow dynamics, particularly relevant for managing windthrow mortality following partial harvesting and riparian buffers, conserving soil, and mitigating the impacts of windthrow events in the face of climate change.

Keywords: dendrochronology jack pine root grafting tree mortality windthrow

3.1 Introduction

Two-thirds of the boreal forest is managed, producing 9% of the world's industrial roundwood (Gauthier et al., 2015; FAO, 2020). Traditionally, clear cuts represented the most popular harvest method in the boreal forest due to their better cost-efficiency (Dussart & Payette, 2002; Keenan & Kimmins, 1993; Montoro Girona et al., 2023). Clear cuts are a group of silvicultural treatments that involve the simultaneous harvest of most or all trees in a stand (Seedre et al., 2018). Riparian buffers are often left unharvested to dampen the effects of clear cuts on nearby freshwater ecosystems, such as the increase in surface water runoff, or the alterations in water chemistry (Carignan et al., 2000; Sørensen et al., 2009; Bahuguna et al., 2010). However, the residual trees left in buffer strips are often affected by windthrows, jeopardizing their beneficial buffering effects (Guimond et al., 2024).

Windthrow is a natural disturbance that influences structural diversity and tree succession (Gromtsev, 2002; Kneeshaw et al., 2011). Windthrow occurs when the force exerted by the wind exceeds the anchorage strength of the tree or the resistance of its stem, leading to tree uprooting or breakage (Klaus et al., 2011; Quine et al., 2021). Tree vulnerability during windthrow events depends on a complex ecological interaction of biotic and abiotic factors, such as topography, substrate type, tree size, tree species, and forest management practices (Xi and Peet, 2011; Montoro Girona et al., 2019). Moreover, interspecific (Pang et al., 2024), and intraspecific differences in root architecture (Danjon et al., 2005; Štofko and Kodrík, 2008), as well as differences in soil properties (Fourcaud et al., 2008; Mansour et al., 2024), and in the root-soil plate (i.e, roots and adhered soil) (Coutts, 1986; Moore, 2000), have been reported to influence root anchorage. Natural root grafting is also often explained as an evolutionary mechanism giving trees better stability against windthrow (Keeley, 1988; Loehle and Jones, 1990).

Natural root grafts are formed when the roots of initially independent trees come into permanent contact, inducing bark breakage at the pressure point and allowing the fusion of cambium, xylem, and phloem to establish vascular continuity (Graham and Bormann, 1966). Root grafting has been reported to influence disease transmission,

carbohydrate transfer, and tree growth (Bloomberg and Reynolds, 1982; Fraser et al., 2006; Tarroux et al., 2010). The presence of root grafts has also been argued to explain the greater resistance of European beech (*Fagus sylvatica* L.) during a rockfall simulation in the French Alps (Stokes et al., 2005). Moreover, increased uprooting resistance due to root grafting has been used to explain why grafted Tabonuco (*Dacryodes excelsa* Vahl.) trees showed lower wind damage than non-grafted trees after a tropical hurricane, while non-grafted trees were uprooted (Basnet et al., 1993).

Natural root grafting has been observed in most pine species, including jack pine (*Pinus banksiana* Lamb.) (Bormann and Graham, 1959; Miller and Woods, 1965; Fraser et al., 2005; Tarroux and DesRochers, 2010). Jack pine is one of the most relevant commercial tree species in Canada and has shown greater windthrow mortality rates (70-82 %) compared to other boreal species due to its self-pruning at a young age, which produces an early transition from a low to high gravity center (Rich et al., 2007; Fleming et al., 2018).

The main objective of this study was to determine if there is a relationship between natural root grafting and windthrow mortality in jack pine stands. We hypothesized that

(1) grafted trees would have a lower probability of uprooting than non-grafted trees,

(2) grafted trees would be more likely to show stem breakage than tree uprooting, and

(3) the root grafting frequency would be greater in trees growing closer to one another (Tarroux and DesRochers, 2010).

3.2 Materials and methods

3.2.1 Study sites

The study sites were located in eastern Canada (Fig. 20), within the spruce-moss bioclimatic domain (MFFP, 2021; MRNF, 2023). The total annual precipitation is 929 mm, with 27% falling as snow, and the annual average temperature is 1.5 ± 2.5 °C (mean ± standard deviation) (Environment Canada, 2024). Sites were located over glacial soils and the glaciolacustrine soils of the esker ecosystems (Hasan et al.,

2023). Esker soils are typically characterized by a sandy and gravelly texture formed by glacial or sub-glacial streams (Syverson et al., 1994; Lindroos et al., 2020). Stands were even-aged and originated after a fire in 1920 for Site 1 and in 1905 for Sites 2, 3, and 4 (Government of Quebec, 2019).

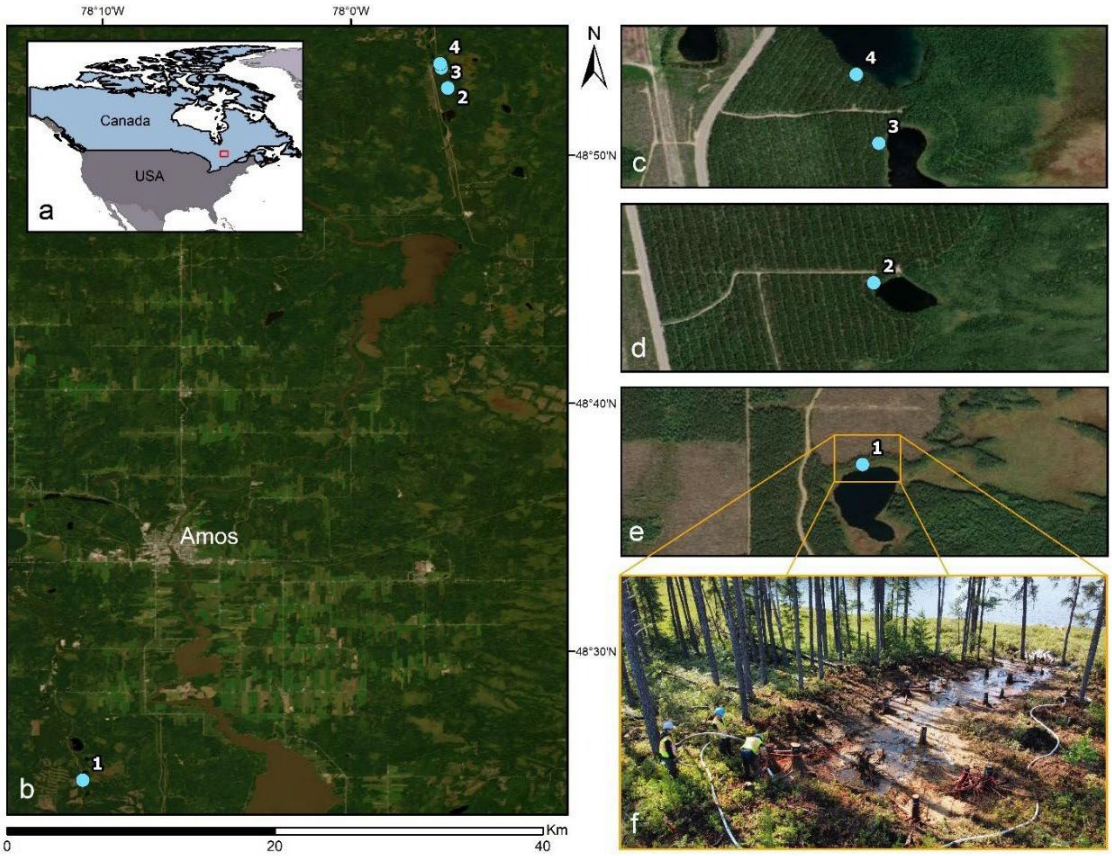


Figure 19
Location (a, b) and satellite view of the study sites (c, d, e), and drone view of excavation Site 1 (f).

3.2.2 Site selection and sampling protocol

We selected a total of 4 jack pine-dominated (> 75 %) stands in riparian buffers based on information from the forest inventories provided by the Ministry of Natural Resources and Forests of Quebec (Government of Quebec, 2019). Nevertheless, different jack pine proportions were obtained when the sites were inventoried during the fieldwork, ranging from 50 % to 95 % (Table 11). Riparian buffer stands were selected as they are located near water bodies required for a continuous water supply

during the hydraulic excavation of root systems. Forest strips located next to recent (4 to 7 years since harvest) clear cuts were prioritized to increase the proportion of tree mortality and to increase the number of cross-sectional disks from dead trees with an adequate conservation state. Sites on sandy and sloping soils were selected to facilitate the excavation and water drainage during the excavation.

Table 12
Site characteristics for the root grafting chapter.
[1]Clear cut year information extracted from Government of Quebec, 2019. [2]SD: standard deviation.

Site	Latitude	Longitude	Clear cut year[1]	jack pine proportion (%)	Stand age (± SD)[2] (years)	Average DBH (± SD)[2] (cm)	Density (trees/ha)	Excavated trees		
								Total	Uprooted	Broken
1	48°24'48.1" N	78°10'47.9" W	2016	95.0	97.70 ± 0.48	25.09 ± 4.67	505	31	4	11
2	48°52'41.9" N	77°56'05.5" W	2020	72.2	111.2 ± 2.22	23.05 ± 2.43	833	23	3	4
3	48°53'31.0" N	77°56'20.9" W	2020	50.0	113.0 ± 0.82	18.38 ± 4.35	442	25	4	5
4	3'40.4" N	3'24.0" W	2020	61.9	111.7 ± 0.76	18.89 ± 4.41	595	23	6	3

Sampling was done in August 2023, labeling jack pine trees and stumps and distinguishing between live, broken, uprooted trees, and snags (i.e., standing dead). Trees were felled with a chainsaw, and cross-sectional disks were extracted at the base to estimate tree age. The area surrounding all the selected trees was manually cleaned from the moss and *Kalmia spp* layer, bushes, and saplings with shovels, hoes, garden rakes, and pruning shears. The distance between each stump was measured. Root systems were exposed by removing the superficial soil layer using high-pressure water from a hydraulic pump (Mark III; Wajax, Lachine, Canada) (Tarroux et al., 2010)

(Fig. 19 f). All possible root grafts were collected, and the root systems of the trees that shared root grafts were extracted with a chainsaw and transported to the laboratory. The dimensions of each excavated rectangular plot were measured, and an inventory was performed, noting the length (L) and width (W) of each plot, the number of live jack pines (N_{ajp}), the number of other tree species (N_{other}), and calculating the jack pine proportion in trees per hectare (Equation 5, Table 11).

$$jjDDDDjj\ aaiimmDD\ ddDDmmDDiiDDdd\ (DD\theta\theta DDDDDD/hDD) = \left(\frac{NN_{DDjja\quad a}}{NN_{DDjjaa} + NN_{ooDDhDD\theta\theta}}\right) \times \left(\frac{10000}{LL \times WW}\right) \quad (5)$$

3.2.3 Laboratory work

The laboratory work took place in the GREMA lab at the UQAT campus of Amos, Quebec, Canada. All samples were air-dried, and each root section was carefully labeled to indicate the specific tree from which the root originated. Cross-sectional disks were extracted from all suspected root grafts to verify the existence of vascular continuity among roots. We found no inter-specific root grafts. All cross-sectional and root graft disks were progressively sanded with 100, 200, 300, and 400 grit sandpaper using an industrial PMC-216 Stroke Belt Sander and Polisher (Doucet Machineries Inc., Daveluyville, Canada). If root growth rings were still difficult to visualize, manual sanding was applied with 600 and 1000 grit or cut with an industrial band saw. Due to the narrow rings found, the cross-sectional disks and the graft sections were digitalized with a scanner (Expression 12000XL, Seiko Epson Corp., Suwa, Japan) to obtain a clearer visualization during the dating process and age estimation.

Bark breakage and the formation of root grafts create a region where tree rings are difficult to visualize due to callus formation (Tarroux et al., 2010). Consequently, we identified the first visible shared ring as the one corresponding to the graft formation year (Fig. 21). The age of trees, roots, and the year in which root grafts were formed were determined by dating growth rings from both cross-sectional disks of the trunk

and grafts and by using pointer years to accurately date the samples (Schweingruber, 1988; Tarroux and DesRochers, 2010). For one of our root grafts, estimation of the graft formation year was not possible because the trees were in an advanced decomposition state or no cross-sectional disk from the trunk was available. A total of 91 cross-sectional disks and 19 root grafts were analyzed.

