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Université du Québec en Abitibi-Témiscamingue

VERS UN AMÉNAGEMENT DURABLE DE LA FORÊT BORÉALE CANADIENNE : RÉPONSE À LONG TERME DE LA RÉGÉNÉRATION NATURELLE, DE LA DIVERSITÉ MICROBIENNE ET DU STRESS HYDRIQUE LE LONG D'UN GRADIENT D'INTENSITÉ DE SYSTÈMES SYLVICOLES

TOWARDS SUSTAINABLE CANADIAN BOREAL FOREST MANAGEMENT: LONG-TERM RESPONSE OF NATURAL REGENERATION, MICROBIAL DIVERSITY, AND WATER STRESS AFTER A GRADIENT OF SILVICUTURAL SYSTEMS

Thèse présentée comme exigence partielle du

Doctorat en sciences de l'environnement

Par

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This doctoral thesis represents the culmination of over four and a half years of research in forest ecology within the boreal ecosystems, landscapes of remarkable ecological integrity that have long inspired my academic journey. My research path in this field began in 2017, when I joined Umeå University (Sweden) and the Swedish University of Agricultural Sciences (SLU), where I studied plant and forest biotechnology and conducted my master's research on the impacts of continuous cover forestry versus clearcutting on soil fungal communities. This experience was pivotal—not only for shaping my research interests in forest management and soil microbiology, but also for meeting my current advisor Dr. Miguel Montoro Girona, whose mentorship became instrumental in my continued academic development.

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DEDICATION

To my life partner, Dr. Naharin Sultana Anni,

for standing by me through the sleepless nights and

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This achievement is ours.

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This doctoral research was conducted within the Groupe de Recherche en Écologie de la MRCT d'Abitibi (GREMA) at the Université du Québec en Abitibi-Témiscamingue (UQAT), under the guidance of Miguel Montoro Girona (UQAT), Yves Bergeron (UQAT) and Patricia Raymond (Ministère des Ressources naturelles et des Forêts, MRNF). Funding was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC Alliance), the Ministère des Ressources naturelles et des Forêts (MRNF), the Fondation de l'UQAT, and the Centre d'étude de la forêt (CEF).

The thesis is organized into five chapters. Chapter I offers a general introduction to the research questions and objectives, while Chapter V presents overall conclusions and perspectives. Chapters II, III and IV contain the core studies, each drafted as a manuscript for submission to peer-reviewed journals. References for each article appear at the end of its chapter, together with any supplementary material.

Chapter I – Introduction

Chapter II – Kim, S., Bergeron, Y., Raymond, P., Thiffault, N., & Montoro Girona, M. (2025). Natural regeneration 18 years after experimental silvicultural systems in Canadian boreal forests. *Forest Ecology and Management, 585*, 122655. https://doi.org/10.1016/j.foreco.2025.122655

Chapter III – Kim, S., Bergeron, Y., Martineau, C., Thorn, R. G., Tai, V., Raymond, P., Noualhaguet, M., & Montoro-Girona, M. (Manuscript). Rhizosphere microbial communities 19 years after clearcut and partial-cut treatments in Eastern Canadian boreal forests. Intend to submit to *PLOS ONE.*

Chapter IV – Kim, S., Bergeron, Y., Grosbois, G., DesRochers, A., Raymond, P., & Montoro Girona, M. (Manuscript). Partial harvest reduces water stress in conifer seedlings: An 18-year $\delta^{13}C$ analysis in Canadian boreal forests. Submitted to *Trees.*

Chapter V – Conclusion

This thesis is my original work, developed in close collaboration with my supervisors and co-authors. My supervisors guided the overall research direction and provided critical input in the design and sampling of the fieldwork, data analysis, and academic writing. In **Chapter 1**, the research was conceptualized by Sanghyun Kim and Miguel Montoro-Girona. I was responsible for data curation, formal analysis, and visualization. Miguel Montoro-Girona, Yves Bergeron, Patricia Raymond, and Nelson Thiffault contributed to funding acquisition, validation, and manuscript review. Methodology and project administration were led by Miguel Montoro-Girona, who also provided resources and supervision, together with Yves Bergeron and Patricia Raymond. I prepared the original draft, which was reviewed and edited by all co-authors. In **Chapter 2**, the study was conceptualized by Sanghyun Kim and Miguel Montoro-Girona. I conducted data curation, formal analysis, and visualization, with assistance from Marion Noualhaguet. The methodology was developed collaboratively with Christine Martineau, R. Greg Thorn, and Vera Tai. Field investigation was carried out by myself, Miguel Montoro-Girona, and Yves Bergeron. Miguel Montoro-Girona and Yves Bergeron secured funding and oversaw project administration. Supervision and validation were provided by Miguel Montoro-Girona, Christine Martineau, and Yves Bergeron. I wrote the original draft, and all co-authors contributed to manuscript review and editing. In **Chapter 3**, the research was conceptualized by Miguel Montoro-Girona and myself. I carried out data curation, formal analysis, and visualization. Methodology development involved Miguel Montoro-Girona, Guillaume Grosbois, and Annie DesRochers. Funding acquisition was led by Miguel Montoro-Girona, Yves Bergeron, Patricia Raymond, Annie DesRochers, and Guillaume Grosbois. Project administration, supervision, and validation were primarily undertaken by Miguel Montoro-Girona, with additional supervision by Yves Bergeron and Patricia Raymond. I prepared the original draft, and all co-authors contributed to review and editing. All co-authors have approved inclusion of these manuscripts in the thesis.

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RÉSUMÉ

Les procédés de régénération comportant des coupes partielles, telles que les procédés par coupes progressives, sont des alternatives prometteuses à la coupe totale pour équilibrer les objectifs écologiques, économiques et sociaux en aménagement forestier. Ces méthodes sont au cœur de l'aménagement écosystémique, car elles visent à reproduire les effets de perturbations naturelles modérées. Cependant, les procédés par coupes progressives ont été initialement conçus sur la base de modèles forestiers Européens et peuvent ne pas être totalement adaptés au régime de perturbations naturelles et aux conditions écologiques de la forêt boréale canadienne. Ainsi, la compréhension de la réponse à long terme de la régénération naturelle, de la diversité microbienne du sol et du stress hydrique des semis après coupe partielle est cruciale pour le développement d'une sylviculture adaptée à la forêt boréale. Cette thèse évalue les effets de différents procédés des régénération (coupe totale, coupe avec réserve de semenciers et trois variantes de coupe progressive régulière) sur ces variables, 18 à 19 ans après coupe dans des pessières noires de l'est du Canada. Dans le chapitre 2, l'étude de la régénération naturelle montre que le procédé de régénération par coupes progressives en mini-bandes a considérablement amélioré la densité des semis d'épinette noire (39 765 semis/ha), laquelle était trois fois plus grande qu'en coupe totale. La croissance des semis était cependant deux fois plus grande en coupe totale qu'en mini-bande. Les principaux facteurs environnementaux influençant la réussite de la régénération étaient la disponibilité du sol minéral, le scarifiage, la couverture de mousse *Polytrichum* et la proximité des bandes résiduelles de forêt. Dans le chapitre 3, l'étude des communautés microbiennes de la rhizosphère associées aux semis d'épinette noire n'a révélée aucune différence significative de la diversité microbienne globale entre les procédés de régénération. Cependant, les sites de coupe totale présentaient une plus grande abondance de bactéries fixatrices d'azote (par exemple, *Roseiarcus* spp.), ce qui pourrait contribuer au cycle des nutriments et à la croissance des semis. Les sites de coupe progressive ont montré une augmentation notable de 77 % des champignons ectomycorhiziens bénéfiques (par exemple *Piloderma* spp.), ce qui indique des relations symbiotiques robustes en cas de perturbations modérées. Les changements dans la composition microbienne étaient étroitement liés à l'altération des propriétés physico-chimiques du sol, en particulier la teneur en calcium, la saturation en bases et la présence de métaux dans les couches organiques. Dans le chapitre 4, l'évaluation du stress hydrique chez les semis d'épinette noire et de sapin baumier par analyse des isotopes stables du carbone ($\delta^{13}C$) a révélé que les procédés de régénération à forte intensité de récolte (coupe totale et coupe avec réserve de semenciers) ont des valeurs de $\delta^{13}C$ plus élevées, indiquant un stress hydrique accru. Inversement, les procédés de régénération par coupes progressives ont maintenu des valeurs $\delta^{13}C$ comparables aux contrôles non récoltés, soulignant que leur efficacité à réduire le stress de sécheresse des semis peut être due aux conditions microclimatiques favorables fournies par le couvert partiel formé par les arbres résiduels. Cette thèse démontre les avantages écologiques du procédé de régénération par coupes progressives, qui en maintenant un couvert partiel, favorise la régénération naturelle, les interactions microbiennes bénéfiques et réduit le stress

hydrique physiologique des semis de conifères. Ces preuves intégrées soulignent le potentiel des pratiques de gestion basées sur l'écosystème, telles que les coupes progressives, pour améliorer durablement la résilience et la productivité des forêts.

Mots-clés : épinette noire, métabarcodage de l'ADN, aménagement écosystémique, régénération naturelle, rhizosphère, coupes progressives, microbiote, stress hydrique, sylviculture, isotopes stables du carbone.

ABSTRACT

Silvicultural systems comprising partial harvests, such as shelterwood systems, have emerged as promising alternatives to the conventional and dominant harvesting practice, clearcutting, aiming to balance ecological, economic, and social objectives. These silvicultural systems are central to ecosystem-based forest management to emulate the effects of moderate natural disturbances. However, shelterwood systems were initially designed in European forests and may not be fully adapted to the natural disturbance regimes and ecological conditions of the Canadian boreal forest. Thus, to understand the long-term response of natural regeneration, soil microbial diversity, and drought stress to partial harvest is crucial for the development of a silviculture adapted to the boreal forest. This thesis evaluates the effects of different silvicultural systems (clearcut, seed-tree method, and three variants of uniform shelterwood) on natural regeneration dynamics, rhizosphere microbial communities, and water stress responses of conifer seedlings 18–19 years post-harvest in eastern Canadian boreal forests. 1) The study of natural regeneration highlights that the mini-strip shelterwood system significantly enhanced black spruce seedling density (39 765 seedlings/ha; 50 751 seedlings/ha in younger stands and 28 780 seedlings/ha in older stands), compared to three times lower densities but two times higher growth rates observed in clearcut areas. Key environmental factors influencing successful regeneration included mineral soil, scarification, *Polytrichum* moss cover, and proximity to residual strips. Further, ericaceous shrubs significantly reduced black spruce regeneration, potentially altering future stand structure. 2) The study of rhizosphere microbial communities in black spruce seedlings revealed no significant differences in overall microbial diversity among silvicultural systems. However, clearcut sites displayed higher abundances of nitrogen-fixing bacteria (e.g., *Roseiarcus* spp.), potentially aiding nutrient cycling and seedling growth. Shelterwood sites showed a notable increase in ectomycorrhizal fungi (e.g., *Piloderma* spp.), indicative of robust symbiotic relationships under moderate disturbances. Changes in microbial composition were closely linked to altered soil physicochemical properties, particularly calcium content, base saturation, and metals in organic layers. 3) The study of physiological water stress in black spruce and balsam fir seedlings using stable carbon isotope analysis ($\delta^{13}C$) revealed high-intensity harvest treatments (clearcut and seed-tree) led to enriched $\delta^{13}C$ values, indicating increased water stress. Conversely, shelterwood systems maintained $\delta^{13}C$ values comparable to unharvested controls, underscoring their efficacy reducing seedling drought stress may be due to the favorable microclimatic conditions provided by residual trees. This thesis demonstrates that partial harvest can enhance natural regeneration, produce symbiotic microbial interactions, and reduce physiological water stress on conifer seedling. The integrated evidence underscores the potential of partial harvest to reach sustainable forest management in the boreal forests.

Keywords: Black spruce, DNA metabarcoding, Ecosystem-based management, Natural regeneration, Rhizosphere, Shelterwood system, Soil microbes, Water stress, Silviculture, Stable carbon

INTRODUCTION

Background. ***Importance of Boreal Forests and Climate Change Threats.*** Boreal forests are the largest terrestrial biome on Earth, covering roughly one-third of the planet's forested area (Gauthier et al., 2015). These high-latitude forests harbor immense biodiversity and serve as a critical global carbon sink, sequestering vast amounts of carbon in their soils and biomass (Ameray et al., 2024; Bradshaw & Warkentin, 2015). About two-thirds of boreal forests, supplying significant economic resources, are managed for timber, contributing roughly 37% of the world's wood supply (FAO, 2024). This dual role of boreal forests in providing ecosystem services and economic products makes their health and sustainability globally important. The primary natural disturbances shaping the boreal forest include wildfire, insect outbreaks, beaver activity, moose browsing, and windstorms (Arsenault et al., 2025; Caron et al., 2023; Debaly et al., 2022; Labrecque-Foy et al., 2020; M. Martin et al., 2022; Neumann et al., 2024). However, boreal ecosystems are increasingly under pressure from human activities and climate change (Seidl et al., 2017). Industrial logging have altered extensive areas, while anthropogenic climate change has led to rising temperatures in northern regions at a rate above the global average (FAO, 2024; Labrecque-Foy & Montoro Girona, 2023; Zhang et al., 2020). Consequently, disturbance regimes are changing, wildfire seasons are lengthening, insect outbreaks are more frequent, all of which threaten the stability of boreal forest landscapes (Aakala et al., 2023; De Jager et al., 2025; Hof et al., 2021; Navarro et al., 2018). This global context underpins the urgent need to develop sustainable forest management strategies that maintain boreal ecosystem integrity in the face of environmental change (Girona et al., 2023). Forest scientists warn that boreal forests managed under conventional practices may be less resilient and more vulnerable to these climate-driven disturbances and being thus crucial the adaptation of silvicultural practices to reach sustainable forest management under climate change (Achim et al., 2021; D'Amato et al., 2023; Kim et al., 2021; Puettmann, 2011; Raymond et al., 2023).

Figure 1.1
Landscape of boreal forest in a MISA experimental site
Photo credit: Ruben Leroy

Boreal Forest Management: From Conventional forest management to Ecosystem-Based Management. Clearcutting, the practice of harvesting all or most trees in an area at once, has been the dominant silvicultural method in boreal forests (Aakala et al., 2023; Kim et al., 2021; Lafleur et al., 2018; Puettmann et al., 2011). Clearcutting became widespread because of its operational efficiency and high immediate timber yield, achieving short-term economic objectives providing even-aged forests (Pukkala et al., 2011). Additionally, it replicates the effects of severe natural disturbances such as wildfires by removing the entire canopy and significantly altering environmental conditions (Aszalós et al., 2022). However, clearcutting poses serious challenges for long-term forest sustainability (Beese et al., 2019; Keenan & Kimmins, 1993). Even-aged management simplifies stand structure and often leads to a loss of biodiversity and ecosystem functions (Angelstam, 1998; Hasan et al., 2023; Raymond et al., 2023; Tahvonen & Rämö, 2016). In particular, it causes habitat loss and landscape fragmentation by removing canopy cover and woody debris that many species depend on (Beese et al., 2019; Fuller et al., 2004; Kim et al., 2021).

Figure 1.2
Aerial drone view of MISA experimental site, 19 years post-clearcut
Photo credit: Ruben Leroy

Studies have documented that clearcutting reduces habitat diversity and can homogenize species composition across the landscape (Bouchard & Pothier, 2011; Hasan et al., 2020; Puettmann et al., 2015). The sudden removal of vegetation also disrupts nutrient cycling. Clearcuts can rapidly deplete soil nutrients and organic matter and increase soil erosion rates on exposed sites (Kohout et al., 2018b). As a result, clearcut areas may experience declines in soil fertility and water quality over time (Callahan et al., 2022; Grosbois et al., 2023; Guimond et al., 2024). Furthermore, clearcutting tends to create hotter, drier microclimates by removing shade and transpiration from the canopy, lowering soil moisture retention, and hindering regenerating vegetation, particularly shade-tolerant species and understory communities, in the short-term (Lafleur et al., 2010; Mallik, 2003). Importantly, such structurally simplified forests are less resilient to external stressors and have been found to be more vulnerable to wind damage and climate extremes than forests with more complex structure (Halpern & Urgenson, 2021). These issues have prompted

criticism of conventional clearcutting and sparked societal concern about the long-term integrity of boreal forests (Gauthier, 2009).

Foresters in Europe began developing uneven-aged silviculture using partial harvesting to emulate natural gap dynamics in boreal and temperate forests, aiming to support sustainable regeneration (Jaloviar et al., 2020). The uneven-aged silviculture was especially prominent in mixed hardwood forests with relatively mild climates, where canopy gaps favored continuous natural regeneration (Kenefic & Kern, 2013). However, these approaches often do not translate well to the Canadian boreal region, advance regeneration is often too sparse in Canadian boreal forests to support European-style selection or gap-based silviculture. In Quebec, most sites require customized prescriptions such as careful logging, fill-planting, or scarification, especially where balsam fir or black spruce are dominant (Greene et al., 2002). Another study in Quebec also argued that partial harvest needs fine-tuning for irregular boreal structures, where disturbance regimes and stand development are highly variable (Ruel et al., 2007). Their integrated experiments showed that even moderate harvesting intensity required adaptation for regeneration success and biodiversity conservation (Ruel et al., 2007).

Figure 1.3
Aerial drone view of MISA experimental site, 19 years after mini-strip shelterwood
Photo credit: Ruben Leroy

Ecosystem-based management (EBM) in the boreal context emphasizes maintaining ecological integrity and biodiversity while allowing for resource extraction (Gauthier et al., 2023). This approach aims to emulate natural disturbance patterns and preserve key structural elements of the forest (Bergeron et al., 1999; Girona et al., 2023; Klenk et al., 2009; Kuuluvainen & Grenfell, 2012). Within an EBM framework, silvicultural systems are designed to balance economic objectives with the conservation of habitat provision, nutrient cycling, and climate regulation (Gauthier, 2009).

Bose et al., (2014) classify partial harvest in the Canadian boreal forest into four main types: commercial thinning (20-30%, basal area removal), regular shelterwoods (30-70%), diameter-limit cutting (30-60%), and variable retention (10-60%). Each treatment varies in harvest intensity and structural goals, ranging from thinning for growth enhancement to retaining mature trees for biodiversity. By retaining a portion of the trees and structural features in harvested areas, partial harvest seeks to protect soil and microclimate conditions and sustain wildlife habitats (Pukkala, 2016). Canadian provinces and other boreal regions have increasingly incorporated sustainable forest management practices, including retention forestry, into their policies to address concerns about clearcutting (Ameray et al., 2023; Girona et al., 2016; Kim et al., 2021, 2025; Santaniello et al., 2016).

Among those silvicultural treatments, the uniform shelterwood system removes approximately 30–40 % of stand basal area in each entry (cumulatively up to 60–70 %), thereby maintaining a relatively even overstory cover to promote natural regeneration for shade tolerant species (Hannah, 1988). By contrast, the irregular shelterwood functions as a spatially explicit retention system, removing 30–60 % of basal area in staggered, patchy patterns to emulate natural gap dynamics (Raymond et al., 2009). Each approach balances harvest intensity with structural objectives, uniformly in the uniform shelterwoods and heterogeneously in the irregular shelterwood, so as to protect soil and microclimate conditions, sustain wildlife habitats,

and promote continuous cover (Pukkala, 2016). According to the National Forestry Database, Québec's annual allowable cut currently stands at roughly 34 million m³. In 2022, about 2.5 million m³ (approximately 7 % of that volume) was harvested under partial harvest systems (irregular shelterwood, uniform shelterwood, and other retention methods), up from just 4 % in 2010 (Canadian Council of Forest Minsters, 2023). In recognition of these benefits, Quebec and other boreal jurisdictions have formalized shelterwood system guidelines within their ecosystem-based management policies to address both production and conservation goals (Ameray et al., 2023; Kim et al., 2021; Larouche & Saucier, 2013; Raymond et al., 2010; Santaniello et al., 2016; Shorohova et al., 2023).

The overarching challenge now is to adapt partial harvest to the Canadian boreal forest conditions and verify that they effectively mitigate the ecological drawbacks of clearcutting. Long-term studies are crucial to evaluate whether ecosystem-based silviculture can achieve the intended balance between timber production and ecological integrity (Gauthier et al., 2015).

Clearcutting vs. Partial Harvest in boreal forests. *Natural Regeneration*. Clearcutting has profound impacts on forest regeneration by altering species composition, disrupting microsite conditions, and modifying microclimates that are critical for seedling recruitment (Walker & Mallik, 2009). Specifically, clearcutting can hinder the regeneration of shade-tolerant conifers such as black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill) and white cedar (*Thuja occidentalis* L.), which dominate mature boreal stands in Canada (Lafleur et al., 2019; Maleki et al., 2020). The complete removal of canopy and associated root networks can create harsh microclimatic conditions, including increased temperature fluctuations, reduced soil moisture retention, and higher wind and solar exposure that impede seedling establishment and survival (Kohout et al., 2018a; Lafleur et al., 2010). Furthermore, the elimination of mature seed trees necessitates reliance on seed influx from adjacent stands or advance regeneration, which is frequently inconsistent or insufficient for ensuring adequate natural regeneration (Mallik, 2003; Thiffault et al., 2024). These constraints

often lead to regeneration delays and may require artificial regeneration such as tree planting.

In contrast, partial harvest have gained traction over the past few decades as silvicultural alternatives to clearcutting in boreal forests (Gauthier, 2009; Gauthier et al., 2023). Retention of overstory trees moderates post-harvest abiotic conditions by buffering soil temperatures, reducing moisture loss, and protecting understory seedlings from wind exposure (Bescond et al., 2011). These legacy trees can also contribute to protecting seeds, organic layer, and sustaining mycorrhizal networks that may enhance regeneration (Bell-Doyon et al., 2022; Simard et al., 2021). Additionally, the heterogeneous canopy structure promotes a more diverse understory, supporting biodiversity and ecosystem functions (Hernández-Rodríguez et al., 2021). Research has shown that partial harvests help maintain species associated with mature or old-growth conditions by avoiding the full reset of forest structure (Moussaoui et al., 2020b). By maintaining structural complexity, microclimates and residual seed sources, partial harvest fosters more stable microenvironments that are better suited to shade-tolerant and late-successional species (Kim et al., 2021; Lafleur et al., 2019). For instance, in mixedwood forests of northeastern North America, Bose et al. (2023) reported species-specific regeneration responses, where shade-tolerant and mid-tolerant species (e.g., balsam fir, red spruce) responded favorably to intermediate retention levels. Environmental factors also shape regeneration outcomes following partial harvest. Larger gaps created by partial harvest increased both density and diversity of early-successional and shade-intolerant species due to improved soil temperature and light availability (Mallik et al., 2014).

Despite growing knowledge, several gaps remain in our understanding natural regeneration under partial harvest treatments. First, most studies focus on short- to medium-term outcomes, whereas long-term studies (> 5 years post-harvest) are rare. Second, partial harvest responses are highly variable and context-dependent, influenced by site moisture, species composition, intensity, pre-harvest condition and spatial configuration of harvests (Moussaoui et al., 2020b), making them difficult to generalize and underscoring the need for adaptive, site-specific prescriptions. Third,

some stands display uneven or sparse seedling distribution, especially where seedbed conditions are suboptimal or seed sources are limited, thus it is important to study the microsite-level constraints (soil compaction, competing understory, seed rain) that drive regeneration gaps. These gaps highlight the need for adaptive management strategies, such as targeted site preparation or enrichment planting, to complement partial harvest and ensure consistent regeneration across different microsites at the long term.

Soil Ecosystem (Physicochemistry, Bacteria, and Fungi. Forest soils are critical to post-harvest natural regeneration success because they host the physical and biological processes that underpin nutrient cycling, seedling establishment, and ecosystem recovery (Qin et al., 2017). In boreal forests, soils are often characterized by acidic pH, low base saturation, and high organic matter accumulation in the organic horizon (Kyaschenko et al., 2017). These properties are closely linked with vegetation type, canopy cover, and disturbance history (Bastianelli et al., 2017). Silvicultural systems are able to modify canopy structure and alter organic matter inputs can trigger cascading effects on soil microclimate, chemical composition, and microbial assemblages (Clemmensen et al., 2013; Kim et al., 2021; Obase et al., 2025) (Figure 1.4). Over time, repeated clearcutting can simplify landscape age structure, reduce the presence of old-growth features, and raise concerns about biodiversity loss at both stand and landscape scales (Gauthier et al., 2015; Keenan & Kimmins, 1993; Noualhaguet et al., 2023).

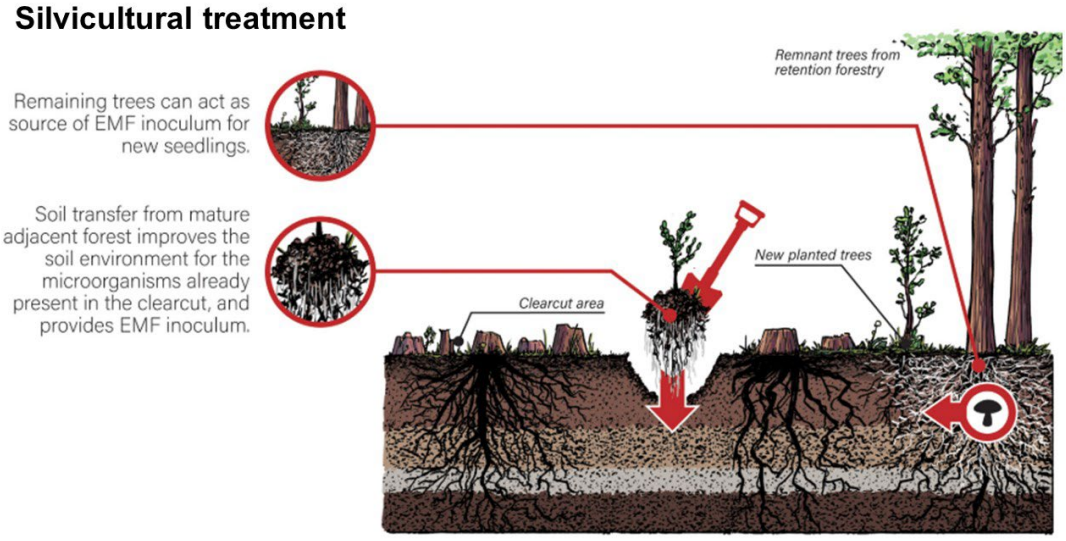

Figure 1.4
Retention forestry and soil translocation: enhancing seedling establishment through mycorrhizal network access and improved soil conditions
Source: (Policelli et al., 2020)

Soil microbial communities are highly responsive to disturbances such as harvesting (Hartmann et al., 2012). While some shifts may be transient, many leave persistent legacies on microbial composition and function (Hartmann et al., 2014). Clearcutting can disrupt root-microbe interactions by removing tree hosts, which reduces the prevalence of ectomycorrhizal fungi (Bell-Doyon et al., 2022). Moreover, changes in soil pH, moisture, and nutrient availability following clearcuts can favor fast-growing, disturbance-tolerant bacterial and fungal taxa, altering the balance of functional groups (Hannam et al., 2006). These microbial community shifts can affect not only decomposition rates but also the bioavailability of nitrogen and phosphorus that are key nutrients for seedling development and growth (Philippot et al., 2023).

Soil physicochemical properties and microbial communities differ significantly between clearcut and partial harvest systems, influencing forest regeneration trajectories (Policelli et al., 2020). Clearcutting typically results in increased soil temperature, decreased moisture, and altered nutrient cycling dynamics due to substantial

exposure to sunlight and greater evaporation (Bell-Doyon et al., 2022; Kim et al., 2021). These physical changes, combined with the removal of organic matter, can lead to reduced soil fertility, erosion, and decreased organic carbon content (Kohout et al., 2018b). Therefore, clearcutting significantly alters soil microbial communities, reducing beneficial microbes such as ectomycorrhizal fungi, critical for tree nutrition and soil health (Policelli et al., 2020). Opportunistic bacteria and saprotrophic fungi often increase following clearcuts, rapidly decomposing residual organic matter but potentially reducing long-term nutrient availability (Bell-Doyon et al., 2022).