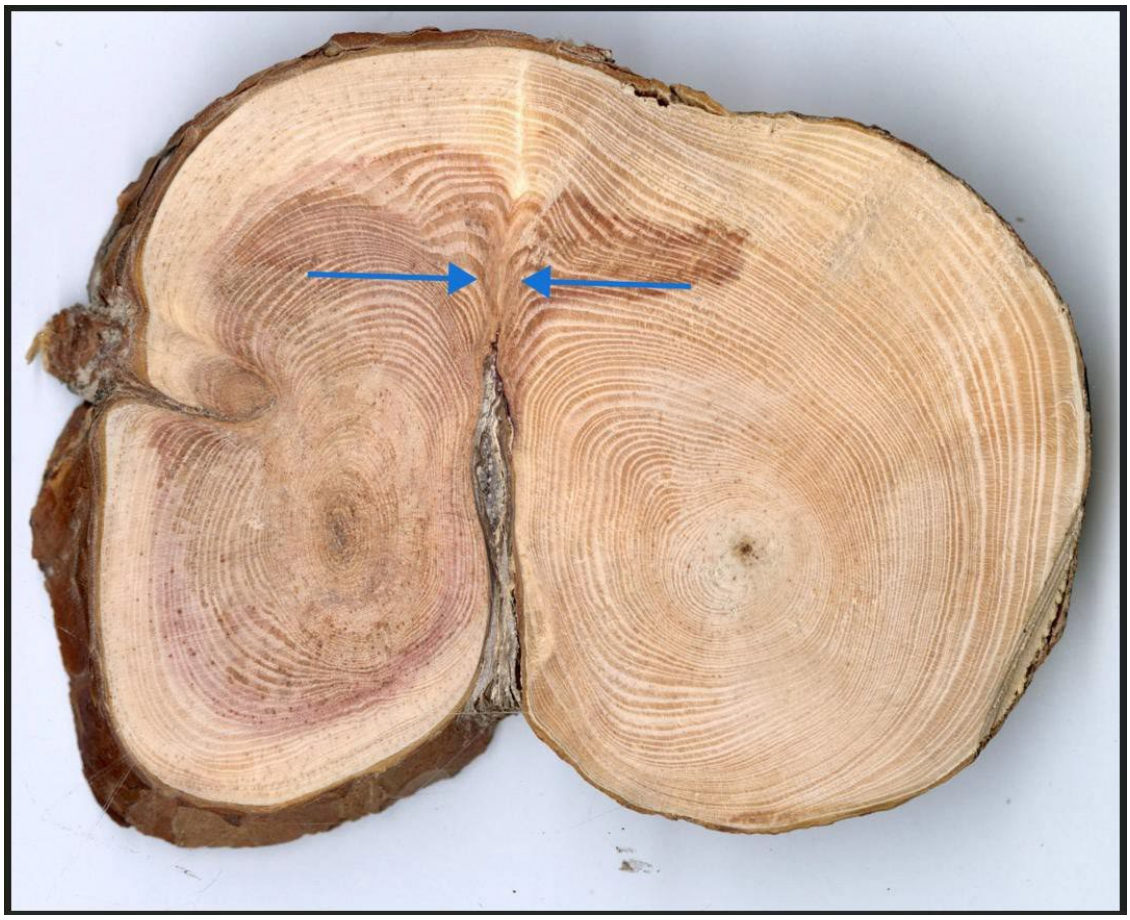


Figure 20
Natural root graft formed between roots of two different jack pines. Arrows indicate the first visible shared ring considered as the one belonging to the graft formation year.

3.2.4 Data analysis

A first contingency table was created to assess the influence of root grafting on uprooting probability. It included the number of grafted and non-grafted trees from

each of the two status classes: standing (including live, broken, or snags), and uprooted trees. A second contingency table was used to analyze the influence of root grafting on the probabilities of stem breakage and tree uprooting. Fisher's exact test was applied in each contingency table due to the lower expected frequencies detected (Mcdonald, 2009; Nowacki, 2017). Site 4 was not considered due to the absence of

root grafts. Proportions of grafted and non-grafted trees in each category were included in each contingency table to facilitate the interpretation of Fisher's test results.

A Pearson's correlation test was used to assess the relationship between the distance among trees and the grafting frequency. All statistical analyses were conducted using R version 4.3.3, with a significance level set at $p = 0.05$ for all response variables.

3.3 Results

Our results show that natural root grafting decreased the likelihood of tree uprooting (Table 12, Fisher's exact test: $p < 0.01$). Grafted trees represented 48 % of the jack pines in Site 1, while this proportion was 8 % for Sites 2 and 3. The number of root grafts also showed marked differences between sites, ranging from zero to 15 grafts (Table 13). Our dendrochronological analysis revealed that all uprooted trees were uprooted after the clear cut was done in the adjacent stand. The proportion of uprooted trees varied among riparian buffers, with Site 1 showing the lowest uprooting mortality rates (10 %) and Site 4 the greatest (20 %) (Table 3).

We also found an influence of root grafting in the windthrow mortality type, with grafted trees being more prone to stem breakage than tree uprooting (Table 14, Fisher's exact test: $p < 0.05$). The proportion of broken trees ranged from 18 % of the total amount of dead jack pines to 50 % depending on the site (Table 13). The minimum distance between grafted trees was 0.06 m, while the maximum reached 1.56 m (Table 13). Moreover, 89 % of the grafts were located among trees closer than 1 meter from each other. A trend was found between the proximity among trees and the year of graft formation, showing that greater distances between trees delayed graft formation. However, the correlation was weak (rho = 0.32) and not significant ($p = 0.24$).

Table 13
Contingency table displaying the counts of standing and uprooted jack pine trees categorized by grafting status (grafted vs. not grafted). Proportions of grafted and non-grafted trees in each category are in parentheses.

Standing			**Uprooted**		Total
	Observed	Expected	Observed	Expected	
Grafted	23 (1.0)	19.13	0 (0.0)	3.87	23
Not grafted	61 (0.78)	64.87	17 (0.22)	13.13	78
Total	84		17		101

Table 14
Jack pine mortality rates and grafts found per site.

	Site 1	**Site 2**	**Site 3**	**Site 4**
Total mortality (%)	54	44	67	57
Windthrow mortality (uprooted) (%)	10	13	12	20
Proportion of broken to total mortality (%)	50	40	23	18
Proportion of snags to total mortality (%)	32	30	60	47
Windthrow to total mortality (%)	68	70	41	53
Trees with no cross-sectional disk	23	5	4	4

analyzed (%)				
Number of grafts	15	4	4	0
Number of non-dated grafts	1	0	0	0
Grafted trees (%)	48	9	8	0
Shortest distance among grafted trees (m)	0.25	0.30	0.06	-
Greatest distance among grafted trees (m)	1.35	1.56	0.14	-

Table 15
Contingency table displaying the counts of broken and uprooted trees categorized by grafting status (grafted vs. not grafted). Proportions of grafted and non-grafted trees in each category are in parentheses.

	Broken		**Uprooted**		Total
	Observed	Expected	Observed	Expected	
Grafted	9 (1.0)	5.18	0 (0.0)	3.82	9
Not grafted	14 (0.78)	17.82	17 (0.22)	13.18	31
Total	23		17		40

3.4 Discussion

Our results revealed that natural root grafting reduced the likelihood of tree uprooting in agreement with our first hypothesis. This study is the first to explore the relationship

between root graft presence and tree uprooting and supports the general assumption of greater mechanical resistance to uprooting during windthrow events due to root grafting (Graham and Bormann, 1966; Keeley, 1988). Aligned with our second hypothesis, we present novel evidence that root grafting influences the mortality type, with grafted trees affected by strong wind gusts being more prone to stem breakage. Similarly, Štofko & Kodrík (2008) found less extensive root-soil plates in Norway spruce (*Picea abies* L.) trees that were uprooted during windthrow events, while Moore (2000) related greater root-soil plates in Monterrey pine (*Pinus radiata* D. Don) with greater bending moments (i.e., greater maximum resistance of the tree stem to failure or the root system to overturn). In addition, an increase in the number of lateral roots has been reported to reduce the uprooting frequency in boreal black spruce stands (Krause et al., 2014). The formation of natural root grafts expands the root-soil plate surface of trees and increases the number of lateral roots sustaining the stem, which could enhance tree anchoring, increasing the bending moment that the tree can resist before being uprooted and, thus, reducing uprooting likelihood. When a tree is subjected to wind forces, the root system experiences differential stresses: on the lee side, the roots endure bending and compressive forces, while on the windward side, where the root-soil plate is lifted, the roots are subjected to tensile and shear forces (Coutts, 1986; Mattheck and Bethge, 1991). By increasing the size of the root plate and the number of lateral roots, the formation of root grafts reduces the movement capacity of the leeward and windward sides of the root system, creating a more rigidsystem that can reduce the capacity to absorb mechanical energy, deviating it to the stem and increasing stem breakage probability. However, this reduction in the movement capacity of the root system may only apply when the wind direction is aligned with the imaginary line connecting the grafted trees. Nevertheless, the overall increase in the root-soil plate area provided by the grafts could stabilize the root system irrespective of the wind direction. We encourage future research to investigate the dynamics between root-soil surface, number of lateral roots, wind direction, and root grafting, which was beyond the scope of this study. Moreover, our study focused on jack pine, a species presenting a tap-root system that has been reported to be more resistant to uprooting than that of other genera characterized by shallow roots, such

as the *Picea* or *Abies spp.* (Dupuy et al., 2007; Lavoie et al., 2012; Taylor et al., 2019; Guimond et al., 2024). This should be considered when interpreting our results as the influence between root grafting on uprooting probability or stem breakage or its magnitude could differ depending on the tree species considered. Root grafting frequency increased with trees being closer to one another. These results matched the expectations included in our third hypothesis and are consistent with previous research that revealed that distance among trees is an adequate predictor of root grafting (Reynolds and Bloomberg, 1982; Külla and Lõhmus, 1999; Fraser et al., 2005; Tarroux and DesRochers, 2010; Gaspard and DesRochers, 2020).

The application of clear cuts has been associated with alterations in stand structure (Bouchard and Pothier, 2011), biodiversity (Rosenvald and Lõhmus, 2008), deadwood abundance, deadwood diversity (Nirhamo et al., 2023), soil properties (Sağlam and Gökbulak, 2024), and the carbon cycle (Jamroz and Jerzykiewicz, 2022), along with a lack of social acceptance (Bliss, 2000). This context is rising the interest in the use of partial cuts as promising silvicultural alternatives to clear cuts (Gauthier et al., 2023). Partial cuts harvest a proportion of trees in the stand, reducing the wind-dissipating effect of forest canopies which can also lead to greater windthrow mortality among the remnant trees (Achim et al., 2005; Lavoie et al., 2012; Montoro Girona et al., 2019). The influence of root grafting on tree stability during windthrow events could provide valuable insights for developing strategies to reduce the increased vulnerability of residual trees following partial cuts.

Moreover, our results could be of practical use when managing stands located in areas where soil integrity is of particular interest, such as steep slopes or where freshwater ecosystems and hydric resources are very vulnerable to forest practices. Retaining trees close to one another could represent an adequate alternative to silvicultural treatments such as crown thinning or thinning from above, where competing trees are selected and removed (Cameron, 2002).

The number of grafts found ranged from 0 to 15, and the proportion of grafted trees varied between 0 and 48 %, depending on the site, both of which were lower than in

previous studies focusing on pure jack pine stands (Tarroux and DesRochers, 2010). This could have been related to the fact that our sites were mostly mixed with black spruce, which could have increased the distance between trees, reducing the grafting frequency. Jack pine is a tree species that presents an early self-thinning that starts 15 years after the establishment (Yarranton and Yarranton, 1975; Béland et al., 2003). Tarroux & DesRochers (2010) found proportions of grafted jack pines ranging from 29

% to 71 % with 95 % of the graft being formed when the trees were 45 years old. Moreover, 50 % of the trees in pure lodgepole pine (*Pinus contorta* Douglas) stands were reported to be grafted with 92 % of the trees forming the graft at 20 years of age (Fraser et al., 2005). The advanced age of the trees in our study sites (98-113 years) could imply that grafts were formed in the past, but they were already decomposed when the fieldwork was done, reducing the number of grafting observations or the proportion of grafted trees.

3.5 Conclusion

Our study provides novel scientific evidence that root grafting reduces uprooting while increasing the likelihood of stem breakage. These findings can contribute to advancing current ecological knowledge of tree mortality by windthrow, which is particularly relevant given the increasing interest in partial harvesting and the associated after-harvest windthrow rates. Furthermore, our results could be of practical interest to forest managers in stands with conservation purposes, such as freshwater ecosystems. A better understanding of the windthrow dynamics could be of notable importance in the following decades due to the expected increase in frequency and severity of windthrow events under climate change scenarios, especially in the boreal regions, where windthrow plays a relevant role in forest dynamics (Girard et al., 2014; Saad et al., 2017).

Author contribution statement

MAP, MMG, and AD conceived and designed the experiment. MAP conducted the field and laboratory work, analyzed and interpreted the data, and wrote the first draft of this manuscript. MMG and AD provided funding, supervision, and administrative support for this research, as well as reviewed and edited the manuscript. All the authors approved the final version of the paper before submission.