In contrast, partial harvest retains canopy cover and structural elements, buffering soils against temperature extremes and preserving soil moisture, leading to less disruption of soil physicochemical conditions (Ameray et al., 2021; Moussaoui et al., 2020b). Partial harvest methods typically preserve greater quantities of organic matter and nutrients, enhancing soil fertility and stability, and better maintaining soil carbon storage compared to clearcuts (Noualhaguet et al., 2023). For this reason, it is expected that partial harvest maintains more diverse and stable soil microbial communities (Purahong et al., 2015). Retention of mature trees and litter layer sustains beneficial ectomycorrhizal fungi, which support seedling nutrition and enhance regeneration success (Urbanová et al., 2015). Additionally, partial harvest can better preserve nitrogen-fixing bacteria and diverse bacterial communities, contributing to sustained nutrient cycling and improved soil resilience following disturbance (Sukdeo et al., 2019). However, the long-term trajectories and functional recovery of microbial communities after partial harvest remain poorly understood compared to clearcut. There is a critical gap in assessing whether partial harvest fully supports the re-establishment of microbial networks essential for seedling performance, which requires evaluating plant-microbe feedback in long-term post-harvest conditions.

Water Stress Responses of Conifer Seedlings. In forest ecosystems, water availability is a primary environmental factor influencing seedling establishment, physiological performance, and long-term survival (Battaglia et al., 2000; Gabira et al., 2024). Seedling and water relationships are shaped by both climatic conditions and

site-specific microenvironments, which are in turn strongly affected by silvicultural practices (Roy et al., 2000). As climate change continues to increase the frequency and intensity of droughts (Fettig et al., 2013), understanding how silvicultural systems mediate water stress is critical to ensuring successful forest regeneration (Pappas et al., 2022; Sohn et al., 2016).

Silvicultural systems such as clearcutting and partial harvest alter forest structure and microclimate, influencing soil temperature, moisture retention, and evaporative demand (Allman et al., 2023). Post-harvest conditions typically result in elevated transpiration rates and reduced stomatal conductance in seedlings, potentially leading to greater physiological stress under drought-prone conditions (Roy et al., 2000).

The physiological status of seedlings under different moisture regimes can be assessed using various methods, with stable carbon isotope composition ($\delta^{13}C$) being one of the most robust (Zhang et al., 2023). The $\delta^{13}C$ value represents the ratio of heavy (^{13}C) to light (^{12}C) carbon isotopes in plant tissues, expressed relative to an international standard (VPDB). The $\delta^{13}C$ serves as an integrative proxy for intrinsic water-use efficiency and long-term stomatal behavior (Di Matteo et al., 2017). Under water-limited conditions, seedlings tend to exhibit higher $\delta^{13}C$ values due to reduced stomatal aperture and increased water-use efficiency (Parker & Dey, 2008). Thus, $\delta^{13}C$ analysis provides insight into how forest microclimate, shaped by harvest intensity, affects seedling physiology over extended periods.

In addition to canopy structure, other biotic and abiotic factors such as seedling size, soil texture, and ground vegetation affect water stress outcomes (Taeger et al., 2015). For example, coarse soils like sand can cause more negative water potential than fine soils, increasing seedling stress under dry conditions (Nainanayake & Bandara, 2008). Moreover, moss-dominated forest floors often act as a moisture buffer, slowing evaporation and stabilizing the water supply to roots (Fenton & Bergeron, 2006). Larger seedlings with greater leaf area and transpiration demands may also be more sensitive to drought, especially in exposed microsites (Fischer & Toit, 2019).

Physiological assessments of naturally regenerating seedlings are rarely integrated into forest management evaluations. As boreal regions face increasing climatic variability, silvicultural systems that maintain or enhance microclimatic stability may offer greater support for seedling resilience (Girona et al., 2023). Partial harvest could therefore contribute to more drought-resilient forest regeneration by minimizing physiological water stress in establishing seedlings, however no research has previously carried out to confirm this question.

Objectives and hypotheses. The general objective of this doctoral thesis to evaluate the long-term response of natural regeneration, microbial community dynamics, and seedling water stress to a gradient of silvicultural systems in Canadian boreal forests, to guide the implementation of partial harvest as silvicultural option for ecosystem-based management practices.

The general hypothesis is that silvicultural systems using partial harvest promote enhanced natural regeneration, more beneficial microbial interactions, and lower physiological water stress in conifer seedlings compared to conventional clearcutting methods. Additionally, mid-term ecological impacts of silvicultural systems are significantly influenced by interactions regeneration methods, forest structure, soil properties, and physiological responses of tree seedlings. The specific objectives and hypotheses for each thesis chapter are:

Natural Regeneration after Silvicultural systems along a gradient of harvest intensity

Objectives:

1) To evaluate the effects of a gradient of silvicultural systems (clearcut, seed-tree, uniform shelterwood systems) on the density, growth, and establishment success of naturally regenerated black spruce seedlings 18 years post-harvest.

2) To determine the key environmental and site-specific factors driving natural regeneration and seedling growth after silvicultural interventions.

Hypotheses:

1) Partial harvest, represented by shelterwood treatments, combined with spot scarification will produce higher densities of naturally regenerated black spruce seedlings compared to clearcutting due to better preservation of residual trees as seed sources and favorable microsites.

2) Seedling growth (terminal shoot length, height) will be greater in treatments with higher canopy openness (clearcut, seed-tree), driven by increased light availability.

Rhizosphere soil Microbial Communities after Clearcut and Partial cut

Objectives:

1) To assess the long-term effects of clearcut and partial-cut treatments on the diversity, structure, and composition of rhizosphere microbial communities associated with naturally regenerated black spruce seedlings.

2) To determine the microbial indicators behind the complex relationship between silvicultural systems, altered soil physicochemical properties, and rhizosphere microbial community dynamics.

Hypotheses:

1) Partial harvest sites will result in greater rhizospheric soil microbial diversity compared to clearcut sites due to increased environmental heterogeneity and preserved soil conditions.

2) Specific microbial taxa, such as nitrogen-fixing bacteria and ectomycorrhizal fungi, will significantly differ in abundance between clearcut and partial cut treatments, reflecting their sensitivity to disturbance intensity and altered soil chemistry.

3) Changes in microbial communities are strongly correlated with specific soil physicochemical properties altered by silvicultural systems.

Seedling Physiological Responses to Water Stress using $\delta^{13}C$

Objectives:

1) To evaluate the impact of silvicultural systems on physiological water stress in conifer seedlings 18 years after harvest using stable carbon isotope ($\delta^{13}C$) analysis.

2) To determine the factors involved in the relationship between the harvest intensity in silvicultural treatment and seedling physiological stress indicators ($\delta^{13}C$).

Hypotheses:

1) Seedlings regenerating under clearcut and seed-tree method, characterized by greater canopy removal, will exhibit elevated foliar $\delta^{13}C$ values, indicating increased physiological water stress compared to seedlings in partial harvest and unharvested control areas.

2) Larger seedlings (diameter) will exhibit higher $\delta^{13}C$ values due to greater transpiration demands, and the presence of bryophyte cover (*feathermosses*) will significantly reduce physiological water stress by moderating soil moisture conditions.

Study sites and experimental design. This study was conducted in the boreal forest region of Quebec, Canada, within the northern Saguenay–Lac-Saint-Jean and North Shore regions. The study area spans two bioclimatic domains: the balsam fir–white birch (*Abies balsamea* and *Betula papyrifera*) and the black spruce–feathermoss (*Picea mariana* and *feather moss*) regions, representative of the eastern Canadian

boreal forest ecosystem (Figure 1.5). The climate in these regions is subhumid continental to subpolar, characterized by long, cold winters and short growing seasons of approximately 140 days (Rossi et al., 2011). Average annual temperatures range from 2.2°C to 2.8°C, with summer highs reaching 18.4°C and winter lows dipping to –15.7°C and annual precipitation varies from 931 mm to 1,081 mm (Environment and Climate Change Canada, 2015). Geologically, the study area is underlain by thick glacial till deposits and frequent rock outcrops on steeper slopes (Robitaille & Saucier, 1998). Soils are predominantly humo-ferric podzols, with textural classes ranging from sandy clay loam to sandy loam (Montoro-Girona, 2017). These acidic, nutrient-poor soils are typical in Eastern Canadian boreal forests and play a central role in seedling establishment and microbial dynamics.

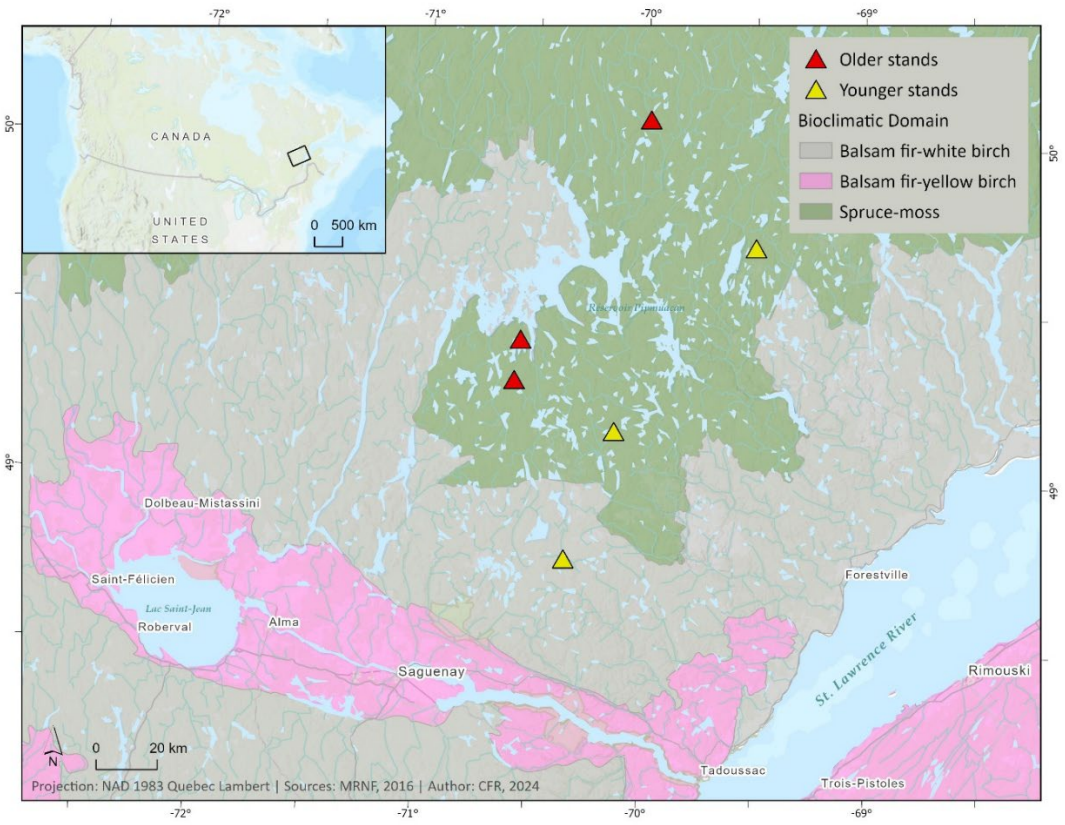

Figure 1.5
Study blocks of experimental silvicultural systems in Quebec, Canada.

The study stands are natural, even-aged black spruce-dominated forests, with stand ages ranging from 80 to 150 years. The canopy composition is over 90% black spruce, accompanied by scattered balsam fir, white birch, and trembling aspen (*Populus tremuloides*). The homogeneity of these stands in terms of species composition and structure is attributed to shared wildfire histories, confirmed through dendrochronological analysis.

The MISA (Managing Innovative Silvicultural Alternatives) experiment, to favor natural regeneration of even-aged stands, features a novel and structured design comprising two fully randomized block experiments, each set in even-aged black spruce stands of different ages and regeneration levels—one in younger stands (80–100 years, 2,595 trees/ha) with limited advance regeneration, and the other in older stands (120–150 years, 1,537 trees/ha) with abundant regeneration. Each design included three blocks, with six silvicultural systems, featuring innovative shelterwood variants, randomly assigned to 3-hectare units, for a total of 36 experimental units. While this setup enables strong within-stand comparisons, stand types were not replicated across different landscapes, limiting broad-scale generalization.

A key innovation of this experiment lies in its integration of structurally distinct shelterwood systems such as regular progressive cuts, designed to emulate natural disturbance dynamics and maintain ecological continuity. These shelterwood variants go beyond conventional methods by varying spatial patterning, intensity, and temporal progression of canopy removal, thereby providing new insights into regeneration pathways under managed disturbance regimes.

The homogeneity of both stand types, shaped by similar fire histories, was confirmed through dendrochronological analysis, strengthening the internal consistency of the design (Girona et al., 2016). To track natural regeneration and ecosystem responses, one permanent 10 × 60 m sampling plot was established in each unit, complemented by two transects of 21 circular microplots (4 m²) per plot, resulting in 1 512 microplots

across the experiment. Ecological data was previously collected one year before and after harvest as well as 10 years after (Montoro Girona et al., 2018). Prior to harvesting, black spruce overwhelmingly dominated the canopy (younger stands: 95.8%; older stands: 96.1%), with minor presence of balsam fir, trembling aspen, and white birch. In our study, we revisited the MISA experiment 18 and 19 years after harvest to capture the long-term ecological trajectories often overlooked in short-term studies. By assessing regeneration dynamics, seedling physiological traits, and soil microbial communities nearly two decades post-treatment, we aimed to evaluate the lasting impacts of novel shelterwood systems on boreal forest resilience and ecosystem recovery, providing insights critical for informing adaptive silviculture under changing environmental conditions.

Thesis outline. This doctoral thesis is the result of research conducted within the GREMA (Groupe de recherche en écologie de la MRC Abitibi) research group at the Université du Québec en Abitibi-Témiscamingue (UQAT), as part of the four-year doctoral program in Environmental Sciences the Université du Québec à Montréal (UQAM) and UQAT.

The thesis is structured in five chapters, following a manuscript-based format. Chapter I provides a general introduction, outlining the theoretical framework, research context, and main objectives of the study. It also details the study sites and experimental design throughout the project. Chapters II to IV consist of independent scientific studies developed during the course of the doctoral research. These chapters are presented in the format of scientific articles intended for peer-reviewed publication. Each chapter contributes to a comprehensive understanding of the long-term impacts of silvicultural systems on natural regeneration, rhizosphere microbial dynamics, and seedling physiological responses in boreal forests: Chapter V offers a general conclusion that synthesizes the findings, highlights the major contributions of the research, discusses methodological limitations, and offers recommendations for future studies.

Bibliographic references and supplementary materials are included at the end of the thesis.