GENERAL CONCLUSION

This thesis enhances the understanding of how boreal forest ecosystems respond to partial cut treatments. Specifically, we investigated the effects of partial cuts on jack pine–dominated esker forests, focusing on thinning shock, post-harvest growth release, changes in aboveground carbon stocks, and windthrow mortality. Furthermore, we explored the role of natural root grafting in shaping windthrow-related mortality, providing novel insights into the biomechanical mechanisms that influence tree stability during windthrow events.

Thinning shock and growth response. Our results revealed that thinning shock was more frequent near skidding trails and more intense in the shelterwood treatment. This implies that thinning shock is a tree growth phenomenon that can be linked to density reductions resulting from tree harvest. Moreover, the longer duration of thinning shock observed in trees located near skidding trails, as well as the inverse pattern detected in the shelterwood treatment, are likely attributable to higher windthrow-related mortality in shelterwood stands. This increased windthrow risk may result from greater tree removal intensity and/or older stand age compared with thinning stands, leading to continued reductions in stand density well beyond the harvest year.

The $\delta^{13}C$ analysis further deepens the understanding of the physiological causes behind thinning shock. The more negative $\delta^{13}C$ following harvest suggests that thinning shock is not produced by a temporary stomatal closure following harvest, as previously hypothesized (French et al., 2023), and thus that there is not a carbon uptake limitation following harvest. Hence, the carbon uptake following harvest may have been invested in other sinks rather than stem growth. One possible explanation is the expansion of the root system, increasing coarse and fine root growth, as it has been previously observed in other tree species following harvest (López et al., 2003; Vincent et al., 2009). Another possible explanation may be related to the diversion of assimilates from residual trees to the root systems of grafted trees that were harvested, as described for jack pine in previous work (Tarroux et al., 2010). Given

that root grafts are common in jack pine–dominated forests, as shown in Chapter IV, this mechanism may have contributed to the observed patterns.

We found greater radial growth rates in residual jack pine trees compared to those from control stands and in trees located near skidding trails, which is in accordance with findings revealing improved tree growth in jack pine stands following partial cuts (Moulinier et al., 2015), and with the improved growth conditions of trees near trails (Montoro Girona et al., 2016). However, our hypothesis of greater radial growth with increasing harvest intensity was not met, as trees in the thinning treatment (30-35 % of removal) presented greater radial growth rates during the 8-year post-harvest period compared to trees from the shelterwood (40-50 % of removal). These results may be related to a priority of harvesting trees from greater-diameter classes in the shelterwood treatment (i.e., harvest from above), leaving a greater proportion of smaller and slower-growing trees, which would explain the initially lower growth rates in the shelterwood treatment. In addition, shelterwood stands were generally older, and age-related declines in growth potential may have further constrained post-harvest radial growth compared with the younger thinning stands, as older stands have been shown to exhibit weaker growth responses to canopy openings in other boreal species (Montoro Girona et al., 2016). An additional explanation is that the greater harvest intensity in the shelterwood treatment created a larger imbalance between the remaining root biomass and the leaf area available to supply carbohydrates. In stands with many existing root grafts, residual trees may have needed to maintain or support portions of the interconnected root systems left behind after harvest. This increased imbalance between carbon supply and root demand could have temporarily heightened the constraints on stem growth in the remaining trees. Once maintenance of the root biomass of previously harvested trees ceased to be a priority, resources could be redirected aboveground. On the edge, the lower tree competition, in addition to a likely increase in sun irradiance and soil moisture (Bladon et al., 2006; Delgado et al., 2007), may have created better conditions for growth, explaining the greater radial growth rates compared to those found in trees located in the interior. In addition, the greater harvest intensity of the shelterwood treatment may have further benefited

the post-harvest growth conditions, explaining the greater radial growth rates of edge shelterwood trees compared to edge thinning trees.

Carbon stocks and windthrow mortality. Live aboveground carbon stocks were similar between the control and thinning treatments but were reduced in the shelterwood treatment. This implied that in the shelterwood treatment, post-harvest tree growth did not compensate for the biomass loss due to harvest.

Moreover, carbon gains were strongly associated with tree characteristics, particularly larger pre-harvest DBH and proximity to skidding trails, with trees within 5 meters of a trail showing higher carbon gains, following the results of Chapter II that revealed greater tree growth in trees located closer to skidding trails. This could be explained by the greater crown dimensions in trees with greater DBH and the more favourable growth conditions for trees near skidding trails due to the lower inter-specific competition (Dronova et al., 2011; Montoro Girona et al., 2016; Chase et al., 2016; Mensah et al., 2020).

The shelterwood treatment also exhibited lower carbon content in deadwood. This was likely due to a preference for targeting large DBH trees during harvest operations (i.e., harvest from above), leaving thinner trees that, once dead, contributed less to the deadwood carbon pool. Partial cut stands also showed a greater proportion of windthrow mortality (i.e., broken and uprooted trees) than control stands, probably due to the reduction in the wind-dissipating effect of stems with harvest and the increase in wind speed following harvest (Achim et al., 2005; Russell et al., 2018). Nonetheless, the alterations differed among mortality classes. The proportion of uprooted trees increased in all partial cut treatments compared to controls, which could be due to the reduction in neighbour tree support following stand density reductions (Peterson and Cannon, 2021). Conversely, the proportion of broken trees remained constant across treatments. This may be related to the strong anchorage provided by the tap-root system of jack pine or to the presence of root grafts, which are frequent in jack pine pure stands like the ones considered for this study, and increase stem breakage while reducing uprooting likelihood (Dupuy et al., 2007; Alcalá-Pajares et al., 2025). Snag

proportions were lower in partial cut stands relative to controls, which was likely due to the removal of snag trees to ensure safety during thinning operations, and due to the extension of the lifespan of suppressed trees when harvesting preferentially trees from the dominant and codominant social status in the shelterwood treatment.

Our study also exposes the complexity of assessing tree mortality, with each mortality type being driven by a different set of variables. Uprooting mortality was greater on null-slope sites, likely due to the reductions in shear strength due to the greater moisture accumulation (Singh and Thompson, 2016). Both uprooting and broken mortality increased with tree height, likely explained by a lower stem taper in taller trees and, thus, a lower mechanical stability following harvest (Moore, 2000). Broken mortality also increased with increasing stand age, likely due to the correlation between age and tree height (Béland and Bergeron, 1996). Snag trees increased with tree exposure, with snag proportions increasing in areas with lower Topex values, lower competition, and greater wind speeds. This may be related to greater wind speeds in more exposed areas, which would increase evapotranspiration rates in already weakened trees due to tree suppression (Jiao-Jun et al., 2004).

Natural root grafting. This thesis also advances our understanding of the factors governing windthrow mortality by assessing the interaction between natural root grafting and post-harvest windthrow mortality. It offers the first empirical evidence linking natural root graft presence with a reduced likelihood of tree uprooting during windthrow events. Additionally, the results reveal a second trade-off in mechanical behaviour, whereby trees with root grafts may be more prone to stem breakage when exposed to wind forces. These results may be attributed to the expansion of the root-soil plate with the formation of root grafts and the increase in tree anchorage through an increase in the number of lateral roots supporting each stem. The study provided additional evidence showing that graft frequency increases with decreasing distance between trees, suggesting spatial structure as a key determinant of belowground connectivity. Differences in graft incidence between study sites likely reflect variations in species composition, stand structure, and tree age, highlighting the influence of ecological and developmental context on graft formation.

Implications for forest management. Some models commonly used to project tree growth and to justify forest management interventions in managed even-aged stands are typically based on variables such as basal area or stem density before and after thinning (Burkhart and Tomé, 2012). Consequently, these models represent the effect of thinning as an immediate reduction in stand density and basal area, followed by continued growth along a new trajectory. While this captures the structural effects of thinning, it does not explicitly account for the short-term physiological growth reductions that can occur immediately after harvest (i.e., thinning shock). Our findings challenge the common assumption of growth release starting immediately following harvest (Thorpe and Thomas, 2007). It is thus important to include the thinning shock in future growth and yield models in forests where dominant species reveal thinning shock, such as the jack pine-dominated esker forests. This could be done by including a coefficient, which could range from 0 to 1, to reduce the estimated growth during the first years following harvest. This coefficient will depend on the thinning intensity, and also on the species, and site, as growth, as tree growth responses to canopy openings can differ significantly across species and site conditions (Juodvalkis et al., 2005; Pretzsch, 2020). Thus, additional research is needed to reveal how thinning shock varies across sites, forest management, and species. This will improve model accuracy while avoiding underestimations of tree growth and anticipated rotation periods, which could lead to economic losses. We recommend that forest managers begin by assessing whether thinning shock is present in their stands and evaluating how growth stagnation may vary with harvest intensity or proximity to trails.

This work provides evidence that thinning shock may result from resource allocation to root systems rather than from post-harvest physiological stress caused by changes in the canopy microenvironment (French et al., 2023). However, it remains unclear whether these resources are directed toward expanding root systems or sustaining grafted roots from harvested trees, as previously described for jack pine (Tarroux et al., 2010). If thinning shock arises from root system expansion, forest managers should favour low- to medium-intensity harvests, such as the thinning treatment examined in this thesis, since our findings show that harvest intensity directly

influences both the duration and intensity of thinning shock. Because thinning shock appears to be more pronounced near skidding trails, an alternative management option would be to maintain harvest intensity while reducing skidding trail density. This could be achieved by felling trees throughout the stand using chainsaw operators and extracting logs with a cable skidder, which can reach up to 50 m, substantially farther than the boom of a forest harvester, thereby allowing wider trail spacing and reducing overall trail density. However, the feasibility of this approach may be limited in sparsely populated regions or areas with constrained labour availability, such as the Canadian boreal forest, and its economic viability would need to be carefully evaluated. Alternatively, if thinning shock is driven by resource sharing through grafted roots, operators should avoid harvesting trees in close proximity and instead target individuals less surrounded by conspecifics. These changes may translate into reductions in stand-level growth, as grafted trees have been shown to exhibit lower radial growth rates after thinning in jack pine trees that did not reveal a thinning shock (Tarroux et al., 2010). Therefore, comparing radial growth responses between stands where grafted trees are retained and stands managed under business-as-usual practices could provide valuable insight into the consequences of this suggested management strategy.

The similar live aboveground and deadwood carbon stocks found in the thinning treatment when compared to unharvested stands could suggest that this treatment could be considered as a potential candidate for sustainable forest management when carbon-oriented objectives are to be achieved. This could be of special interest given the involvement of Canada in the Nationally Determined Contribution, which lies under the umbrella of the Paris Agreement and aims at lowering by 45-50 % the carbon emissions compared to 2005 by 2035, or Canada’s commitment to net-zero emissions by 2050 (UNFCCC, 2025). Moreover, we recommend that forest managers avoid harvesting trees belonging to the largest DBH classes when maintaining forest carbon stocks is a management objective, as our results indicate that larger pre-harvest DBH is associated with greater post harvest carbon gains. In unharvested stands, we registered a more balanced proportion of snag and windthrow mortality. However, in

partially cut stands, snag mortality decreased. This was likely due to the removal of snag trees during harvest operations to ensure safety. In the case of shelterwood treatments, the removal of large DBH trees could have altered self-thinning dynamics, extending the lifespan of suppressed trees that could have become snags in the absence of harvest. Snag trees are important components as they represent important niche and feeding sources for a wide variety of organisms, are key components of tree succession towards old growth forests and decompose more slowly than other mortality types (Aakala et al., 2007; Staniaszek-Kik et al., 2019). Thus, when performing partial cut treatments, forest managers should adopt measures to maintain the proportions of snags, such as leaving high stumps, which is a known practice by some forest practitioners in Sweden when biodiversity is prioritised (Lindhe and Lindelöw, 2004).

Based on the reduction in uprooting likelihood observed in naturally grafted trees and the greater grafting frequency found in trees closer to one another, it may be of interest to forest managers to retain trees in closer proximity to one another (i.e., trees likely grafted) to improve average residual tree anchorage. This may be particularly relevant in areas with high windthrow risk following harvest. In addition, preserving potentially grafted trees could also be of interest to forest managers in stands where maintaining soil integrity is a priority, such as those located on steep slopes adjacent to aquatic systems, as tree uprooting generates sediment displacements, and this sediment flux increases with increasing land steepness (Strzyżowski, 2021). In such contexts, promoting belowground connectivity through selective retention strategies could minimize soil disturbance by reducing uprooting, thus preserving slope stability and protecting water quality.

Research limitations. Our study was conducted in the balsam fir–white birch bioclimatic domain, whereas jack pine–dominated esker forests also occur in other boreal domains where differences in climate, topography, and species composition may influence post-harvest dynamics (Rudolph and Laidly, 1990; Storrar et al., 2014). In addition, during our expeditions to select study sites, we also observed black spruce–dominated forests on esker soils. Black spruce shows different growth responses and windthrow susceptibility than jack pine (Elie and Ruel, 2005). Thus, the generalization of our findings regarding the esker forests should be made with caution, as this work is focused only on jack pine-dominated stands. Additional constraints included the absence of pre-harvest mortality data, which complicates the distinction between windthrow-related mortality and the breakage of pre-existing snags. While jack pine snags are highly resistant to breakage, often remaining intact for approximately 30 years (Angers et al., 2010), our evidence suggests that mortality patterns in partially cut stands may differ from those in unharvested forests. These limitations highlight the need for further research to better capture species-specific responses and treatment effects in esker forests.