Chapter I introduces the research background, presents key scientific and management challenges in forest management in the boreal forests as well as the state of knowledge of partial harvests, outlines the specific research objectives and hypotheses, describes the study sites and experimental design, and concludes with an overview of the thesis structure.

Chapter II investigates the natural regeneration 18 years after the application of various experimental silvicultural systems in boreal forests of eastern Canada. The study evaluates seedling and sapling density, species composition, and growth attributes across clearcut, seed-tree, and shelterwood systems. It also explores how microenvironmental factors, including ground cover and substrate type, influence regeneration outcomes under different canopy retention levels. This chapter was published in Forest Ecology and Management journal with the title of “Natural regeneration 18 years after experimental silvicultural systems in Canadian boreal forests” (Kim et al., 2025).

Chapter III assesses the composition and diversity of rhizosphere microbial communities associated with black spruce seedlings 19 years after clearcutting and partial cutting (mini-strip shelterwood) treatments. Using DNA metabarcoding, this chapter compares bacterial and fungal assemblages among treatments and examines the relationship between microbial communities and soil physicochemical properties. The study highlights the legacy effects of forest management on soil microbial ecology and identifies indicator taxa that may influence seedling establishment. This chapter will be submitted to PLOS One journal.

Chapter IV evaluates the long-term water stress responses of naturally regenerated black spruce and balsam fir seedlings across different silvicultural systems. By analyzing foliar stable carbon isotope ratios ($\delta^{13}C$), this chapter quantifies intrinsic water-use efficiency as a proxy for physiological drought stress in conifer seedlings. The analysis explores how harvesting intensity, canopy structure, seedling size, and bryophyte ground cover affect water stress responses in seedlings. This chapter will be submitted to Trees journal from Springer.

Chapter V synthesizes the main findings of the thesis and discusses their implications for sustainable forest management and climate change adaptation strategies in boreal ecosystems. It also identifies limitations of the current research and outlines directions for future studies focusing on the implementation of partial harvest as promising options in boreal forests.

1. REGENERATION NATURELLE 18 ANS APRES DES TRAITEMENTS SYLVICOLES EXPERIMENTAUX DANS LES FORETS BOREALES CANADIENNES

NATURAL REGENERATION 18 YEARS AFTER EXPERIMENTAL SILVICULTURAL SYSTEMS IN CANADIAN BOREAL FORESTS

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1.1 Résumé

Au Canada, la coupe à totale est le procédé de régénération le plus utilisé dans les forêts boréales, malgré les impacts potentiels sur la simplification des forêts et la perte de biodiversité. Il est suggéré de conserver les arbres matures pour maintenir la structure des peuplements et la biodiversité, en particulier pour favoriser la régénération des espèces tolérantes à l'ombre. La récolte partielle est considérée comme une alternative prometteuse à la coupe totale pour intégrer les objectifs écologiques, économiques et sociaux dans la planification sylvicole. Cependant, cette approche doit être développée pour être utilisée dans les forêts boréales naturelles. Nous évaluons ici les effets des traitements sylvicoles sur la régénération naturelle dans des peuplements naturels équiennes d'épinette noire (*Picea mariana* (Mill.) B.S.P.) matures, 18 ans après la coupe. En 2003, dans les régions du Saguenay et de la Côte-Nord du Québec, un plan expérimental de blocs entièrement randomisés a été établi sur six sites, chacun contenant deux types de peuplements forestiers (jeunes et vieux) et six traitements sylvicoles. Dans 1 512 micro parcelles, nous avons inventorié tous les semis d'arbres par espèce et par classe de hauteur et nous avons évalué un semis dominant en fonction de variables liées à la croissance et au microenvironnement. Nous avons constaté que 18 ans après le traitement, la coupe progressive par mini-bandes produisait la plus forte densité de semis d'épinette noire (39 765 semis/ha). En revanche, la coupe totale a produit une densité de semis trois fois plus faible que la coupe progressive uniforme, mais a permis de multiplier par deux la croissance des pousses terminales des semis. Le sol minéral, la scarification ponctuelle, la couverture de mousse avec *Polytrichum* spp. et la distance par rapport aux bandes résiduelles étaient corrélés positivement avec la densité des semis d'épinette noire. Notre étude met en évidence le procédé de régénération par coupes progressives comme alternative sylvicole à la coupe totale pour promouvoir la régénération de l'épinette noire dans les forêts boréales canadiennes.

Mots clés: aménagement écosystémique, aménagement durable des forêts, procédé de régénération par coupes progressives, scarifiage, arbustes éricacées, régénération naturelle.

1.2 Abstract

In Canada, clearcutting is the most widely used silvicultural system in boreal forests despite potential impacts on forest simplification and biodiversity loss. Retaining mature trees is suggested to maintain stand structure and biodiversity, especially for promoting the regeneration of shade-tolerant species. Partial harvesting is considered a promising alternative to the clearcutting system as a means of integrating ecological, economic, and social objectives into silvicultural planning; however, this approach must be developed for use in natural boreal forests. Here, we evaluate the effects of silvicultural systems on natural regeneration in stands of natural even-aged mature black spruce (*Picea mariana* (Mill.) B.S.P.), 18 years after cutting. In 2003, in the Saguenay and North Shore regions of Quebec, an experimental design of fully randomized blocks was established across six sites, each containing two forest stand types (younger and older stands) and six silvicultural systems. In 1 512 microplots, we categorized all tree seedlings by species and height class and assessed a dominant seedling for growth-related variables, and microenvironment. We found that 18 years after treatment, mini-strip shelterwood harvesting produced the highest black spruce seedling density (39 765 seedlings/ha). In contrast, clearcutting produced a seedling density that was three times lower than uniform shelterwood harvesting but demonstrated a twofold increase in seedling terminal shoot length. Mineral soil, spot scarification, moss cover with *Polytrichum* spp., and distance from residual strips positively correlated with black spruce seedling density. Our study highlights the potential of shelterwood systems as a silvicultural alternative to clearcutting for promoting black spruce regeneration in Canadian boreal forests.

Keywords: ecosystem-based management, sustainable forest management, shelterwood systems, scarification, ericaceous shrubs, natural regeneration

1.3 Introduction

Despite the global forest area shrinking annually by approximately 10 million ha—the size of South Korea—between 2010 and 2020, the demand for wood products has surged, with industrial roundwood production projected to increase 4%–8% by 2030 (FAO, 2024; Q. Zhang et al., 2020). Increased logging to support this demand significantly alters forest ecosystems (Park & Wilson, 2007). Even-aged management based on the clearcut system may favor the decline of old-growth forest areas (Martin et al., 2020), the simplification of stand structures (Angelstam, 1998; Bouchard & Pothier, 2011; Raymond et al., 2023), and the loss of biodiversity (Fuller et al., 2004; Kim et al., 2021). Thus, the boreal biome is currently facing challenges stemming from the increasing homogenization and simplification of forest structure across various countries (Puettmann et al., 2015). For instance, in Canada, clearcutting has been the dominant forest management practice across the country. On average, 4000 km^2 of boreal forest is clearcut each year in the country (Girona et al., 2023a; National Forestry Database, 2024). Promoting more diversified forest structures, however, can simultaneously support wood supply needs while enhancing biodiversity and ecosystem services (Girona et al., 2023a; Waldron et al., 2020).

Using partial harvesting as a silvicultural alternative to clearcutting can help integrate ecological, economic, and social objectives, while narrowing the gap between natural and managed forests, and hence align with the ecosystem-based management framework (Bose et al., 2014; Gauthier et al., 2023). Although shelterwood systems support ecosystem-based management objectives, achieving successful natural regeneration remains a significant challenge because of factors such as variability in seedling recruitment, competition from understory vegetation, and site-specific conditions (Bose et al., 2023; Lafleur et al., 2010, 2019; Moussaoui et al., 2020a). Furthermore, altered fire regimes or increased severity and frequency of extreme droughts because of climate change threaten successful natural regeneration establishment (Boucher et al., 2020; Molina et al., 2022). Thus, the continuous evaluation and refinement of silvicultural systems are necessary to ensure the efficacy and sustainability of forest management practices adapted to future climate change (Ameray et al., 2024).

MISA (Managing Innovative Silvicultural Alternatives) is a large-scale experiment in the boreal black spruce region of Quebec, Canada, designed to evaluate various silvicultural systems, including novel variants of uniform shelterwood, that differ in their overstory removal and scarification intensities. Earlier results have shown that the uniform shelterwood system is effective in promoting the radial growth of residual trees (Montoro Girona et al., 2016, 2017) with moderate tree mortality by windthrow (Montoro Girona et al., 2019), whereas seed-tree systems promote the establishment of black spruce regeneration over balsam fir (*Abies balsamea*) (L.) Mill (Montoro Girona et al., 2018). However, the factors involved in natural regeneration are not yet fully understood, highlighting the need for long-term ecological monitoring to fully understand and optimize these systems for wider implementation in Canadian boreal forests.

Regeneration success is influenced by a complex interplay of biotic and abiotic factors (Thiffault et al., 2024): belowground intra- and inter-specific competition, interaction with ground-cover species, soil characteristics, disturbances, and light availability, all of which critically affect seedling establishment and growth in boreal forest ecosystems (Bose et al., 2023). For instance, intra- and interspecific competition between seedlings and understory vegetation for light and nutrients has been a major factor affecting post-shelterwood regeneration processes in North American and European forests (Brose and Van Lear 1998; Joanisse et al. 2018). In eastern Canadian boreal forests, ericaceous shrubs, such as bog Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron and Judd) and sheep laurel (*Kalmia angustifolia* L.), impede seedling establishment and growth through a combination of mechanisms, including competition for soil nutrients and potential allelopathic interactions (Mallik, 2003). Ground-cover vegetation, such as bryophyte species, also plays a pivotal role in influencing tree regeneration by aiding seed germination by providing and maintaining optimal moisture conditions (Ohlson & Zackrisson, 1992). In a greenhouse experiment, *Sphagnum* spp. ground cover provided an optimal substrate for black spruce germination and early development, although *Sphagnum*-covered substrates eventually inhibited the growth of two-year-old seedlings (Lavoie et al., 2007; Pacé et

al., 2018). Soil characteristics also shape the success of natural regeneration in the Canadian boreal forest (Nagati et al., 2020). Black spruce prefers acidic, moist, well-drained soils and is resilient to occasional drought and waterlogged conditions because it is physiologically and mycorrhizally adapted to low-nutrient, acidic environments; however, this species also thrives in diverse soil conditions, from rich humus to rocky, shallow soils over bedrock (Viereck & Johnston, 1990). Nonetheless, more intense drought conditions combined with anthropogenic disturbances may significantly alter the composition, structure, and biogeography of forests and produce profound shifts in various ecosystem processes and services (Walker et al., 2015).

Mechanical site preparation by scarification favors successful regeneration by creating favorable microsites for seed germination for light-seeded tree species (Prévost, 1997; Sikström et al., 2020), including black spruce. Seedbed conditions that optimize the survival and growth of conifer seedlings remain poorly understood (Montoro Girona et al. 2023a). To elucidate the synergistic effects of scarification and canopy opening on seedling establishment and subsequent growth, there is a pressing need for more comprehensive and long-term studies (Béland et al., 2000; Drössler et al., 2017; Raymond et al., 2000).

Our study aimed to assess the dynamics of natural regeneration and their driving factors in even-aged natural black spruce stands of eastern Canada, 18 years after treatments related to overstory removal and spot scarification. Stands were subjected to six silvicultural systems: three variants of the uniform shelterwood system (close-selection, distant-selection, mini-strip), one seed-tree cutting, and one clearcut as well as unmanaged as a control. We hypothesized that the shelterwood system offers an optimal balance between light availability and seed sources and that scarification creates adequate seedbeds while controlling competing vegetation for seedling density. Moreover, greater seedling growth can be expected to higher harvest intensities, i.e., seed-tree and clearcut treatments, which enhance light availability in the understory. Relying on these hypotheses, we predicted that (i) the combined application of partial harvesting and scarification would ensure successful conifer regeneration, with higher conifer seedling densities in uniform shelterwood systems

than in the clearcut stands; (ii) seedling growth rates would be higher in seed-tree and clearcut systems relative to shelterwood systems; (iii) competitive interactions between black spruce seedlings and the surrounding vegetation would substantially influence black spruce seedling density.

1.4 Materials and methods

1.4.1 Study area

The study area comprises natural even-aged black spruce stands located in the northern Saguenay-Lac-Saint-Jean region and North Shore regions of Quebec, Canada (Montoro Girona et al., 2023c). The study sites are located within two bioclimatic domains, namely the balsam fir–white birch (*Betula papyrifera* Marsh.) and the black spruce–feathermoss bioclimatic domains (Saucier et al., 2009) (Figure 2.1). Regional climate is subhumid continental, with a short growing season of 140 days (Rossi et al. 2011). The annual mean temperature is 2.8 °C and is characterized by cold winters (–15.7 °C) and cool summers (18.4 °C) in the data collection year (2021). Average annual precipitation is 931 mm in the form of snow or rain (Environment and Climate Change Canada 2015). Surface deposits are mainly composed of thick glacial tills, and rock outcrops are frequent at the top of steep slopes (Robitaille & Saucier 1998). The predominant soil type is humo-ferric podzol (Montoro Girona et al., 2018). In the experimental sites, the soil texture ranges from sandy clay loam to sandy loam.