Due to the limited number of sites representing each treatment in our study region, we were required to select stands that varied in age, post-harvest density, and jack pine proportion. This structural heterogeneity may have influenced our results, as stand age and residual density can directly affect post-harvest growth responses (del Río et al., 2008; Hood et al., 2018). Likewise, variation in stand structure and species composition may have influenced windthrow susceptibility, given their documented effects on windthrow mortality (Elie and Ruel, 2005; Rich et al., 2007; Montoro Girona et al., 2019). Finally, differences in stand age can also affect snag abundance and mortality dynamics (Metsaranta et al., 2008; Moroni and Harris, 2010), potentially confounding treatment effects on post-harvest snag mortality. Consequently, some of the observed responses may reflect underlying stand characteristics rather than the effects of harvest treatments alone.

The present thesis includes two partial cutting treatments: a thinning treatment, likely conducted from below, and a shelterwood treatment, likely implemented using a

harvesting approach from above. These treatments were selected because they were the only partial cutting practices applied in jack pine stands within the balsam fir–white birch bioclimatic domain of the Abitibi–Témiscamingue region. However, the inclusion of different partial cutting intensities and harvesting approaches made it difficult, in some cases, to disentangle the effects of harvest intensity from those of harvest approach. We therefore strongly recommend that future studies incorporate all combinations of harvest intensities and management approaches to better isolate their respective influences.

We defined thinning shock as the period when tree-ring widths were equal to or less than the average of the ten pre-harvest years. Growth typically declined in the first post-harvest year and gradually recovered, though still below pre-harvest levels during the shock period and technically falling into the thinning shock period. Because of narrow rings, $\delta^{13}C$ analyses were conducted on tree-ring blocks that combined declining and recovering growth phases, which may have blurred short-term physiological signals. Future studies facing similar challenges could address this by applying technologies that allow $\delta^{13}C$ measurements while reducing increment core manipulation, such as laser-based $\delta^{13}C$ analyses at annual resolution (Rinne-Garmston et al., 2023). Although our $\delta^{13}C$ results suggest that temporary stomatal closure is unlikely to underlie the thinning shock, the absence of tree-ring, source water, and atmospheric vapour $\delta^{18}O$ data limits our ability to robustly interpret the underlying physiological mechanisms (Roden and Siegwolf, 2012). Incorporating $\delta^{18}O$ would have provided complementary insights into stomatal behavior and transpiration dynamics, thereby strengthening our understanding of the processes influencing $\delta^{13}C$ variations during the thinning shock period.

Moreover, because thinning shock was identified by comparing post-harvest tree-ring widths with the mean growth over the 10 years preceding harvest, thinning shocks were also detected in control stands. This likely introduced additional noise into our estimates of thinning shock. Such noise could have been reduced by estimating thinning shock through a direct comparison of post-harvest radial growth in harvested stands with that of control stands and defining a thinning shock when growth in

harvested trees was lower than in control trees. This approach is consistent with methods commonly used in studies that compare the radial growth of stands affected by natural disturbances, such as defoliation events (Camarero et al., 2018), with that of the unaffected stands. However, this approach was difficult to implement because harvest years differed among the partially cut stands. We therefore strongly recommend that future studies, when possible, select stands with synchronized harvest years to facilitate robust comparisons with control stands.

Finally, our radial growth analysis covered only the first eight years post-harvest, not extending to the peak of growth release, which prior research indicates occurs around the tenth year after harvest (Barrette et al., 2018). This constraint should be considered when interpreting the growth responses exposed in this work.

Our windthrow analysis included wind speed measurements taken at 30 meters above ground level as a potential explanatory variable since it was the only available information in historical records. While this height can serve as a proxy for wind conditions beneath the canopy, it may not accurately capture the wind dynamics experienced by trees, particularly in partially cut stands. Wind speed data collected closer to the forest floor, such as at the standard 10-meter above-ground height (Harper et al., 2010; Taylor et al., 2019), would have provided a more accurate representation of the actual forces acting on tree stems. The absence of such information (e.g., from public sources) represents a limitation of our study, potentially affecting the accuracy of our windthrow risk assessments. In addition, our analysis did not account for extreme or anomalous wind events, as such data were, to the best of our knowledge, unavailable. This represents another limitation, particularly given that our sites were harvested in different years. Access to records of anomalous wind events could have been critical for distinguishing differences in mortality rates across sites and better understanding the role of wind disturbance in post-harvest tree mortality.

The reduction in tree uprooting and the increase in stem breakage likelihood in grafted trees may be attributed to an expansion in the root-soil plate with root grafting.

However, due to time constraints, we were unable to collect data on root-soil plate area or volume. This data could have been useful to directly investigate the underlying mechanisms driving the observed influence of root grafting on windthrow mortality. Furthermore, the limited availability of study sites suitable for root system excavation restricted our sampling to mature jack pine riparian buffers, where natural root grafts were scarce, probably due to advanced decomposition of grafted trees. Another important limitation of this study is its species-specific focus. Our analysis was limited to jack pine, whereas other boreal conifers, such as black spruce, are known to be more susceptible to uprooting during windthrow events (Elie and Ruel, 2005). Therefore, caution should be exercised when extrapolating our findings to other forest compositions, as the influence of root grafting on windthrow susceptibility may vary across species.

Contributions. This thesis presents several findings that enhance our understanding of the effects of partial cuts in the Canadian boreal forest and support the development of more sustainable and adaptive silvicultural treatments.

This chapter provides novel evidence that thinning shock in jack pine may not be attributable to stomatal closure, as previously hypothesized (French et al., 2023), but rather to shifts in carbon allocation following harvest. In doing so, it advances our understanding of tree physiological responses to disturbances. Our results further demonstrate that the occurrence, length, and intensity of thinning shock are conditioned by the type of silvicultural treatment applied and the position of the tree with respect to the skidding trail. These results show, for the first time, that thinning shock is not a uniform response but can be modulated by harvest approach and tree spatial position within the stand. This constitutes a significant contribution to growth and yield research, as it challenges the common assumption of an immediate growth increase after harvest and highlights the need to account for shock dynamics when modeling stand development. Moreover, the findings reveal that tree growth does not necessarily scale with harvest intensity, as higher post-harvest growth was observed under thinning than under shelterwood, likely due to differences in the size-class

distribution of removed trees. Thus, the harvest approach itself can alter or even counteract the expected effects of harvest intensity on radial growth.

Overall, this chapter contributes new insights into the physiological responses of residual trees to partial cuts, enriching our conceptual understanding of thinning shock and its variability. In addition, our results assess for the first time the growth responses of jack pine-dominated stands located on esker soils. Finally, it provides the first assessment of growth responses in jack pine–dominated stands on esker soils. This represents a major contribution, as silvicultural prescriptions for this forest type remain largely unsupported by empirical evidence.

This chapter provides critical insights into how partial-cut treatments affect jack pine aboveground carbon stocks, an important indicator of sustainable forest management (Sabatini et al., 2019), and tree mortality patterns, which are closely tied to timber revenue and ecosystem dynamics (Martin et al., 2014). This work demonstrates that low-intensity thinning treatments harvesting 30–35 % of stand basal area effectively preserve both live and dead aboveground carbon stocks at levels comparable to unharvested controls in mature jack pine esker forests. This is a significant contribution, as it provides scientific support for prescribing low-intensity thinning when carbon preservation is a management priority. The study further highlights that trees with larger pre-harvest diameters exhibited greater post-harvest carbon accumulation, underscoring the importance of retaining large trees in carbon-oriented silviculture. Moreover, trees located near skidding trails showed significantly higher radial growth and carbon gains, confirming the influence of microsite conditions on stand-level carbon dynamics. At the same time, the spatial analysis of mortality types revealed increased uprooting and stem breakage near trail edges, emphasizing the role of trail layout and design in carbon dynamics.

Overall, this research advances our understanding of how partial cuts influence aboveground carbon stocks in both live and dead biomass pools. Additionally, the results underscore the need to incorporate skidding trail characteristics into carbon

modeling frameworks to accurately capture post-harvest stand dynamics in boreal forests.

In this work, we revealed that the presence of natural root grafts in jack pine trees reduces uprooting likelihood and increases the propensity of stem breakage. These results represent a major and pioneer contribution as they imply that windthrow mortality is not only influenced by individual tree traits, as previous research has revealed, but also by the influence of interactions among neighbouring trees. The lower uprooting probability in grafted trees and the higher grafting frequency observed in trees closer to one another could be of special interest in silvicultural interventions aimed at reducing tree uprooting, such as in those scenarios where preserving soil attributes is considered a priority.

Future research directions. Although our work provides key and novel information in the understanding of the thinning shock, it does not fully answer the origins of this growth phenomenon. Since our findings suggest that it may be related to a change in the carbon allocation patterns following thinning (Tarroux et al., 2010), future research should verify this hypothesis by combining the radial growth trends with root growth trends and root grafting presence, an approach previously followed by Tarroux et al. (2010). Moreover, our work focused on trees presenting thinning shocks following partial cuts. Since not all the sampled trees were exhibiting thinning shock, we believe that it would be of interest to explore the reasons behind its absence. This, in turn, will help to improve growth predictive models and could influence the harvesting criterion of forest managers when improving tree growth is a priority.

The reduced retention of live and dead carbon stocks observed in the shelterwood treatment appears to result not only from its harvest intensity but also from the harvest approach itself. Therefore, we recommend that future research on the effects of partial cuts on carbon stocks include both thinning and shelterwood treatments, each applied using from-below and from-above approaches, to more precisely disentangle and assess the specific influence of harvest approach on carbon stock dynamics. Similar experimental designs have been previously tested in growth analysis focused on Scots

pine (*Pinus sylvestris* L.) in Europe, and could serve as an example to follow this research line (Saarinen et al., 2020). The inclusion of a shelterwood-from-below treatment, with the same harvest intensity used in our study, could also help determine whether this silvicultural treatment, which seeks to promote natural regeneration and emulate small-scale natural disturbances, can be considered sustainable from a carbon stocking perspective. Moreover, the impact of partial cuts on carbon stocks in the Canadian boreal forest should be assessed across a broader range of regions as, to the best of our knowledge, our study, focused on jack pine forests, and that of Lee et al. (2002), focused on trembling aspen–balsam fir mixedwoods, are among the very few empirical studies that have addressed this question in the context of the Canadian boreal forest.

Our estimations of carbon stocks were based solely on overstory live residual tree biomass, as well as standing and fallen dead tree biomass. Although existing literature indicates that soil carbon is largely unaffected by partial cuts (Zhang et al., 2018a), several studies have documented changes in carbon pools within litter and understory biomass following these interventions (Lee et al., 2002; Ruiz-Peinado et al., 2016). Therefore, future research should also aim to include biomass fractions that were excluded from the present study. We detected the absence of allometric equations specific to mature jack pine that include the root biomass. Developing such equations is essential for improving the accuracy of biomass estimation for one of the most ecologically and economically significant species in Canada. Finally, future studies should consider spanning a full rotation period and incorporating climate change projections. This would help clarify not only how partial cuts currently affect jack pine carbon stocks, and by extension, how forestry contributes to meeting Canada's international climate commitments, such as the Paris Agreement, but also how these effects might evolve under future climate scenarios.

Future research on windthrow mortality should incorporate detailed historical records of windthrow events or past storm events, as these data can offer valuable insights into long-term mortality patterns and the legacy effects of past harvesting practices. Additionally, the development of wind maps, including key variables such as prevailing

wind direction and wind speed, is essential. Such tools would enable forest managers to tailor silvicultural practices to site-specific wind exposure, for instance, by aligning skidding trails with the dominant wind direction to reduce windthrow risk. The projected increase in the intensity and frequency of extra-tropical cyclones and their current displacement northward (Saad et al., 2017; Altman and Korznikov, 2025), combined with climate-induced changes such as reduced soil frost duration and increased precipitation, could elevate windthrow risk in the coming decades (Saad et al., 2017; Csilléry et al., 2017). Consequently, it is essential to explore the sensitivity of boreal forest landscapes to windthrow under various climate change scenarios through modeling and spatial analyses. Such efforts will help identify and prioritize high-risk areas, thereby informing adaptive forest management strategies aimed at mitigating future windthrow-related mortality.