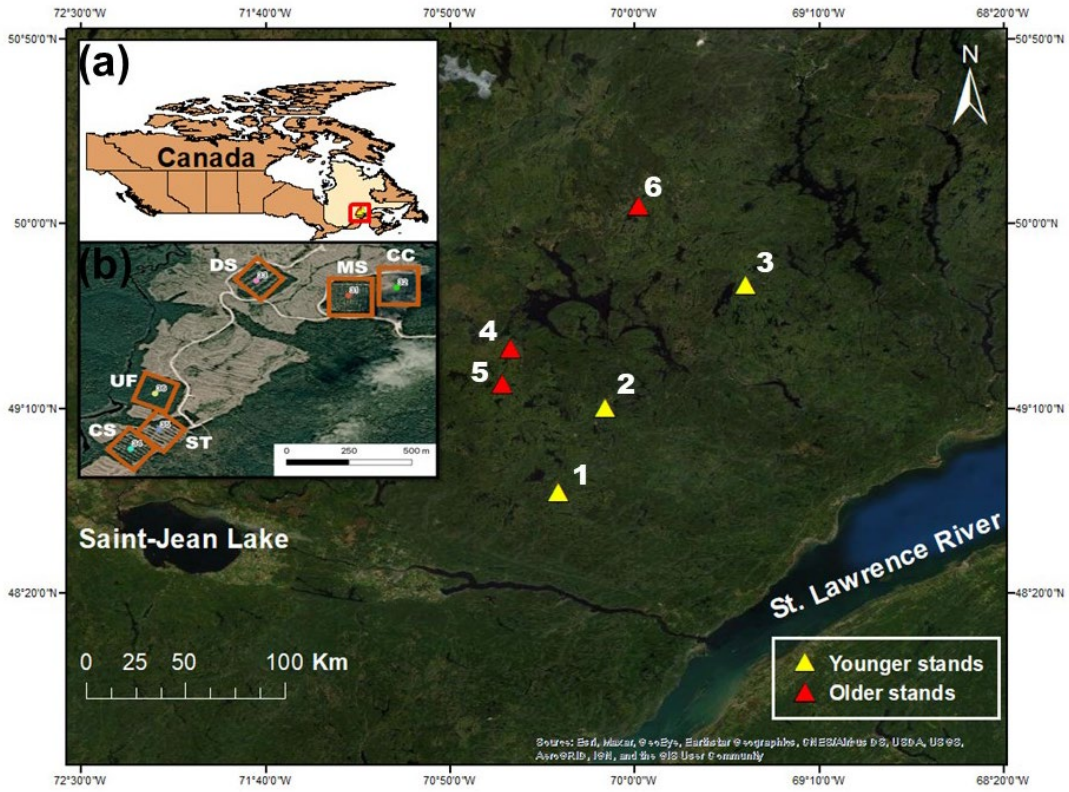

Figure 1.1
Location of the MISA experimental sites (1–3: younger stands; 4–6: older stands). (a) The northern Saguenay-Saint-Jean-Lake and North Shore regions of Quebec, Canada; (b) Orthophotography depicting the 3 ha experimental units (brown squares) of one block (replicate) as an example. UF, unmanaged forest; MS, mini-strip shelterwood; DS, distant-selection shelterwood; CS, close-selection shelterwood; ST, seed-tree system; CC, clearcut harvesting.

1.4.2 Experimental design

The MISA experiment was structured as two separate fully randomized block designs (Figure S1). One design was implemented in younger even-aged black spruce stands (80–100 years; average density of 2 595 trees/ha), considered to have a low level of advanced regeneration, and the other in older stands (120–150 years; average density of 1 537 trees/ha) considered to have a high level of advanced regeneration. Each design included three blocks, with six silvicultural systems randomly assigned to 3-hectare units in each block, resulting in 36 experimental units (6 sites × 6 treatments). While this design enables comparisons of treatment effects within each stand type

(younger vs older), the stand type itself is not independently replicated across different sites. Therefore, potential site-specific conditions may influence the observed stand type effects, limiting the ability to generalize these effects across broader regions.

Both stand types were homogeneous because of their fire history; this was confirmed through dendrochronological dating of the trees. To study natural regeneration, each experimental unit included one permanent sampling plot (10 × 60 m) with two transects of circular microplots (4 m^2) perpendicular to the main plot (2 transects × 21 microplots × 36 experimental units = 1 512 microplots; Figure 3). Sampling and measurements were conducted one year before and after harvesting, as well as 10 years (Montoro Girona et al., 2018) and 18 years after harvesting (this study). Prior to cutting, the tree species composition was dominated by black spruce (younger: 95.8%; older: 96.1%, total number of stems), with balsam fir (younger: 1.6%; older: 3.6%), trembling aspen (*Populus tremuloides* Michx; younger: 2%; older: 0.2%), and white birch (younger: 0.5%; older: 0.1%) making up the remainder.

1.4.3 Silvicultural systems

Three variants of the uniform shelterwood system differ in their respective spatial and scarification patterns: 1) mini-strips (MS) created narrow corridors (5 m wide skid trails) of 50% harvested areas with unharvested strips in between, and the highest scarification proportion (average scarified area of 1 296 m^2/ha); 2) distant selection (DS) with the harvester boom created a more spaced and irregular pattern of 50% tree removal along the 30 m wide skid trails, resulting in the greatest spatial heterogeneity and the lowest scarification proportion (average scarified area of 539 m^2/ha). DS also featured short secondary trails oriented perpendicular to the main skid trails, with each secondary trail spaced 10 m apart; 3) close selection (CS) involved a harvester boom removing trees in a 50% partial cut up to 20 m on each side of the skid trail (average scarified area of 752 m^2/ha), which resulted in a denser pattern of tree removal than DS (Montoro Girona et al., 2016, 2017) (Figure 2). The other silvicultural systems were 4) seed-tree harvesting (ST), where all the merchantable-sized (>9 cm, diameter at breast height) trees were removed, except for a few selected trees (basal area of 10 m^2/ha) for seed production in 15 m cut strips (average scarified area of 848 m^2/ha);

5) clearcutting with the protection of advanced regeneration (CC), which consisted of the complete removal of all merchantable-size trees from the stand without scarification (business as usual); and 6) unmanaged forest (UF), which were control areas without harvesting (Figure 2) (Montoro Girona et al., 2017; Montoro Girona et al., 2018). The proportion of harvested basal area was 50% for the three shelterwood systems, 75% in ST, and 100% for CC. In 2004, spot scarification was conducted in the seed-tree and shelterwood treatments by creating 2 m^2 rectangular spots with a 10-ton excavator equipped with a 1 m^3 bucket, following a spatial pattern adapted to each treatment (Figure 2). Overall, partial harvest treatments differ mainly in the spatial distribution of skid trails, residual strips, and scarification spots.

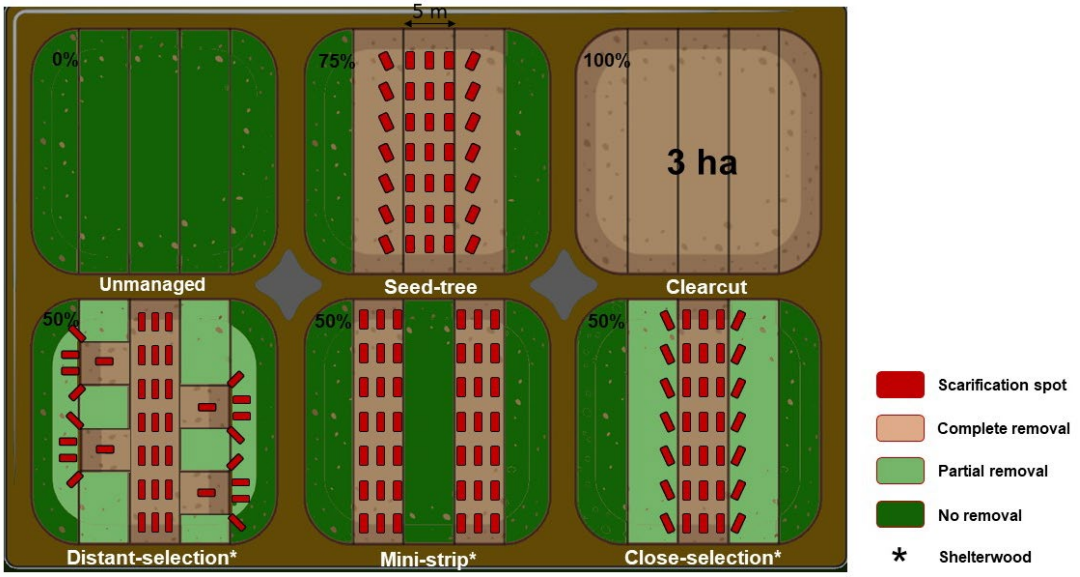

Figure 1.2
Spatial patterns of each experimental silvicultural system. The fully harvested areas or skid trails are represented by brown areas, whereas the intact residual strips are shown in dark green. The partially harvested residual strips are depicted in bright green, and red rectangles are used to indicate the scarification spots, each 2 m^2. Scarification was not carried out in the clearcut treatment and unmanaged forests.

1.4.4 Regeneration assessment

In 2021, we conducted two inventories to study seedling density, growth, and competition between shrubs (e.g., ericaceous species), coniferous (e.g., *A. balsamea*), and deciduous trees (e.g., *B. papyrifera, Salix* spp., *Prunus pensylvanica* L.f., *Sorbus americana* Marshall., *Populus tremuloides*, *Amelanchier* spp., and *Alnus* spp.). The spatial positioning of microplots in relation to harvesting trails was recorded, categorized as strip, edge, or trail. The edge area was defined as the surface within 1.25 meters on either side of the trails (Figure 3). First, all seedlings in each microplot (4 m^2) were counted and categorized by species and height class (A: 0–5 cm; B: 5–30 cm; C: 30 cm to 1 m; D: >1 m with a diameter at breast height (DBH) <1 cm; E: same height but a DBH of 1–5 cm; F: same height but a DBH of 5–9 cm). Seedling and sapling (height class D, E, F) densities were calculated at the microplot level. We also estimated the percent cover of ericaceous shrubs (*Kalmia angustifolia*, *Rhododendron groenlandicum*). Second, we selected one dominant conifer seedling in each microplot on the basis of growth condition (the largest crown or diameter) (Montoro Girona et al., 2018). For each of the selected seedlings, we measured age (determined by whorl count), diameter, height, terminal shoot length (encompassing three years of growth from 2019 to 2021, measured as the upper internodes of the three most recent annual increments), origin (asexual or sexual), rooting substrate (classified as woody debris, mineral soil, deadwood, and vegetation cover by stratum), and dominant bryophyte species. Five preliminary quality classes were established based on easily measured morphological features commonly associated with survival and growth response (Ruel et al., 1995). We also documented the disturbance types (rut, mound, scarification, windthrow, or intact forest floor) observed in the microplots.

We also assessed the presence and absence of neighboring vegetation groups. The major groups were selected on the basis of their frequency in the microplots; they had to appear in more than 151 of the 1 512 microplots (i.e., >10%) containing black spruce seedlings. These groups included ericaceous shrubs (Group Ericaceous: *K. angustifolia*, *R. groenlandicum*), conifer seedlings (Group Conifer: *Abies balsamea, Larix laricina* (Du Roi) K. Koch), and deciduous seedlings (Group Deciduous: *Betula*

papyrifera, Prunus pensylvanica, Salix sp.). Venn diagrams were used to visualize the number of black spruce seedlings associated with each neighboring group.

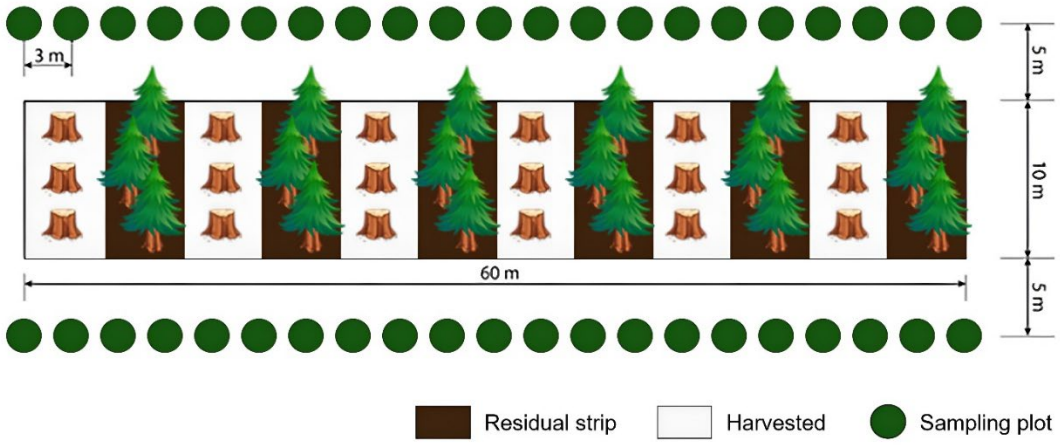

Figure 1.3
Illustration of the sampling design for regeneration assessment in a mini strip, featuring two transects of 4 m² circular microplots arranged perpendicularly to the main plot.

1.4.5 Statistical analysis

To evaluate the effects of silvicultural systems on conifer seedling and sapling density and competing vegetation cover, we performed an analysis of variance (ANOVA) based on a linear mixed model. Blocks (cluster variable) were considered as a random effect and stand type, silvicultural treatment, and their pairwise interaction, as fixed effects. The mixed effects model accounted for the nested structure of the data, where transects were nested within blocks, and blocks were nested within stand types.

We also used a multiple linear regression analysis to predict the annual growth (terminal shoot length in the last three years) of black spruce seedlings. Stepwise regression by backward selection was conducted to extract the optimal combination of predictors (sapling density, harvesting intensity, *Polytrichum* spp. cover, mound, and seedling condition) for the model selection. In addition, we calculated Pearson's correlation coefficients to investigate the relationship between black spruce seedling density/growth and various environmental factors assessed at the microplot level.

Principal component analyses (PCA) were performed to investigate the influence of environmental factors affecting seedling density and growth of black spruce and balsam fir. PCA was conducted using the Factoextra package in R, using all the variables assessed at the microplot level. All statistical analyses were performed using R software version 3.6.0 (R Core Development Team, 2024).

1.5 Results

1.5.1 Seedling density

We found that the three most regenerated tree species 18 years after silvicultural treatment were black spruce, found in 1 222 microplots (80.8% detection frequency), balsam fir (464 microplots; 30.7%), and white birch (318 microplots; 21%) (Figure 4). Overall, the dominant species was black spruce, with a density of 28 376 seedlings/ha, followed by balsam fir (8091 seedlings/ha) and white birch (2 066 seedlings/ha). We also found other regenerated tree species, including *Larix laricina,* and deciduous species, such as *Salix* spp., *Prunus pensylvanica*, *Sorbus americana*, *Populus tremuloides*, *Amelanchier* spp., and *Alnus* spp. However, their abundance was insufficient for detailed species-level analysis.

The ANOVA results indicated a significant interaction between stand type and treatment for all three tree species (Table 2.1). Therefore, the effect of silvicultural systems on seedling density varied between younger and older stands. For black spruce, mini-strip shelterwood treatment increased seedling density the most, particularly in younger stands ($t = -11.9$, $p < 0.001$), relative to unmanaged forests (Figure 2.4). Similarly, other shelterwood variants, i.e., close-selection ($t = -3.9$, $p < 0.001$) and distant-selection ($t = -4.6$, $p < 0.001$), as well as seed-tree harvesting ($t = -3.5$, $p < 0.001$), also significantly enhanced seedling density in younger stands relative to unmanaged forests in older stands. Conversely, seedling density in clearcuts was generally lower than in other treatments, particularly in younger stands. For balsam fir, distant-selection shelterwood increased the seedling density in older stands relative to unmanaged ($t = -5.4$, $p < 0.001$), close-selection ($t = -6.1$, $p < 0.001$), mini-strip ($t = 5.6$, $p < 0.001$), seed-tree ($t = 7.1$, $p < 0.001$), and clearcut treatments ($t = 3.4$, $p < 0.001$). In younger stands, the mini-strip shelterwood treatment

significantly increased seedling density relative to unmanaged (t = −4.9, p < 0.001), close-selection (t = −5.5, p < 0.001), distant-selection (t = −6.9, p < 0.001), seed-tree (t = 5.6, p < 0.001), and clearcut treatments (t = 7.3, p < 0.001). For white birch, seedling density was more influenced by stand type (F = 7.5, p = 0.05) than by conifer species. Seed-tree harvesting significantly improved seedling density relative to the control (t = −12.1, p < 0.001) and clearcutting (t = 10.3, p < 0.001) in younger stands but did not produce significant differences with the older unmanaged stands (t = −0.7, p = 0.52).

Table 1.1

Results from ANOVA with a linear mixed model for the effects of silvicultural treatment and stand type on the seedling density of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera)*. The analysis included site as a random effect.

		Black spruce		Balsam fir		White birch	
Effect (fixed)	df	*F*	Pr > *F*	*F*	Pr > *F*	*F*	Pr > *F*
Stand type	1	0.08	0.148	1.75	0.26	7.46	0.05
Treatment	5	29.644	**<0.001**	7.69	**<0.001**	24.21	**<0.001**
Stand type × Treatment	5	9.39	**<0.001**	19.14	**<0.001**	20.51	**<0.001**

We then compared seedling density for black spruce, balsam fir, and white birch between younger and older stands. Younger stands showed higher regeneration densities for black spruce (23 238 seedlings/ha) and white birch (3 620 seedlings/ha) than older stands (21 067 seedlings/ha for black spruce, 512 seedlings/ha for white birch). Older stands had a higher balsam fir density (3 411 seedlings/ha) than younger stands (1 981 seedlings/ha).

The silvicultural treatment that promoted the most black spruce regeneration was the mini-strip shelterwood, with 50 751 seedlings/ha in younger stands and 28 780 seedlings/ha in older stands. This treatment also produced the highest balsam fir regeneration in younger stands (5 639 seedlings/ha). However, in older stands,

distant-selection harvesting led to the highest balsam fir seedling density (6 767 seedlings/ha). For white birch, the seed-tree treatment was most effective in younger stands (8 375 seedlings/ha), whereas mini-strip harvesting promoted the most regeneration in older stands (1 232 seedlings/ha).

Clearcutting resulted in the lowest seedling densities across treatments and species, particularly in younger stands. For black spruce, clearcutting produced the lowest seedling densities in both stand types (younger: 11 299 seedlings/ha; older: 17 836 seedlings/ha). Similarly, for balsam fir, clearcutting led to the lowest seedling density in younger stands (334 seedlings/ha), although in older stands, clearcutting produced the second-highest balsam fir seedling density. For white birch, clearcutting produced the lowest seedling densities in both younger (1 441 seedlings/ha) and older stands (167 seedlings/ha).

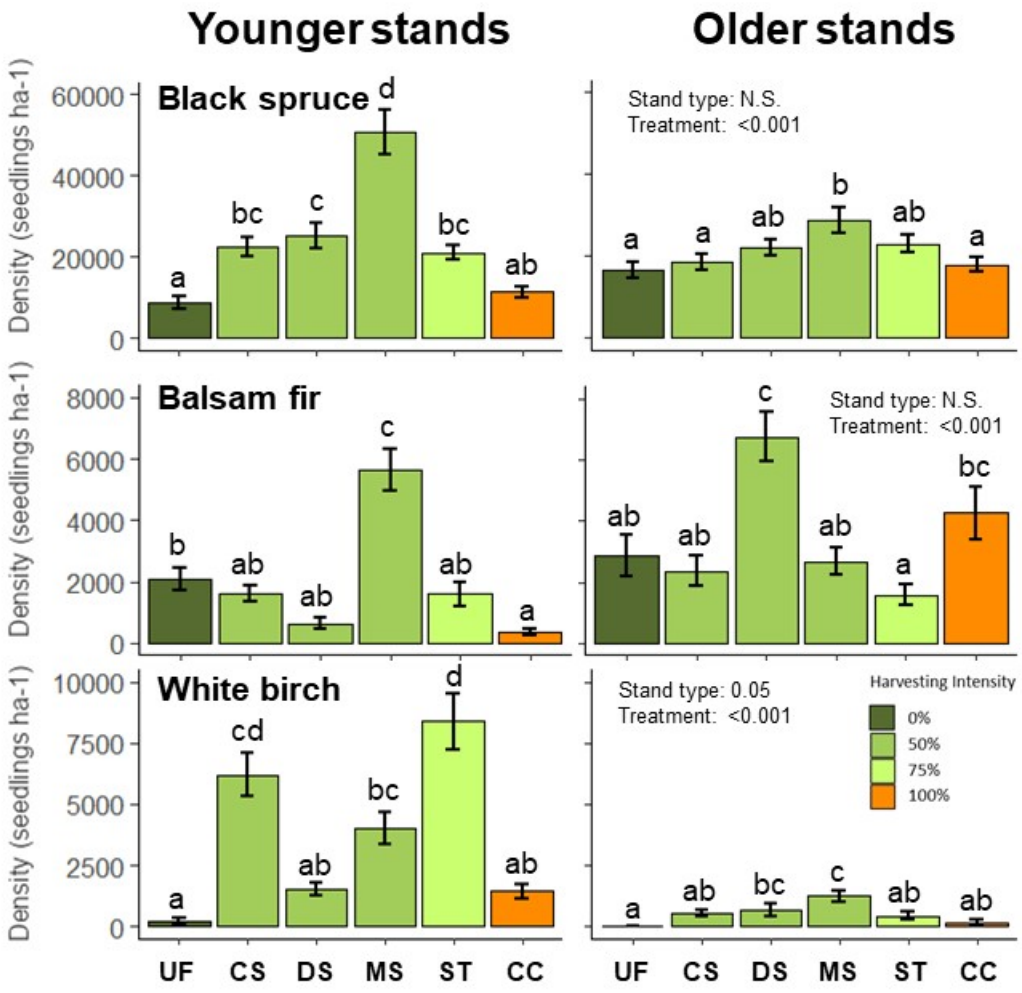

Figure 1.4
Seedling density of black spruce, balsam fir, and white birch in younger and older stands, 18 years after silvicultural systems in black spruce stands. For a given species and stand type, bars with similar letters are not significantly different at α = 0.05. UF, unmanaged forest; CS, close selection; DS, distant selection; MS, mini-strip; ST, seed tree; CC, clearcut.

1.5.2 Conifer seedling growth

Mean annual conifer seedling growth differed in interaction with silvicultural systems and stand types for both species (Table 2.2). For black spruce, clearcutting resulted in the highest seedling growth across both younger ($t = -9.8$, $p < 0.001$) and older stands ($t = -9.3$, $p < 0.001$). Seed-tree harvesting produced the second-highest

growth in both stand types (younger: $t = -5.7$, $p < 0.001$; older: $t = -5.8$, $p < 0.001$), representing a 224% increase relative to the control. For balsam fir, seed-tree harvesting led to the greatest seedling growth in younger stands ($t = -4.0$, $p < 0.001$; Table S2.2), although this was not observed in older stands ($t = -0.2$, $p > 0.05$). Conversely, mini-strip harvesting resulted in the highest growth increase in older stands ($t = -2.4$, $p < 0.05$).

Table 1.2
Results from ANOVA with a linear mixed model for the effects of silvicultural systems and stand types on mean annual black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) seedling growth between the 16th and 18th growing seasons after harvesting (2019–2021). The analysis included site as a random effect.

		Black spruce		Balsam fir	
Effect (fixed)	df	*F*	Pr > F	*F*	Pr > *F*
Stand type	1	0.16	0.709	0.82	0.26
Treatment	5	45.42	**<0.001**	5.56	**<0.001**
Stand type × Treatment	5	8.53	**<0.001**	3.57	**<0.01**

For black spruce, the mean annual shoot growth varied from 2.5 to 13.4 cm across both stand types. Most silvicultural systems (close-selection, distant-selection, seed-tree, clearcut in younger stands and close-selection, seed-tree, clearcut in older stands) resulted in greater annual shoot growth than in the unmanaged conditions (Figure 2.5). Clearcutting, in particular, produced the highest annual shoot lengths in both stand types, with growth 426% higher in younger stands and 257% higher in older stands than in unmanaged conditions.

For balsam fir, mean annual shoot growth ranged from 4.1 to 12.9 cm across both stand types. All harvesting treatments produced higher annual shoot growth than unmanaged forests, except in older stands harvested through clearcutting, which

showed similar values (unmanaged: 4.8 cm; clearcut: 4.9 cm). No clear pattern emerged among the harvesting treatments in either stand type.

The multiple linear regression analysis demonstrated the influence of ecological and management factors on the mean annual growth of black spruce seedlings (Table 2.3). The significant model ($F = 108.6$; $p < 0.001$) included total sapling density (number of seedlings with more than 1 m in height), harvesting intensity, *Polytrichum* spp. cover, presence of a mound, and seedling quality class as predictors. Total sapling density and harvesting intensity had a positive effect on growth, whereas seedling conditions were negatively associated with growth. Although *Polytrichum* spp. cover and the presence of a mound were less significant, they still contributed to the most robust model, which explained approximately 44% of the variation in annual growth. The model's R^2 was 0.44, with all *p*-values <0.05.

Table 1.3
Multiple linear regression models for predicting the annual shoot growth of black spruce seedlings on the basis of regeneration.

Predictors	Coefficients	Std. Error	*t* value	Pr(>|*t*|)
(Intercept)	5.574	0.644	8.654	**< 0.001**
Total sapling density	0.706	0.056	12.591	**< 0.001**
Harvesting intensity	0.057	0.006	9.691	**< 0.001**
Polytrichum sp. cover	0.697	0.392	1.78	0.076
Mound	1.016	0.537	1.891	0.059
Seedling quality class	−0.989	0.126	−7.861	**< 0.001**

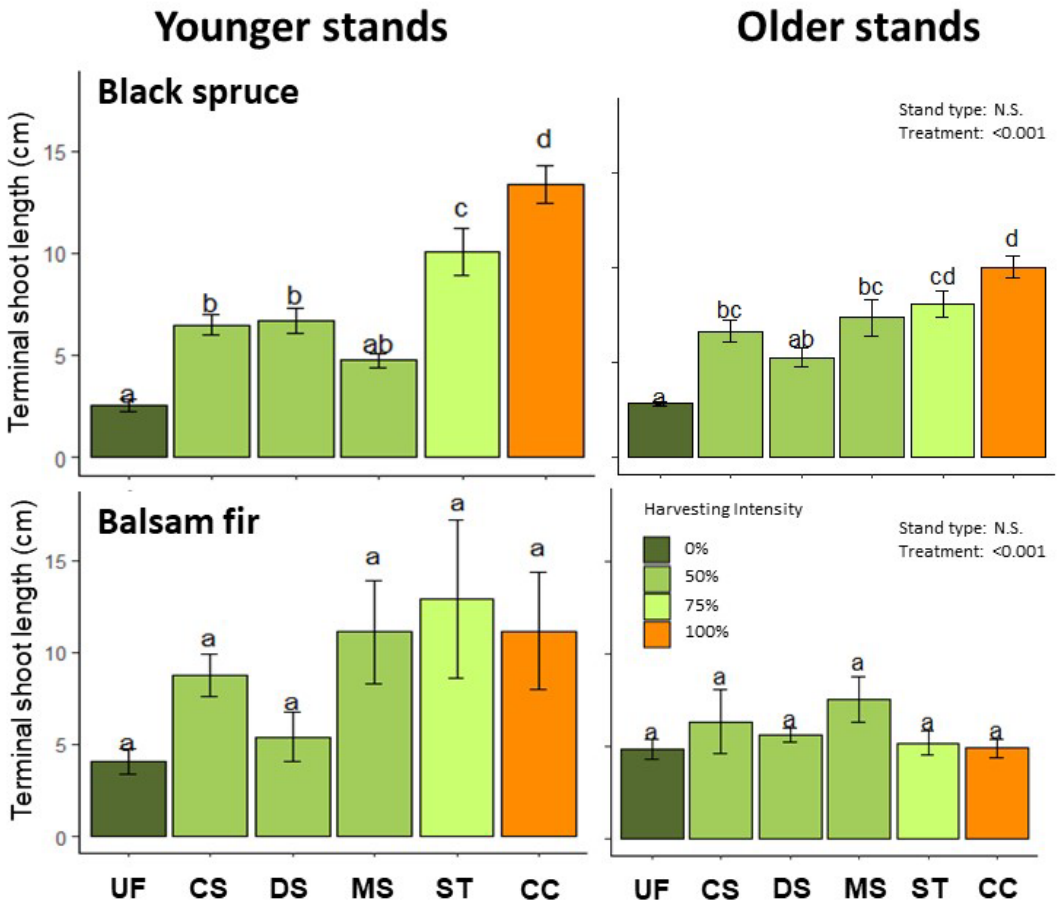

Figure 1.5
Mean annual conifer seedling growth between the 16th and 18th growing seasons after harvesting (2019–2021) by silvicultural treatment and stand type. For a given species and stand type, bars with same letters are not significantly different at α = 0.05. UF, unmanaged forest; CS, close selection; DS, distant selection; MS, mini-strip; ST, seed tree; CC, clearcut.