Our study reveals a relationship between natural root grafting and windthrow mortality, demonstrating that the presence of root grafts reduces the likelihood of uprooting while increasing the incidence of stem breakage. However, further investigation is needed to clarify the underlying mechanisms. It remains uncertain whether the observed effect stems from an expansion of the root–soil plate, as suggested in Chapter IV, or from changes in other architectural traits of the root system influenced by grafting that contribute to enhanced anchorage. The adaptive significance of root grafting remains uncertain, with one common hypothesis being improved root anchorage (Basnet et al., 1993). Based on the root grafts observed during our field campaign, we hypothesize that grafting may result from sustained contact among large roots. Because root allocation tends to increase with wind speed (Nicoll and Dunn, 2000), graft formation could also be promoted in wind-exposed trees, suggesting that wind may play a role in this process. Although this topic lies beyond the scope of this thesis, further research is needed to clarify the mechanisms and adaptive functions underlying root graft formation.

Beyond its potential role in reducing windthrow risk, natural root grafting may also play a critical role in mediating tree responses to other natural disturbances, particularly drought. In unharvested stands, grafted trees have been shown to exhibit higher radial

growth rates compared to their non-grafted counterparts (Tarroux et al., 2010). This graft-induced growth advantage may enhance tree resilience during drought episodes, potentially by enabling resource sharing among interconnected individuals. Nevertheless, a significant knowledge gap remains regarding the broader ecological functions of root grafting in natural forest ecosystems, particularly in the context of increasing drought stress driven by climate change. Addressing this gap could yield valuable insights into forest resilience and adaptive capacity. Given the widespread drying observed across much of the Canadian boreal forest, the projected intensification of drought conditions in several regions (Wang et al., 2014), and the decline in drought resilience observed in the 20th century throughout the Canadian boreal forest (Marchand et al., 2025), we suggest examining whether natural intraspecific root grafting contributes to drought resilience in boreal tree species. Such research could provide valuable insights into the adaptive capacity of forest stands under increasing climatic stress and inform management strategies aimed at enhancing forest resistance and resilience to future drought scenarios.

A significant challenge in advancing research on natural root grafting lies in the need for sometimes expensive and time-consuming soil excavations to expose tree root systems. These logistical and financial constraints have limited the scope and pace of progress in this field. To overcome these limitations, we recommend the development of innovative, non-invasive methodologies for detecting root grafts before excavation. Such approaches would greatly enhance the efficiency of field operations, enabling broader and more systematic investigations into the ecological roles and distribution of natural root grafts.

Moreover, further research is necessary to assess the long-term suitability of partial cuts in different aspects of forest dynamics, such as regeneration and vegetation dynamics (Noualhaguet et al., 2025). Although regeneration and advanced regeneration in our study sites were mostly composed of black spruce, field observations indicated that their presence was limited. This scarcity may be explained by the fact that black spruce typically regenerates following fire disturbances (Montoro Girona et al., 2023), and that in the balsam fir–white birch bioclimatic domain, black

spruce establishment tends to be less successful on mineral soils, such as those found in the study area, compared to fibrous, poorly drained soils (Henneb et al., 2020). Given these findings, we strongly recommend that post-harvest regeneration in esker forests be carefully evaluated to determine the effectiveness of partial cutting strategies. Additionally, the economic sustainability of partial cuts should be assessed to determine whether a viable balance between timber revenue and ecosystem conservation can be achieved. Such evaluations should account for the full range of economic factors across an entire rotation period, including timber yields, operational costs, post-harvest site preparation, and the potential need for artificial regeneration interventions, if identified as needed during regeneration assessments. Furthermore, comparative studies between managed esker stands dominated by jack pine and stands of the same species established on other substrate types, such as clayey substrates or sandy soils with differing properties, should be conducted. Although previous studies may have included jack pine stands growing on esker or fluvioglacial substrates (e.g., Moulinier et al., 2015), substrate type has rarely been explicitly reported or examined as a defining stand characteristic, likely because it was not considered functionally relevant in those contexts. By explicitly focusing on esker substrates, the present work does not assume their uniqueness, but rather highlights the need to assess whether these landforms exhibit distinct structural or functional responses to management compared with other surface deposits. Clarifying this point would help determine whether esker forests warrant specific consideration in ecological analyses and the creation of specific silvicultural prescriptions.

ANNEXE A - SUPPLEMENTARY MATERIAL FOR CHAPTER I

List of candidate models employed during the model selection to test the differences in the $\delta^{13}C$ and their corresponding hypothesis. Interactions among predictors are noted with an asterisk (e.g., competition * distance). Tree diameter at breast height (dbh), tree height (H), competition with surrounding trees (competition), tree age (age), tree social class (sclass), harvest intensity (Treatment), and the block of tree rings (Period). Note that the site was included in all models as a random effect and has been omitted in the model structure column.

ID	Model structure	Biological hypothesis
mnu	$\delta^{13}C \sim 1$	Null model
mgl	$\delta^{13}C \sim$ dbh + H + competition + distance + age + sclass + Treatment + Period	Global model
1	$\delta^{13}C \sim$ dbh	Positive effect of diameter
2	$\delta^{13}C \sim$ H	Positive effect of height
3	$\delta^{13}C \sim$ competition	Positive effect of competition
4	$\delta^{13}C \sim$ distance	Positive effect of distance to skidding trail
5	$\delta^{13}C \sim$ age	Positive effect of tree age
6	$\delta^{13}C \sim$ sclass	Positive effect of tree social status
7	$\delta^{13}C \sim$ Treatment	Positive effect of the treatment

8	$\delta^{13}C$ ~ Period	Positive effect of the period of tree rings
	$\delta^{13}C$ ~ H + distance	Positive effect of height with an additive effect of the distance to the skidding trail
10	$\delta^{13}C$ ~ H + competition	Positive effect of tree height with an additive effect of competition
	$\delta^{13}C$ ~ H + sclass	Positive effect of tree height with an additive effect of tree social status

12	$\delta^{13}C \sim H$ + Treatment	Positive effect of tree height with an additive effect of the treatment
	$\delta^{13}C \sim H$ + Period	Positive effect of tree height with an additive effect of the period of tree rings
14	$\delta^{13}C \sim H$ + distance + sclass	Positive effect of tree height with an additive effect of distance to the skidding trail and tree social status
15	$\delta^{13}C \sim H$ + distance + Treatment	Positive effect of tree height with an additive effect of distance to the skidding trail and the treatment
16	$\delta^{13}C \sim H$ + distance + Period	Positive effect of tree height with an additive effect of distance to the skidding trail and the period of tree rings
17	$\delta^{13}C \sim H$ + distance + sclass + Treatment	

		Positive effect of tree height with an additive effect of distance to the skidding trail, tree social status, and the treatment
18	$\delta^{13}C \sim H + distance + sclass + Period$	Positive effect of tree height with an additive effect of distance to the skidding trail, tree social status, and the period of tree rings
19	$\delta^{13}C \sim H + distance + Treatment + Period$	Positive effect of tree height with an additive effect of distance to the skidding trail, the treatment, and the period of tree rings
20	$\delta^{13}C \sim dbh + dbh * sclass$	Positive effect of diameter and
21	$\delta^{13}C \sim competition + competition * distance$	Positive effect of competition, but different impact according to the distance to the skidding trail
22	$\delta^{13}C \sim distance + competition * distance$	Positive effect of the distance to the skidding trail, but different impact according to the distance to the competition

23	$\delta^{13}C \sim sclass + dbh * sclass$	Positive effect of tree social status, but different impact according to the diameter
24	$\delta^{13}C \sim H + distance + competition * distance$	Positive effects of height and additive effect of the distance to the skidding trail, but different impact of the distance depending on the competition
25	$\delta^{13}C \sim H + competition + competition * distance$	Positive effect of height and additive effect of competition, but different impact of competition depending on the distance to the skidding trail
26	$\delta^{13}C \sim H + sclass + dbh * sclass$	Positive effect of height and additive effect of tree social status, but different impact of the social status according to the diameter
27	$\delta^{13}C \sim H + distance + sclass + dbh * sclass$	
28	$\delta^{13}C \sim H + distance + sclass + competition * distance$	

		Positive effect of height and additive effect of the distance to the skidding trail and tree social status, but different impact of social status depending on the diameter
29	$\delta^{13}C \sim H +$ distance + Treatment + competition * distance	Positive effect of height with additive effect of the tree social status and the distance to the skidding trail, but different impact of the distance according to the competition
		Positive impact of height with additive effect of the treatment and the distance to the skidding trail, but different impact of the distance according to the competition
30	$\delta^{13}C \sim H +$ distance + Period + competition * distance	Positive impact of height with additive effect of the period of tree rings and the distance to the skidding trail, but different impact of the distance according to the competition
		Positive impact of height with additive effect of the distance to the skidding trail, the treatment, and tree social
31	$\delta^{13}C \sim H +$ distance + sclass + Treatment + dbh * sclass	

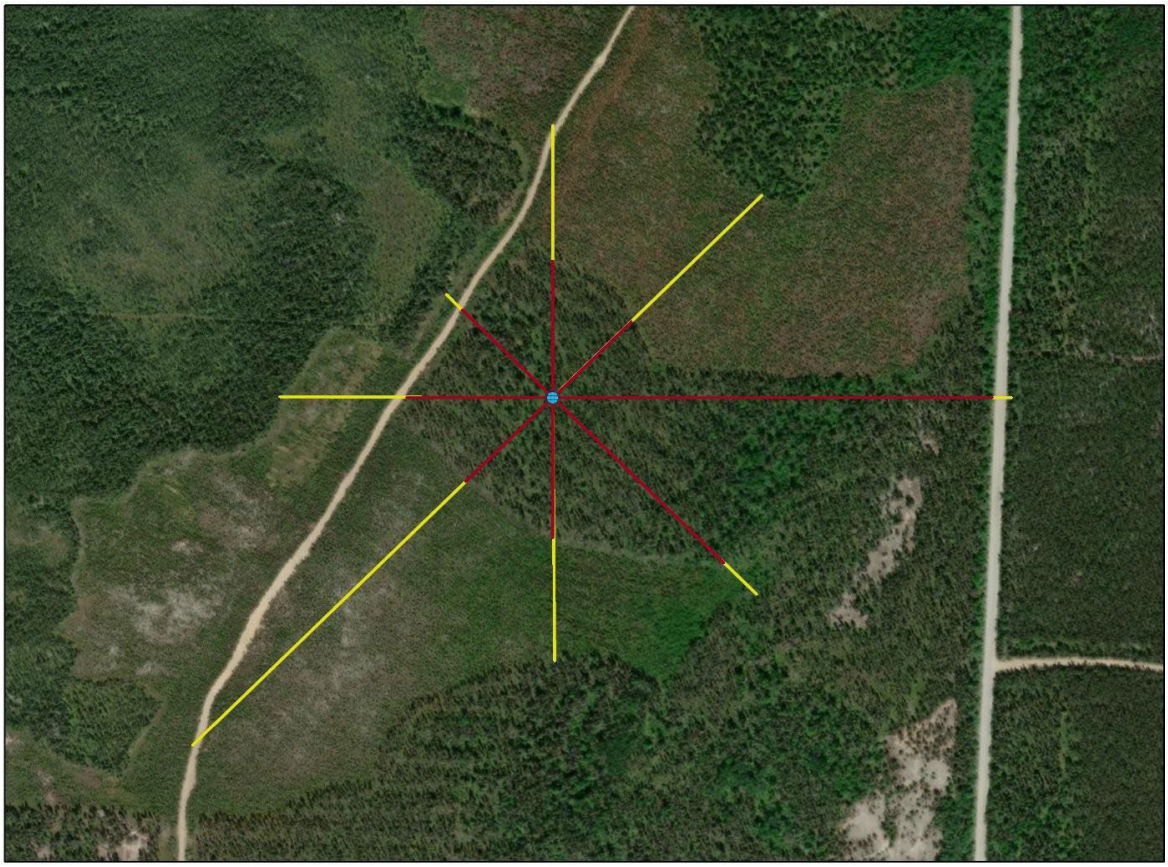
		status, but different impact of tree social status according to the diameter
32	$\delta^{13}C \sim H + distance + sclass + Treatment + competition * distance$	Positive impact of heigh with an additive effect of treatment, tree social status, and distance to the skidding trail, but different impact of distance to skidding trail according to the competition
33	$\delta^{13}C \sim H + distance + sclass + Period + dbh * sclass$	Positive impact of height with an additive effect of the distance to the skidding trail, the period of tree rings, and tree social status, but different impact of tree social status according to the diameter
34	$\delta^{13}C \sim H + distance + sclass + Period + competition * distance$	Positive impact of height with additive effect of tree social status, the period of tree rings, and the distance to the skidding trail, but different impact of the distance according to the competition

Model selection for $\delta^{13}C$ based on AICc criteria. Of the 34 models, only the models with a ΔAICc < 4 are presented. K: number of parameters, AICc: Akaike's

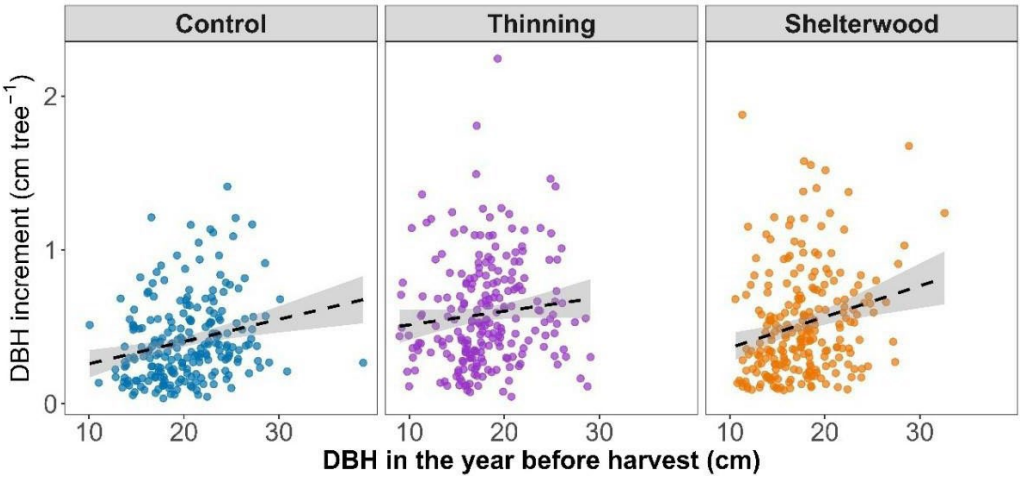
Information Criterion corrected for small samples, ΔAICc: AICc relative to the most parsimonious model, $AICc_{wt}$: AICc weight. Marginal R-squared (R^2_m): proportion of variance explained by the fixed effects alone. Conditional R-squared (R^{2c}): proportion of variance explained by both the fixed effects and the random effects.