1.5.3 Factors influencing conifer seedling density and growth

The first two dimensions of the PCA explained 36.3% of the variance in black spruce seedling density (Figure 2.6a). Mineral soil (Pearson's $r = 0.24$, $p < 0.001$) as a substrate of the seedling, spot scarification ($r = 0.21$, $p < 0.001$) as a main anthropogenic disturbance in the microplot, moss cover with *Polytrichum* spp. ($r = 0.2$, $p < 0.001$), and distance from the residual strip correlated strongly with black spruce seedling density. The PCA indicated that microplot characteristics associated with

spot scarification were positively correlated with black spruce seedling density. For balsam fir, the first two components of the PCA accounted for 41.3% of the variance in seedling density (Figure 2.6b). Organic soil, undisturbed conditions (r = 0.16, p < 0.05), mound conditions, moss cover with *Ptilium* spp. and *Sphagnum* spp. (r = 0.17, p < 0.05), and distance from the residual strip were positively correlated with balsam fir seedling density. The PCA revealed that microplot characteristics related to intact and mound conditions were strongly associated with balsam fir regeneration success.

Considering seedling growth response and environmental characteristics, the PCA explained approximately 42% of the variation for black spruce seedlings and 40% for balsam fir seedlings, highlighting similar variations from PCA, but different responses between the two conifer species (Figure 2.6c, 2.6d). Black spruce seedling growth was positively correlated with moss cover, particularly with *Ptilium* sp., (Pearson's r = 0.1, p<0.05) and negatively correlated with the windthrow disturbance (r = -0.1, p<0.05; Figure 2.6c). In contrast, windthrow disturbance showed a positive correlation with balsam fir seedling growth (r = 0.16, p < 0.05), while the undisturbed (intact) microplot condition exhibited a negative correlation (r = -0.16, p < 0.05; Figure 6d).

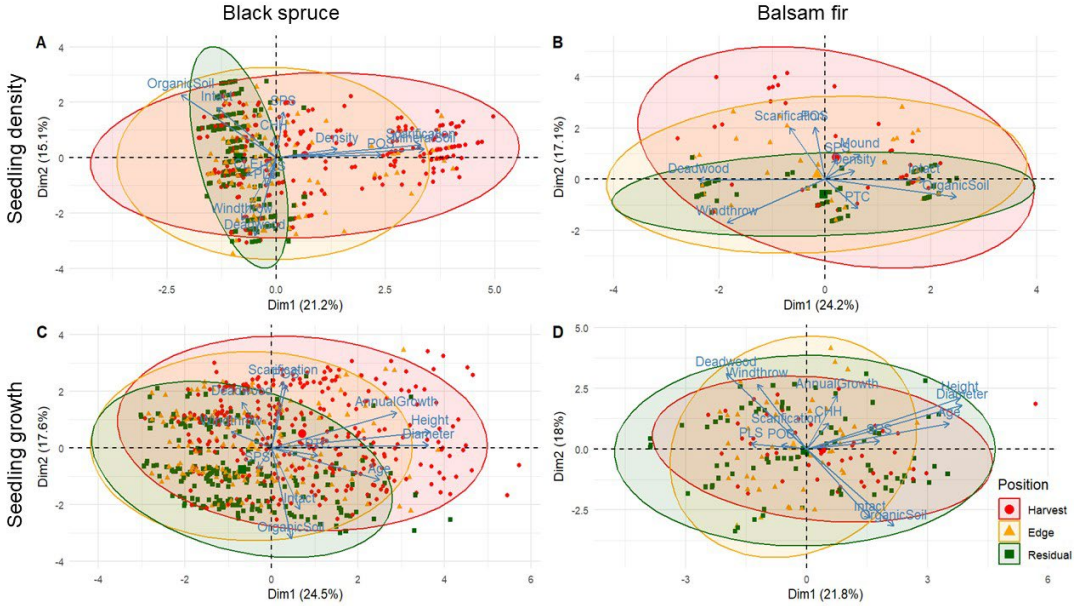

Figure 1.6
Principal component analysis (PCA) of microplot environments, seedling density, and annual seedling growth for black spruce and balsam fir regeneration. Each point indicates a microplot (4 m^2). The proportion of the explained variance is indicated for each axis.

Pleurozium sp. was the most dominant bryophyte covering the soil surface around black spruce seedlings, present in 82% of the 1 512 microplots located in skid trails, 80% in residual strips, and 79% at the edge (Table S3). *Sphagnum* spp. and *Gaultheria hispidula* (L.) Muhl. ex Bigelow (creeping snowberry) were also common on the soil surface around black spruce seedlings, regardless of their position (skid trail, residual strip, or edge). In contrast, *Polytrichum* spp. was more dominant in skid trails (34%) than residual strips (5%). *Cladina* spp. followed this trend, found in 12% in skid trails and 4% of residual strips.

Black spruce was found alongside various neighboring vegetation within 962 of 1 512 microplots (64%) (Figure 2.7). We observed that the highest density of black spruce seedlings, 55 603 per ha, occurred in microplots containing both coniferous and deciduous seedlings (Figure 2.7a). Relative to microplots with only coniferous or only deciduous neighbors, conifer-deciduous vegetation microplots had significantly higher black spruce densities—160% higher than coniferous-only plots, 150% higher than deciduous-only plots, and 110% higher than microplots containing all vegetation. However, black spruce density did not vary significantly with homogeneous species groups. The lowest black spruce seedling density (21 314 seedlings/ha) was found in microplots with *Kalmia*, whereas the highest black spruce seedling density (36 179 seedlings/ha) occurred in microplots with only birch (Figure 2.7b). The presence of *Kalmia* lowered black spruce density by 23% relative to microplots with only black spruce, whereas the presence of birch increased black spruce density by 31% compared to black spruce only microplots, demonstrating species-specific effects on black spruce regeneration.

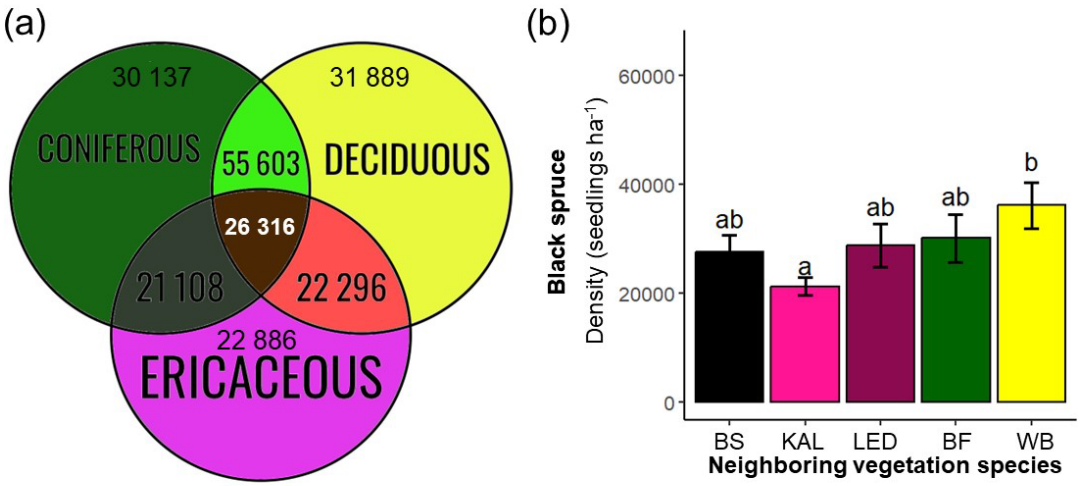

Figure 1.7
Black spruce seedling density in relation to different neighboring vegetation groups. (a) Venn diagram for black spruce seedling density in association with three vegetation groups, separate and combined. (b) Black spruce seedling density in association with the most regenerated single species in this study. The major neighboring vegetation groups include ericaceous shrubs (*Kalmia angustifolia*, *Rhododendron groenlandicum*), conifer seedlings (*Abies balsamea, Larix laricina*), deciduous seedlings (*Betula papyrifera, Prunus pensylvanica, Salix* sp.). BS, black spruce; KAL, *Kalmia*; RHO, *Rhododendron*; BF, balsam fir; WB, white birch.

1.6 Discussion

Our study provides insights into the mid-term response of experimental silvicultural systems on natural regeneration density and growth in Canadian boreal forests. Our findings highlight the different responses of black spruce, balsam fir, and white birch to treatment and stand type, and elucidate the influence of microplot characteristics on conifer seedling density and growth. Additionally, our research provides a predictive perspective on the future structure and composition of the ecosystem under various management practices.

1.6.1 Regeneration density

Our regeneration assessment revealed that black spruce was the most dominant species, significantly surpassing balsam fir and white birch in terms of seedling density 18 years post-harvest. The success of black spruce can be attributed to its adaptability to a variety of silvicultural systems and pre-harvest site conditions, particularly in natural even-aged black spruce–dominated forests. The mini-strip shelterwood treatment, which proved most effective in both younger and older stands, can be credited to the exposure of mineral soil after scarification (Girona et al., 2023c). Specifically, the intermediate shade conditions provided by the residual strips, combined with the reduction of competitive vegetation in scarified areas, created favorable conditions for black spruce seedling establishment. This led to higher seedling densities than the other treatments, highlighting the advantages of the mini-strip shelterwood method in promoting black spruce regeneration. These findings align with previous research showing that increased scarification positively affects conifer seedling establishment (Johansson et al., 2005). The significant interaction between stand type and silvicultural treatment for black spruce density suggests that younger stands benefit more from shelterwood systems. Younger stands may have more favorable pre-harvest conditions, such as higher stand density and thinner organic layers, which improve post-harvest seedling recruitment (Moussaoui et al., 2020a).

Balsam fir performed better in the distant-selection shelterwood treatment in older stands, likely because of its rapid and vigorous growth response to larger canopy openings, in contrast to black spruce (Martin et al., 2020). This aligns with balsam fir's shade tolerance and preference for moist, protected environments (Lavoie et al., 2021). The ecological success of balsam fir is closely tied to its ability to thrive in shaded conditions and its tolerance to cold climates, making it a dominant species in boreal forests, where it often coexists with other conifers. Balsam fir seeds also require a chilling period of 28−60 days (cold stratification) to overcome dormancy and begin germination (Bonner & Karrfalt, 2008), which could affect their natural regeneration outcomes following silvicultural systems.

White birch exhibited a stronger response to stand type than other species, with seed-tree harvesting significantly increasing its density in younger stands. This finding aligns

with previous research showing that canopy openings enhance birch germination and survival, emphasizing the reliance of white birch on increased light for regeneration (Shields et al., 2007). However, successful regeneration requires not only canopy openings but also an adequate level of residual trees to reduce seedling competition and prevent excessively dry soil conditions. This delicate balance shows the important interactions between light availability, soil moisture, and competition in the regeneration of white birch (Messier et al., 1999).

In our study, clearcutting with the protection of advanced regeneration resulted in the lowest seedling densities across all species and stand types, particularly in younger stands. The high disturbance levels associated with clearcutting create harsh environmental conditions, characterized by intense light, temperature fluctuations, and reduced soil moisture; these conditions inhibit seedling establishment, especially for shade-tolerant species (Kim et al., 2021; Kohout et al., 2018b; Roy et al., 2000). In some cases, clearcutting may fail to ensure stand renewal, as indicated by the lower seedling densities and more competitive species observed in our study blocks relative to the controls. This outcome aligns with previous studies that highlight the potential negative impacts of clearcutting on forest ecosystems, including soil erosion, nutrient depletion, and reduced microbial community stability (Kim et al., 2021; Laudon et al., 2011). Over the long-term, clearcutting may increase ecosystem vulnerability to further disturbances, particularly spruce budworm outbreaks exacerbated by climate change (Aakala et al., 2023; Girona et al., 2023b; Montoro Girona et al., 2019; Subedi, 2023).

1.6.2 Seedling growth

Our findings demonstrated the significant impact of silvicultural systems on the annual growth of conifer seedlings in mid-term post-harvest stands, particularly in terms of terminal shoot length in black spruce and balsam fir. The observed growth patterns were inversely related to seedling density, suggesting that intraspecific competition plays a critical role. Densely populated black spruce seedlings compete for limited resources such as soil nutrients, water, and light (Ammer, 2016). In our study, the higher seedling growth rates in clearcut and seed-tree harvesting treatments may be attributed to larger canopy openings and reduced intraspecific competition. For black

spruce seedlings, the number of saplings greater than 1 m in height was a stronger predictor of annual growth than total seedling number; therefore, light availability strongly influences growth. This pattern aligns with previous research showing that increased light availability enhances seedling growth in shade-tolerant species, similar to the response seen in shade-intolerant species (Bebre et al., 2021). These findings underscore the importance of intraspecific competition and light availability as key factors influencing the annual growth of conifer seedlings in these stands. (Marty et al., 2023).

The interaction between stand type and silvicultural treatment further highlights the complexity of forest regeneration processes (Thiffault et al., 2024). For black spruce, the pronounced differences between younger and older stands suggest that the timing and context of harvesting play crucial roles in determining regeneration success (Girona et al., 2023a). Although clearcutting was beneficial in terms of seedling growth across both stand types, the variability in response to other treatments, such as seed-tree and mini-strip harvesting, indicates that stand age and structure are key factors to consider in silvicultural planning. This is particularly relevant for balsam fir, where younger stands responded more favorably to seed-tree harvesting, whereas older stands showed improved growth under mini-strip harvesting (Montoro Girona et al., 2018). The absence of a clear trend among treatments in older balsam fir stands may reflect the species' ecological characteristics, including its shade tolerance and sensitivity to disturbances, such as spruce budworm outbreak and windthrow (Guimond et al., 2024; Lavoie et al., 2021).

Although the influence of *Polytrichum* spp. and mound presence was less pronounced, their inclusion in the optimal model suggests that microsite conditions remain significant in shaping growth outcomes, particularly in environments where soil moisture and temperature are critical limiting factors. Previous research has shown that black spruce height growth tends to be greater on substrates comprising feathermosses and fibrous material, highlighting the importance of bryophyte substrates in influencing black spruce seedling growth (Lavoie et al., 2007). In our study, feathermosses were prevalent across most silvicultural systems, making it

difficult to detect distinct effects attributable to their presence. Although black spruce seedlings were abundant on mineral soil substrate, their growth preference can vary. In some field experiments, black spruce has shown faster height growth on soils covered with moss or a thin organic layer rather than on bare mineral soil (Fleming & Mossa, 1995). Additionally, these microsite conditions can be influenced by understory vegetation, such as ericaceous shrubs, which reduce seedling density and potentially stunt black spruce growth (Martin & Mallik, 2016).

The observed effects may also be attributed to scarification associated with seed-tree and shelterwood harvesting. Although scarification facilitates conifer seedling establishment by exposing mineral soil, it does not necessarily promote seedling growth because of increased nutrient leaching and the promotion of competitive deciduous species such as white birch (Saursaunet et al., 2018). Moreover, the initial benefits of scarification for seedling establishment can be counteracted by its negative effects on subsequent growth and root development.