Model ID	K	AICc	ΔAICc	$AICc_{wt}$	R^2_m	R^2_c
13	7	108.5	0.00	0.38	50.6	81.9
33	11	108.7	0.25	0.34	63.2	81.9
16	16	110.3	1.89	0.15	51.5	81.9
18	18	112.3	3.83	0.16	52.4	81.9

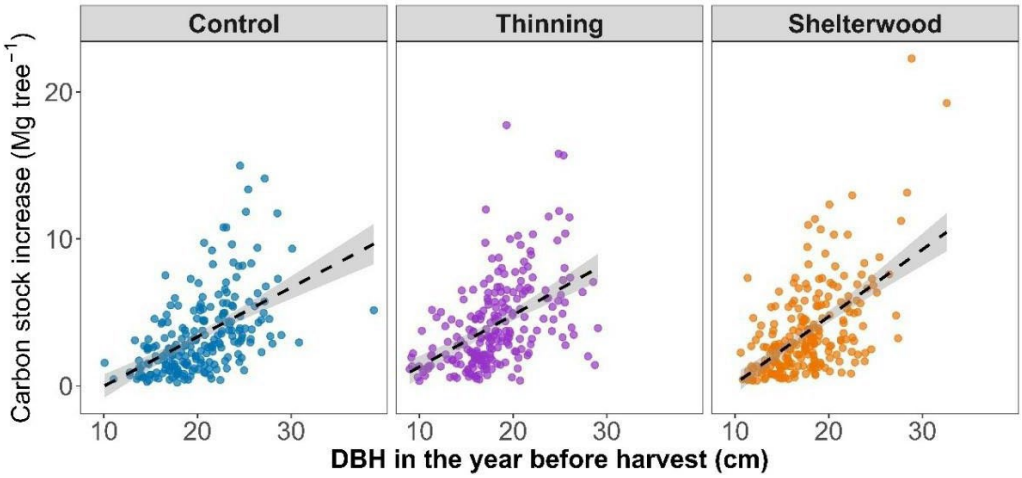
ANNEXE B – SUPPLEMENTARY MATERIAL FOR CHAPTER II



Representation of the first (red) and second (yellow) sets of transects used to determine the adapted Fetch index.

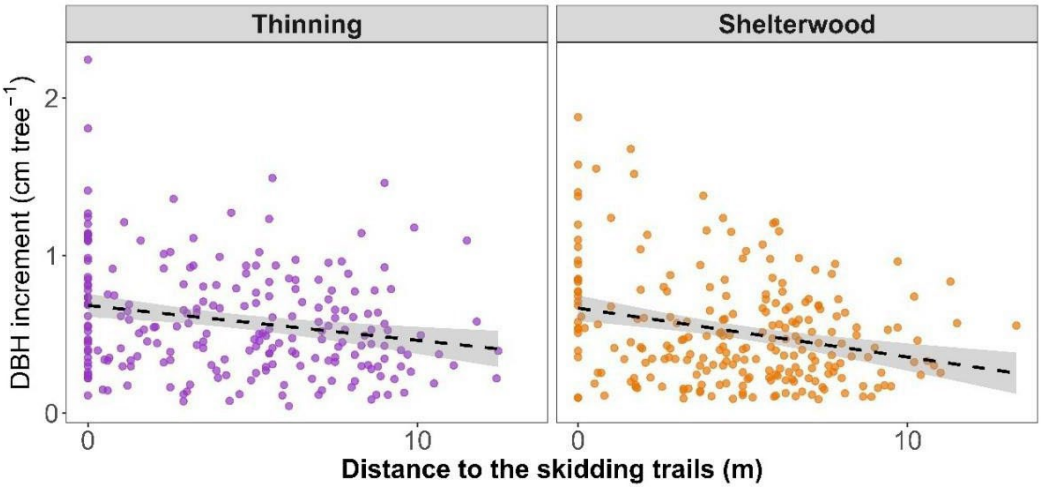


Relationship between the tree DBH in the year before harvest and the DBH increment calculated as the difference between the DBH at the 8th year following harvest and the DBH in the year before harvest. The dashed line represents the fitted linear regression, and the shaded area around the dashed line represents the 95% confidence interval of the regression, indicating the range where the true mean response is likely to fall.

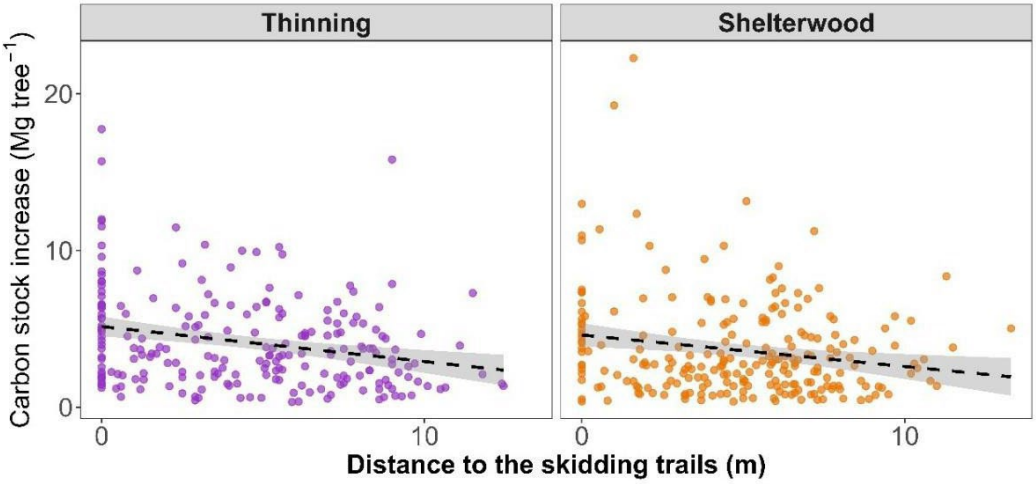


Relationship between the tree DBH in the year before harvest and the carbon stock increase per tree, calculated as the difference between the tree carbon

stock at the 8th year following harvest and that of the year before harvest. The dashed line represents the fitted linear regression, and the shaded area around the dashed line represents the 95% confidence interval of the regression, indicating the range where the true mean response is likely to fall.

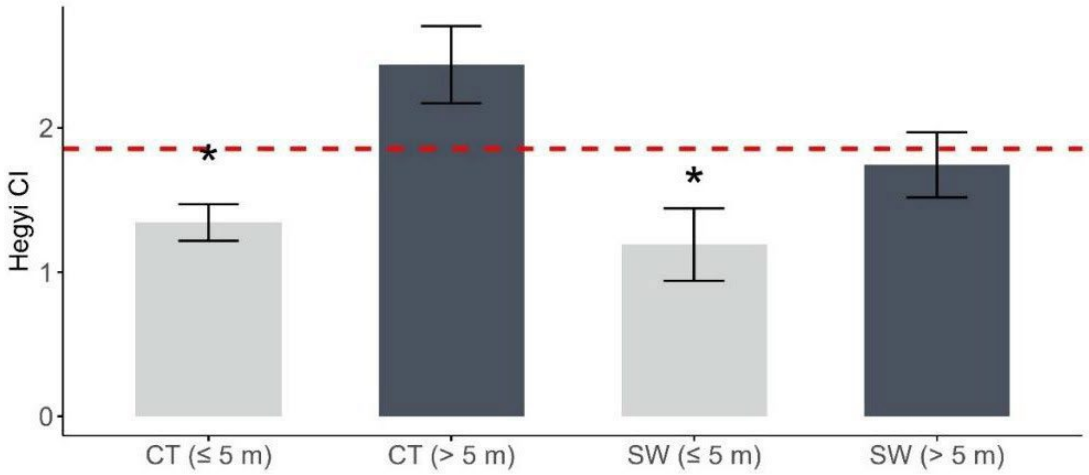


Relationship between the tree DBH increment and its distance to the closest skidding trail. DBH increment is calculated as the difference between the DBH at the 8th year following harvest and the DBH in the year before harvest. The dashed line represents the fitted linear regression, and the shaded area around the dashed line represents the 95% confidence interval of the regression, indicating the range where the true mean response is likely to fall.

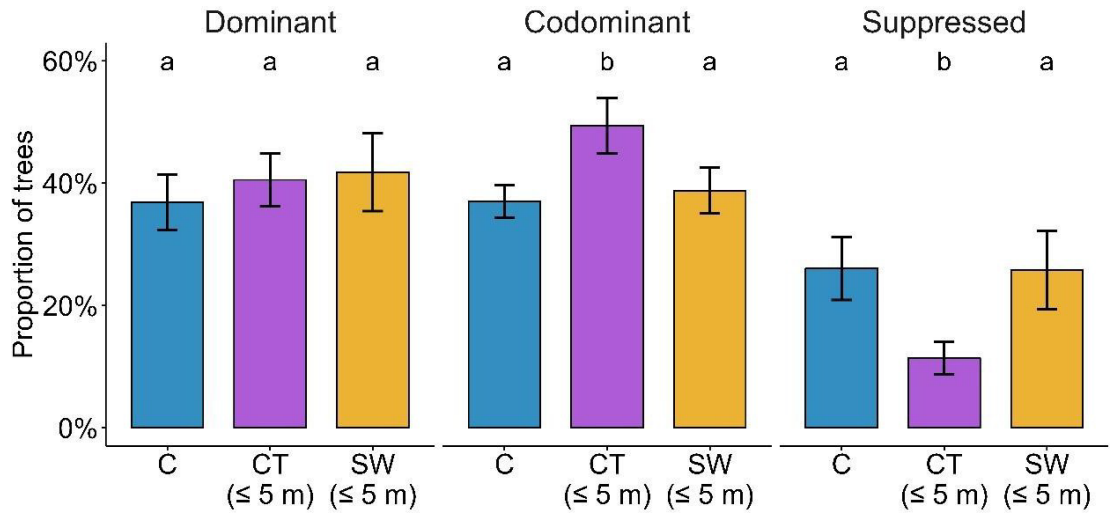


Relationship between the carbon stock increase per tree and its distance to the closest skidding trail, calculated as the difference between the tree carbon stock

at the 8th year following harvest and that of the year before harvest. The dashed line represents the fitted linear regression, and the shaded area around the dashed line represents the 95% confidence interval of the regression, indicating the range where the true mean response is likely to fall.



Mean competition in the edge (≤ 5 m) and interior (> 5 m) of the thinning (CT) and shelterwood (SW) stands in comparison to the mean of the control stands (red dashed line). Asterisks (*) indicate significant ($p < 0.05$) differences among edge and interior competition levels within each treatment.



Average proportion of live trees by crown class and treatment with error bars ± SE. C = control trees, CT = edge trees from the thinning stands, SW = edge trees from the shelterwood stands. Letters indicate significant ($p < 0.05$) differences between treatments within each crown class, determined by Tukey's post-hoc comparisons.

Mean DBH increase per tree across treatments, with standard deviation (SD), standard error (SE), and 95% confidence intervals (CI). The mean DBH increase was calculated as the average difference between each tree's DBH at the 8th year after harvest and its DBH in the year prior to harvest, computed separately for each treatment.

Treatment	DBH increase (cm tree^{-1})	SD	SE	Lower 95 % CI	Upper 95 % CI
Control	0.41	0.27	0.02	0.37	0.44
Thinning	0.58	0.35	0.02	0.54	0.63
Shelterwood	0.52	0.34	0.02	0.47	0.56

Mean carbon stock increase per tree across treatments, with standard deviation (SD), standard error (SE), and 95% confidence intervals (CI). The mean carbon stock increase was calculated as the average difference between each tree's carbon stock at the 8th year after harvest and its carbon stock in the year prior to harvest, computed separately for each treatment.

Treatment	Carbon stock increase (Kg tree^{-1})	SD	SE	Lower 95 % CI	Upper 95 % CI
Control	3.42	2.98	0.20	3.75	4.53
Thinning	4.43	2.71	0.18	3.07	3.79

Shelterwood	3.65	3.10	0.20	3.25	4.04	

Climatic and topographical factors per site. Slope type 1: 0 to 3 %, Slope type 2: 4 to 8%. Wind30: wind speed 30 meters above the ground.

Site	Treatment	Slope type	vation (m)	Wind30 (m/s)	Fetch index	Topex index
C1	Control	1	337	4.16	0.82	1.94
C2	Control	1	330	4.13	1.29	4.36
C3	Control	1	326	4.13	0.83	2.75
C4	Control	2	342	4.17	0.99	4.57
C5	Control	1	333	4.17	1.54	2.73
C6	Control	1	339	4.32	0.77	4.80
C7	Control	2	354	4.10	0.68	3.20
C8	Control	1	333	4.59	1.11	4.47
E1	Thinning	2	337	4.21	0.66	1.16
E2	Thinning	2	356	4.22	1.09	3.57
E3	Thinning	2	337	4.13	0.53	5.63
E4	Thinning	2	351	4.25	1.18	4.05
E5	Thinning	1	327	4.13	1.24	1.74
E6	Thinning	1	376	4.25	1.05	6.30
E7	Thinning	1	362	4.10	1.35	2.84
E8	Thinning	2	328	4.07	0.88	5.64
S1	Shelterwood	1	336	4.13	1.09	3.10

S2	Shelterwood	2	341	4.12	0.82	4.88
S3	Shelterwood	2	339	4.21	1.07	2.78
S4	Shelterwood	1	338	4.13	1.23	3.05
S5	Shelterwood	1	345	4.11	0.84	2.84
S6	Shelterwood	1	320	4.15	0.77	2.34
S7	Shelterwood	1	334	4.13	0.80	2.43
S8	Shelterwood	1	318	4.15	0.54	2.89

Description of all the variables included in the models for assessing the driver factors for live and deadwood aboveground carbon stocks

Category	Variable	Type	ocation in the model	Units	Source	Description
Tree level	DBH_{bh}	Numerical continuous	Predictor	cm	ochronological analyses	Tree diameter at breast height at the moment of harvest.
	Height	Numerical continuous	Predictor	m	Field survey	Tree height.
	Slenderness ratio	Numerical continuous	Predictor	-	Field survey	Tree height divided by diameter at breast height
	Age	Numerical discrete	Predictor	Years	Dendrochronological analysis	Tree age.
	Hegyi Index	Numerical continuous	Predictor	-	Field survey	Competition measured through the Hegyi Index.
	Distance	Numerical continuous	Predictor	m	Field survey	Distance from the tree to the closest skidding trail
	Position	Categorical	Predictor	-	Field survey	Tree position from the skidding trail. Categories: $0 \leq x \leq 5$ m, $x > 5$ m

	Social class	Categorical	Predictor	-	Field survey	Tree social status. Categories: dominant, codominant, and suppressed.
	DBH increase	Numerical continuous	Response	cm	Dendrochronological analysis	The difference between the DBH in the 8^{th} year following harvest and the DBH in the year before harvest (DBH_{bh})

	Carbon increase	Numerical continuous	Response	Mg	Dendrochronological analysis and allometric equations	The difference between the tree carbon stock in the 8th year following harvest and that of the year before harvest (DBHbh)
Stand-level	Treatment	Categorical	Predictor	-	Gouvernement du Quebec, 2019	Silvicultural treatment performed on each site. Categories: control, thinning (CT), and shelterwood (SW).
	Mean DBH	Numerical continuous	Predictor	cm	Field survey	Stand mean diameter at breast height
	Mean H	Numerical continuous	Predictor	m	Field survey	Stand mean height.
	Mean age	Numerical discrete	Predictor	Years	Field survey	Stand mean age
	Mean competition	Numerical continuous	Predictor	-	Field survey	Stand mean competition measured through the Hegyi Index

	Total mortality	Numerical continuous	Response	%	Field survey	Mortality rate, including all mortality classes.
	Uprooted mortality	Numerical continuous	Response	%	Field survey	Mortality rate, including only uprooted trees.
		Categorical	Response	-	Field survey	Categories: uprooted tree =1, rest = 0.
	Broken mortality	Numerical continuous	Response	%	Field survey	Mortality rate, including only broken trees.
		Categorical	Response	-	Field survey	Categories: broken tree =1, rest = 0.
	Snag mortality	Numerical continuous	Response	%	Field survey	Mortality rate, including only snag (standing dead) trees.
		Categorical	Response	-	Field survey	Categories: broken tree =1, rest = 0.

Climatic	Wind30	Numerical continuous	Predictor	m/s	Government of Canada, 2016	Wind speed 30 meters above the ground.
Topographic	Slope	Categorical	Predictor	%	Government of Quebec, 2023	Mean slope. Categories: 1, 0 to 3 %, and 2: 4 to 8 %.
	Elevation	Numerical continuous	Predictor	m.a.s.l.	Government of Quebec, 2023	Mean elevation measured in meters above sea level.
	Fetch index	Numerical continuous	Predictor	-	ArcMap 10.8.1, ESRI 2020.	Represents the wind exposure concerning the area over which wind blows uninterrupted across a surface, like a forest, field, or water body
	Topex index	Numerical continuous	Predictor	-	ArcMap 10.8.1, ESRI 2020.	Represents the wind exposure in the relationship

						between the topography complexity and the stand location.

Model selection for assessing the differences between pre- and post-harvest carbon stocks per hectare based on AICc criteria. Of the 37 models, only the models with a ΔAICc < 4 are presented. K: number of parameters, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: AICc relative to the most parsimonious model, $AICc_{wt}$: AICc weight. Marginal R-squared (R^2_m): proportion of variance explained by the fixed effects alone. Conditional R-squared (R^2_c): proportion of variance explained by both the fixed effects and the random effects.

Model ID	K	AICc	ΔAICc	$AICc_{wt}$	R^2_m	R^2_c
41	6	494.77	0.00	0.46	53.8 %	61.7 %
49	10	497.26	2.49	0.13	55.3 %	63.4 %
Global model	10	497.26	2.49	0.13	55.3 %	63.4 %
47	9	497.56	2.79	0.12	55.2 %	62.4 %

38		4	498.46	3.69	0.07	48.7
%		56.7 %				

Model selection for assessing the driver factors of the proportion of dead trees of each dead tree type based on AICc criteria. Of the 28 models, only the models with a ΔAICc < 4 are presented. K: number of parameters, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: AICc relative to the most parsimonious model, $AICc_{wt}$: AICc weight. Marginal R-squared (R^2_m): proportion of variance explained by the fixed effects alone. Conditional R-squared (R^{2c}): proportion of variance explained by both the fixed effects and the random effects.

Model ID	K	AICc	ΔAICc	$AICc_{wt}$	R^2_m	R^2_c
Uprooted						
5	4	91.08	0.00	0.25	31.1 %	70.5 %
Null model	2	92.50	1.42	0.12	0.0 %	72.8 %
8	3	93.03	1.95	0.10	11.3 %	74.0 %
3	3	93.31	2.23	0.08	9.1 %	74.3 %
4	3	93.95	2.87	0.06	7.2 %	73.7 %
1	3	94.01	2.93	0.06	5.4 %	74.2 %
7	3	94.09	3.01	0.06	7.9 %	74.3 %
2	3	94.09	3.02	0.06	5.2 %	73.1 %

6	3	94.82	3.74	0.04	1.5 %	72.3 %
9	3	94.86	3.78	0.04	1.2 %	73.1 %
11	3	94.98	3.90	0.04	0.8 %	73.3 %
Broken						
13	5	130.37	0.00	0.83	59.19 %	59.19 %
Snag						
7	3	145.02	0.00	0.40	20.7 %	60.2 %

5	4	147.00	1.99	0.55	26.4 %	70.2 %
9	3	147.91	2.89	0.65	14.1 %	67.5 %
Null model	2	148.27	3.25	0.73	0	68.1 %
2	3	148.85	3.84	0.79	8.7 %	69.0 %

Mean proportions of windthrow mortality (broken + uprooted trees) per treatment. Letters indicate significant ($p < 0.05$) differences between treatments within each crown class, determined by Tukey's post-hoc comparisons.

Treatment	Mean windthrow mortality (%)	Standard deviation	andard error	Tukey post-hoc test group
Control	11.9	6.2	2.2	a
Thinning	14.4	5.5	1.9	a
Shelterwood	20.9	7.4	2.6	**b**

Statistics for the presence of the thinning shock. Parameters, coefficients, and confidence intervals (CI) for the linear mixed models for thinning shock presence, including the radial growth and basal area increment before harvest (RG_{BH}, BAI_{BH}). σ1: standard deviation of the random intercept for the site grouping factor. R^2_m: marginal R^2 (variance explained by fixed effects); R^2_c: conditional R^2 (variance explained by fixed and random effects).

Parameter	Coefficient (β)	Std. Dev	Std. Error	*p*-value	Lower 95% CI	Upper 95%

						CI
Radial growth: R^2_m = 4.85 %, R^2_c = 7.28 %						
σ_1		0.2941	-	-	0.00	0.63
Intercept	-0.26	-	0.38	0.49	-1.03	0.50
Distance	-0.09	-	0.04	**< 0.05**	-0.18	-6.0e-03
RG_{BH}	0.20	-	0.32	0.53	-0.42	0.83
Treatment: Shelterwood	0.33	-	0.40	0.41	-0.46	1.14
Distance * Shelterwood	0.09	-	0.06	0.14	-0.03	0.23
Basal area increment (BAI): R^2_m = 4.93 %, R^2_c = 7.84 %						
σ_1		0.3219	-	-	0.00	0.67

Intercept	-0.27	-	0.36	0.44	-1.00	0.41
Distance	-0.09	-	0.04	**< 0.05**	-0.18	-2.0e-03
BAI_{BH}	4.0e-04	-	6.0e-04	0.44	-1.0e-03	2.0e-03
Treatment: Shelterwood	0.33	-	0.40	0.40	-0.45	1.15
Distance * Shelterwood	0.09	-	0.06	0.15	-0.03	0.22

Statistics for delay time of the thinning shock. Parameters, coefficients, and confidence intervals (CI) for the linear mixed models for the delay time, including radial growth and basal area increment before harvest (RG_{BH}, BAI_{BH}). σ1: standard deviation of the random intercept for the site grouping factor. σ2: standard deviation of the residual errors. R_m: marginal R^2 (variance explained by fixed effects); R^2_c: conditional R^2 (variance explained by fixed and random effects).

Parameter	Coefficient (β)	Std. Dev	Std. Error	*p*-value	Lower 95% CI	Upper 95% CI

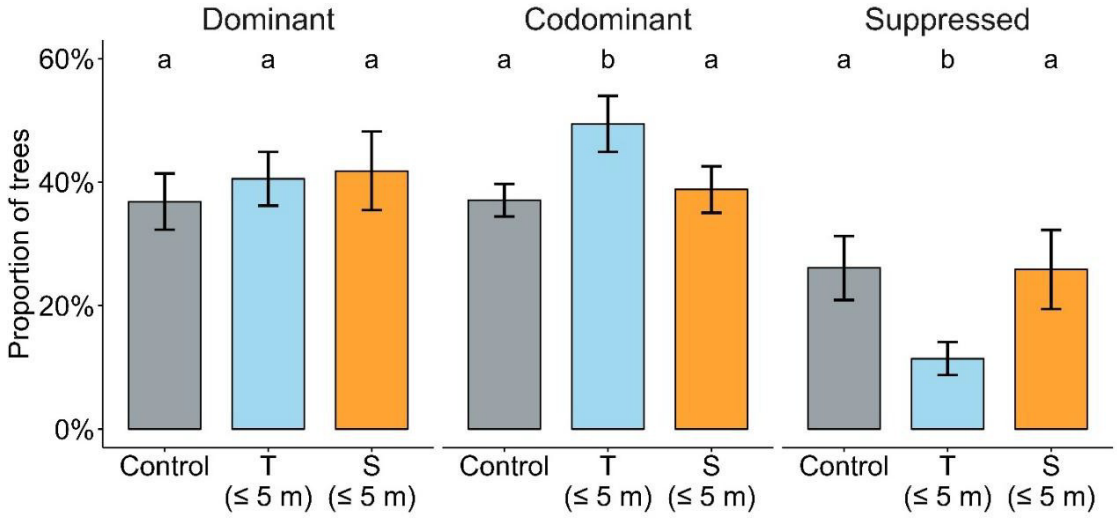
Radial growth: R^2_m = 5.95 %, R^2_c = 20.53 %						
σ_1		0.67	-	-	0.25	1.04
σ_2		1.56	-	-	1.41	1.72
Intercept	2.37	-	0.49	**< 0.01**	1.43	3.32
Distance	-0.03	-	0.05	0.54	-0.14	0.07
RG_{BH}	0.35	-	0.36	0.33	-0.40	1.03
Treatment: Shelterwood	-0.44	-	0.53	0.41	-1.45	0.57
Distance * Shelterwood	0.19		0.07	**< 0.05**	0.05	0.33
Basal area increment (BAI): R^2_m = 6.19 %, R^2_c = 19.91 %						
σ_1		0.65	-	-	0.25	1.01
σ_2		1.56	-	-	1.41	1.73
Intercept	2.43	-	0.43	**< 0.01**	1.60	3.25
Distance	-0.03	-	0.05	0.56	-0.14	0.07
BAI_{BH}	6.9e-04	-	6.4e-04	0.28	-1.0e-03	2.0e-03

Treatment: Shelterwood	-0.49	-	0.05	0.35	-1.46	0.49
Distance * Shelterwood	0.19		0.07	**< 0.01**	0.05	0.33

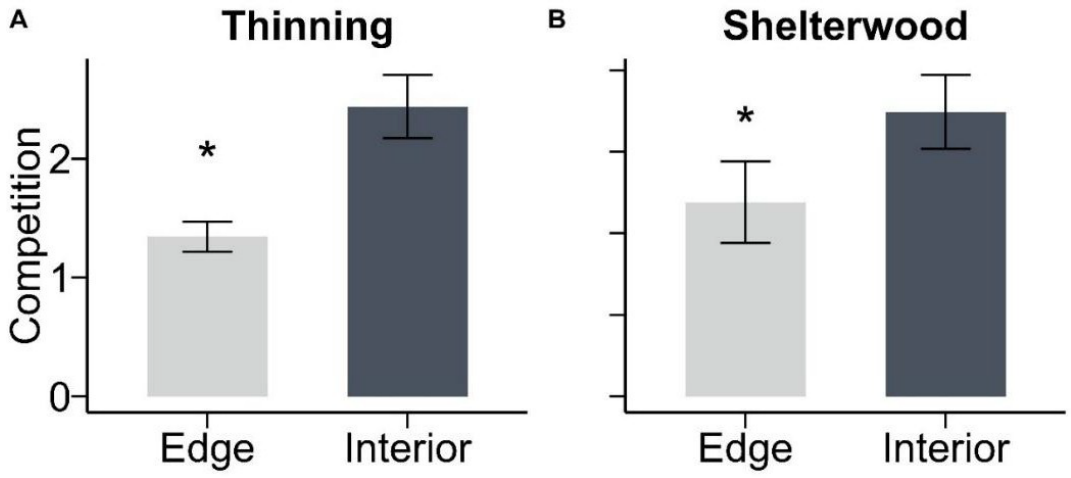
Statistics for the intensity of the thinning shock. Parameters, coefficients, and confidence intervals (CI) for the linear mixed model for thinning shock intensity that included the radial growth and basal area increment before harvest (RG_{BH}, BAI_{BH}). σ1: standard deviation of the random intercept for the site grouping factor. σ2: standard deviation of the residual errors. R_m: marginal R^2 (variance explained by fixed effects); R^2_c: conditional R^2 (variance explained by fixed and random effects).

Parameter	Coefficient (β)	Std. Dev	Std. Error	*p*-value	Lower 95% CI	Upper 95% CI
Radial growth: R^2_m = 10.83 %, R^2_c =12.16 %						
σ_1		0.04	-	-	0.00	0.09
σ_2		0.32	-	-	0.29	0.35
Intercept	1.41	-	0.08	**< 0.01**	1.25	1.56
Distance	-0.01	-	0.01	0.55	-0.03	0.01
RG_{BH}	-0.09	-	0.07	0.18	-0.22	0.04
Treatment: Shelterwood	0.21	-	0.08	**< 0.05**	0.05	0.36
Distance * Shelterwood	-4e-03	-	0.01	0.78	-0.03	0.02
Basal area increment (BAI): R^2_m = 10.88 %, R^2_c = 12.09 %						

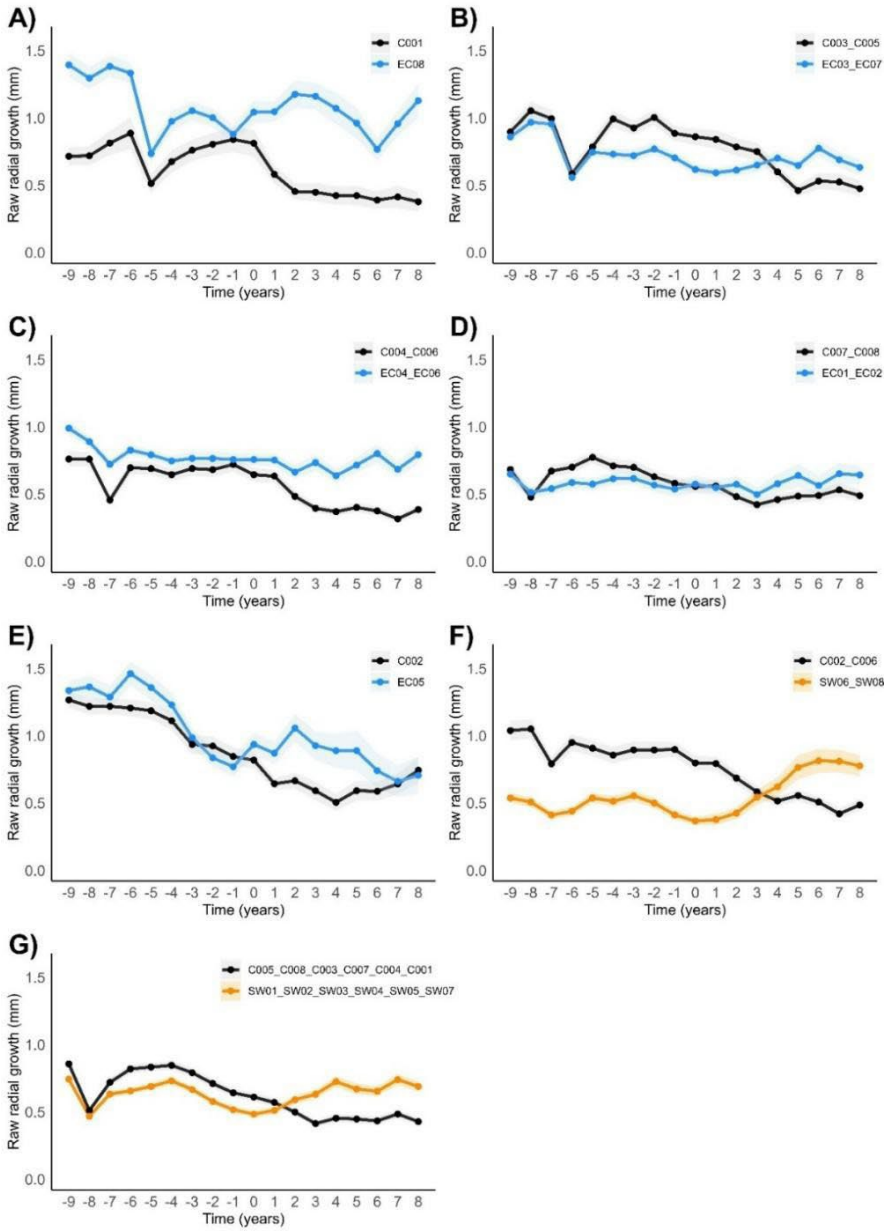
m					c	
σ_1		0.04	-	-	0.00	0.09
σ_2		0.32	-	-	0.29	0.35
Intercept	1.39	-	0.07	**< 0.01**	1.26	1.53
Distance	-0.01	-	0.01	0.48	-0.03	0.01
BAI_{BH}	-1.7e-04	-	1.2e-04	0.17	0.00	1.0e-04
Treatment: Shelterwood	0.22	-	0.08	**< 0.01**	0.065	0.37
Distance * Shelterwood	-3.5e-03	-	0.01	0.80	-0.031	0.02



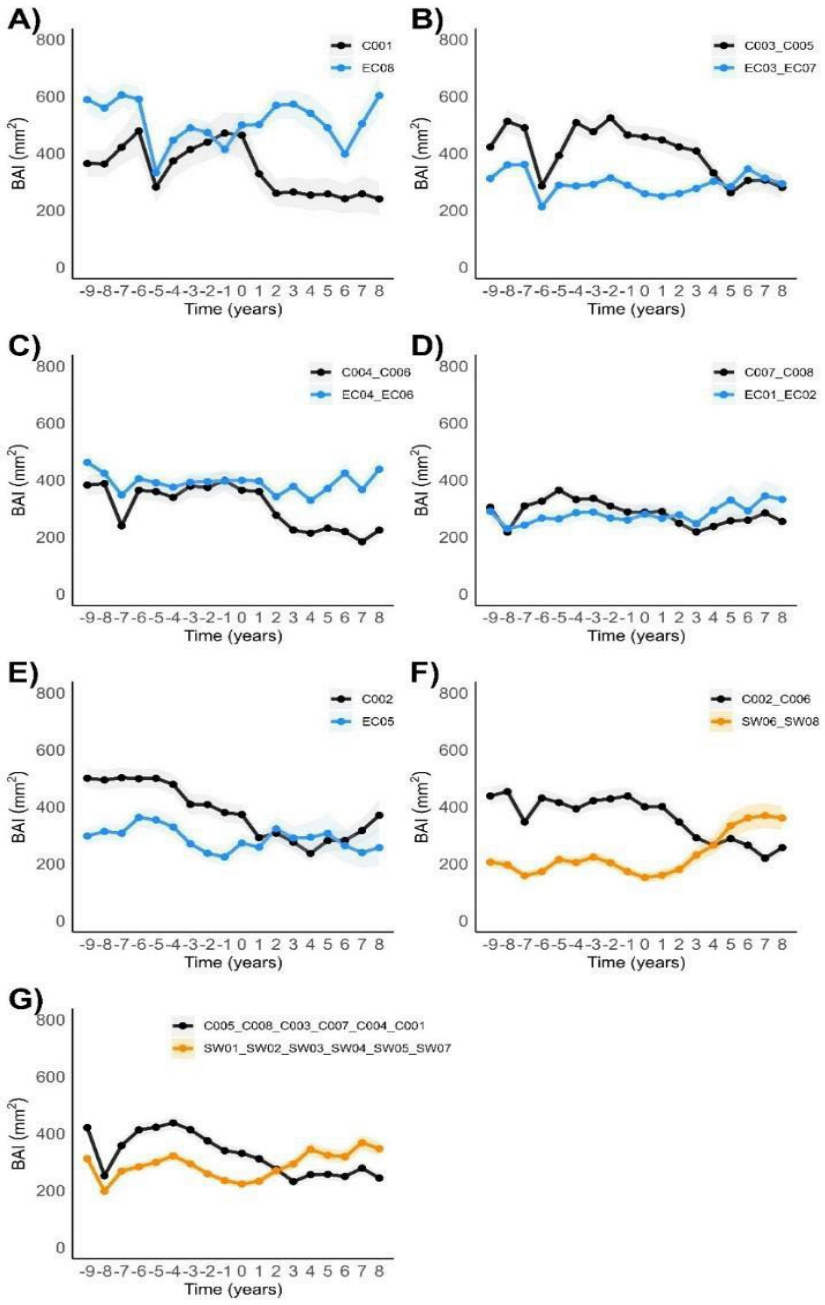
Average proportion of live trees by social class and treatment with error bars ± SE. T = edge trees from the moderate thinning stands, S = edge trees from the shelterwood stands. Letters indicate significant ($p < 0.05$) differences between treatments within each crown class, determined by Tukey's post-hoc comparisons.



Mean competition per treatment and distance to the skidding trail. Vertical bars represent the standard errors (SE). Asterisks (*) represent differences detected between the edge and interior within the thinning (A) and shelterwood (B) treatments revealed by a Tukey post-hoc test.



Paired sites comparing raw radial growth. Thinning sites (EC) are colored in blue. Shelterwood sites (SW) are colored in orange. Control (C) sites are colored in black. Vertical dashed lines represent the harvest year (t = 0). Shaded areas represent the standard error (SE).



Paired sites comparing basal area increment (BAI). Thinning sites (EC) are colored in blue. Shelterwood sites (SW) are colored in orange. Control (C) sites are colored in black. Vertical dashed lines represent the harvest year (t = 0). Shaded areas represent the standard error (SE).

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