Intraspecific competition in black spruce can vary with growth stage. Previous research has demonstrated that the size of neighboring trees is the primary factor influencing competition between black spruce and tamarack, regardless of whether the competition was intra- or interspecific (Roy Proulx et al., 2023). This finding underscores the need for further investigation to confirm this effect.

Additionally, these forest stands may require subsequent phases of structural development, which could significantly influence seedling growth. For example, spatial heterogeneity may create a mosaic of growth rates and stand structures, with some areas rapidly developing into closed-canopy forests, whereas others remain in early successional stages for extended periods (Kanjevac et al., 2023). The long-term trajectory of these stands will depend on the interplay of microsite conditions, ongoing competition, and potential disturbances such as insect outbreaks and windthrow (Peterson & Leach, 2008). Thus, continued monitoring is essential to fully understand the natural regeneration dynamics, as shade-tolerant species typically have a slower

growth response to silvicultural systems, and black spruce forests can take up to 200 years to reach maturity (Frelich et al., 2018).

1.6.3 Factors influencing natural regeneration dynamics in boreal forests

Understanding the driving factors in natural regeneration dynamics after silvicultural systems is essential for preserving ecosystem resilience, biodiversity, and the long-term sustainability of forest landscapes (Martin et al., 2020b). Our analyses revealed that proximity to skid trails significantly affected the regeneration process of conifer species through scarification and canopy opening. This was reflected in a consistent set of environmental factors influencing the presence of sexual seedlings along trails (in areas such as ruts, mounds, and highly disturbed material) and at the edges (involving windthrow and woody debris) and that of vegetative seedlings (through layering) in residual strips (in relation to bryophyte cover and intact microplots). The strong correlation between the mineral soil, spot scarification, and moss cover, e.g., *Polytrichum* spp., with black spruce seedling density highlights the importance of soil disturbance in creating favorable seedbeds for this species and suggests that appropriate site preparation can enhance conifer regeneration (Béland et al., 2000; Lafleur et al., 2011). *Polytrichum* spp. is known for their remarkable hydrophilic properties—retaining up to 646% of their dry weight in water—potentially creating favorable microsites for black spruce seedling establishment in moisture-limited sites, such as these scarified areas (Coelho et al., 2023).

However, the prevalence of *Polytrichum* spp. may also indicate environmental degradation caused by clearcutting practices, as well as the influence of population biology and reproductive strategies (Bao, 2005). Our study demonstrated differing responses between black spruce and balsam fir to environmental conditions. Whereas black spruce regeneration was strongly correlated with mineral soil and negatively correlated with windthrow conditions, these factors did not significantly affect balsam fir seedling growth. For balsam fir, undisturbed soil conditions and mound formations were beneficial; thus microsite stability and moisture retention are critical for its regeneration (Olesinski et al., 2011). This differential response to environmental conditions can be attributed to the contrasting ecological traits of black spruce and

balsam fir, with black spruce being more cold-tolerant and better adapted to poorly drained soils, whereas balsam fir exhibits greater shade tolerance but requires more stable and well-drained microsites for successful regeneration (Messaoud et al., 2019).

Our study shows that the presence of specific vegetation types, such as deciduous trees and *Kalmia*, can significantly affect black spruce regeneration, highlighting the need to manage understory vegetation when implementing shelterwood systems (Thiffault et al., 2013; Walker & Mallik, 2009). The more favorable interaction of deciduous species relative to that of conifers can be explained by black spruce seedlings benefiting from increased light exposure and better access to nutrients and water when deciduous species are leafless in the spring and fall in eastern Canada. Moreover, some deciduous species, like aspen, can enhance soil fertility through the decomposition of their fallen leaf litter (Oboite & Comeau, 2019).

In contrast, *Kalmia* significantly reduced black spruce regeneration in our study, potentially altering future stand dominance. In Newfoundland (Canada), *Kalmia*-dominated heathlands have been shown to decrease the black spruce recruitment rate, with a high proportion of recruited seedlings exhibiting stunt growth (Martin & Mallik, 2016). It is hypothesized that the ectomycorrhizal inoculation of black spruce seedlings could be crucial for their success in *Kalmia* heaths, as stunted growth may be linked to ericoid mycorrhizal fungi (Yamasaki et al., 1998). Further research is needed to better understand how site preparation and management strategies can promote successful black spruce regeneration in the presence of *Kalmia* in boreal stands.

1.6.4 Implications for boreal forest management

Partial harvesting could serve as a next-generation forest management strategy in the Canadian boreal forest. This approach can help balance ecological and economic objectives by preserving key habitat features, reducing soil disturbance, and supporting the recruitment of both shade-tolerant and shade-intolerant species (Moussaoui et al., 2020a). Our findings have significant implications for forest

management practices aimed at enhancing conifer regeneration. High regeneration densities, particularly for shade-tolerant species like black spruce, improve the likelihood of stand success and reduce the need for costly and time-consuming artificial regeneration measures, such as site preparation and planting (Gonçalves & Fonseca, 2023).

The species composition (e.g., black spruce, balsam fir, white birch) and detection frequencies across silvicultural systems and stand types in this study offer valuable insights into future stand development trajectories. These findings can inform management decisions related to vegetation control, thinning interventions, and the necessity of supplemental planting to optimize stand regeneration and long-term forest management sustainability. Accordingly, silvicultural systems should be tailored to the ecological requirements of target species and stand conditions (Girona et al., 2023). For example, mini-strip shelterwood and distant-selection harvesting can be strategically applied to promote black spruce and balsam fir regeneration in younger and older stands, respectively, ranging from 80 to 150 years old. In our study, partial harvesting was particularly effective for black spruce, but its applicability may also extend to other conifer species (Bose et al., 2023).

Conversely, clearcutting can create nutrient-deficient soil conditions detrimental to seedling establishment (Kim et al., 2021; Kohout et al., 2018b; Sharma et al., 2016). Although clearcutting can sometimes promote early seedling growth by reducing seedling density and minimizing intraspecific competition, its effects vary among stand types and species. Without regeneration-assisting treatments, clearcutting can also extend recovery times (Barrette et al., 2022). This variability suggests that a one-size-fits-all approach to silvicultural treatment is inappropriate. Treatments must be carefully balanced with long-term objectives, such as preserving species diversity and maintaining forest structural complexity.

Continuous long-term monitoring is essential to understanding forest succession, assessing the ongoing effects of these treatments, and adapting strategies as needed to ensure sustainable forest regeneration following partial harvesting.

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2. COMMUNAUTÉS MICROBIENNES DE LA RHIZOSPHÈRE 19 ANS APRÈS LA COUPE À TOTALE ET LA COUPE PARTIELLE DANS LES FORÊTS BORÉALES DE L'EST DU CANADA

Rhizosphere soil Microbial Communities 19 Years After Clearcut and Partial cut Treatments in Eastern Canadian Boreal Forests

(*Manuscript*)

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2.1 Résumé

La coupe partielle, une alternative potentielle à la coupe totale, nécessite une évaluation à long terme dans les forêts boréales du Canada afin de comprendre ses effets sur la régénération naturelle et la durabilité des écosystèmes. En particulier, les interactions entre les plantes et les micro-organismes sont essentielles à la régénération naturelle, car elles modifient les conditions du sol afin de favoriser l'établissement des arbres. Cependant, leurs réactions aux traitements sylvicoles restent mal comprises dans les écosystèmes boréaux. Dans cette étude, nous avons évalué les impacts à long terme de la coupe totale et de la coupe partielle sur la diversité microbienne de la rhizosphère et ses facteurs déterminants dans les forêts boréales de l'est du Canada, 19 ans après la récolte. Notre plan expérimental comprenait 12 unités expérimentales réparties en quatre blocs d'étude répliqués et représentant des traitements de coupe totale (100 % de la surface terrière récoltée), de coupe partielle (50 %) et de non-récolte (témoin), avec quatre microparcelles par unité (donnant 48 échantillons de sol composites) sur des semis d'épinette noire (*Picea mariana*) régénérés naturellement. Nous avons appliqué le métabarcodage de l'ADN ciblant les régions 16S rRNA bactériennes et ITS fongiques, en conjonction avec des analyses chimiques détaillées du sol. Bien que la composition globale de la communauté microbienne de la rhizosphère n'ait pas montré de différences significatives entre les traitements après 19 ans, les peuplements en coupe totale et en coupe partielle ont chacun conservé une abondance distincte de certaines espèces qui reflètent les différences entre les traitements. Les sites de coupe totale présentaient une présence élevée de bactéries fixatrices d'azote, notamment *Roseiarcus* spp., qui peuvent contribuer à améliorer la croissance des semis et à enrichir les nutriments, tandis que les zones de coupe partielle présentaient une abondance 77 % plus élevée de champignons ectomycorhiziens tels que *Piloderma* spp., indiquant une association plus forte avec des partenaires fongiques bénéfiques dans des conditions de perturbation modérée. En outre, des différences significatives dans les propriétés du sol, en particulier dans la couche organique (par exemple, la saturation en bases, la teneur en calcium et en métaux), étaient étroitement liées aux changements dans la composition microbienne. Nos espèces indicatrices peuvent

servir de signaux d'alerte précoce en reflétant des changements subtils mais significatifs dans la chimie du sol et les interactions microbiennes résultant des traitements sylvicoles. En identifiant les signatures microbiennes durables des traitements sylvicoles, notre étude fournit une base pour le développement d'interventions microbiennes ciblées qui peuvent accélérer la restauration des sols et promouvoir la régénération durable des forêts.

Mots-clés: aménagement écosystémique, *Picea mariana*, métabarcodage de l'ADN, microbiote du sol, propriétés physico-chimiques du sol, système de coupes progressives

2.2 Abstract

Partial cutting, a potential alternative to clearcutting, requires long-term evaluation in Canada's boreal forests to understand its effects on natural regeneration and ecosystem sustainability. Particularly, plant–microbial interactions are critical for natural regeneration by modifying soil conditions to favor tree establishment, yet their responses to silvicultural systems remain poorly understood in boreal ecosystems. In this study, we evaluated the long-term impacts of clearcut and partial cut on rhizosphere microbial diversity and its driving factors in Eastern Canadian boreal forests, 19 years post-harvest. Our experimental design encompassed 12 experimental units—distributed among four replicated study blocks and representing clearcut (100% basal area removed), partial cut (50%), and unharvested (control) treatments—with four microplots per unit (yielding 48 composite rhizosphere soil samples) on naturally regenerated black spruce (*Picea mariana*) seedlings. We applied DNA metabarcoding targeting bacterial 16S rRNA and fungal ITS regions in conjunction with detailed soil chemical analyses. Although the overall rhizosphere microbial community composition showed no significant differences among treatments after 19 years, clearcut and partial cut stands each retained distinct abundance of some species that reflect difference between treatments. Clearcut sites exhibited an elevated presence of nitrogen-fixing bacteria, notably *Roseiarcus* spp., which may contribute to enhanced seedling growth and nutrient enrichment, whereas partial cut areas showed a 77% higher abundance of ectomycorrhizal fungi such as *Piloderma* spp., indicating a stronger association with beneficial fungal partners under moderate disturbance. Furthermore, significant differences in soil properties particularly within the organic layer (e.g., base saturation, calcium, and metal content) were closely linked to shifts in microbial composition. Our indicator species may act as early warning signals by reflecting subtle yet significant shifts in soil chemistry and microbial interactions resulting from silvicultural systems. By identifying long-lasting microbial signatures of silvicultural systems, our study provides a foundation for developing targeted microbial interventions that can accelerate soil restoration and promote sustainable forest regeneration.

Keywords: Ecosystem-based management, *Picea mariana*, DNA metabarcoding, Soil microbiota, Soil physicochemical properties, shelterwood system

2.3 Introduction

Boreal forests represent the largest terrestrial biome, covering a third of global forest area, and are crucial for carbon sequestration and biodiversity (Gauthier et al., 2023). While two-thirds of this ecosystem is managed for timber, producing 37% of the world's wood, it faces significant challenges in balancing timber production with ecological integrity (Gauthier et al., 2015). Clearcutting remains the dominant harvesting method in global boreal forests, with a significant impact on biodiversity and ecosystem functions (Burton et al., 2010; Gauthier et al., 2015; Girona et al., 2023). In particular, it may lead to habitat loss, fragmentation, and reduced habitat diversity (Fischer & Lindenmayer, 2007; Hasan et al., 2020). It can also deplete soil nutrients and biodiversity while increasing erosion (Laudon et al., 2011). Moreover, clearcut forests could be less resilient and more vulnerable to climate change than other silvicultural systems (e.g., partial harvest, selection cutting) (Lavoie et al., 2021).Alternatively, management frameworks such as ecosystem-based management proposes to diversify silvicultural systems and use partial harvest to better balance ecological integrity, economic viability, and social values in forest management (Aakala et al., 2023; Gauthier, 2009; Kuuluvainen, 2009; Martin et al., 2020).

Partial harvest has been proposed again in the last 30 years in boreal forests as a silvicultural alternative to clearcutting, as it selectively removes trees to reduce stand density while retaining the forest's structural complexity and biodiversity (Bose et al., 2023; Girona et al., 2023). Partial harvest retains a mosaic of canopy elements and deadwood, which helps maintain habitat heterogeneity and supports a greater diversity of flora and fauna compared to clearcutting (Gauthier et al., 2023; Kim et al., 2021; Noualhaguet et al., 2023). Moreover, the increased light penetration and reduced competition in gaps created by partial cutting can promote enhanced growth of residual trees and stand vigor over time (Girona et al., 2016; Lemay et al., 2018; Moussaoui et al., 2020a). Partial harvest can also create favorable microclimatic conditions for shade-tolerant species' seedling establishment and recruitment, provided that retention levels are optimized, thus sustaining long-term forest regeneration (Fenton & Bergeron, 2006; Gauthier, 2009).

In this context, silvicultural systems play a crucial role in shaping the natural regeneration, particularly the rhizosphere of seedlings - the critical interface between plant and soil. This dynamic zone is essential for plant-microbial interactions that drive nutrient cycling, carbon sequestration, and overall forest health (Clemmensen et al., 2013; Philippot et al., 2013). Silvicultural practices, such as clearcutting and partial harvesting, can significantly alter the rhizosphere environment by modifying stand density, light penetration, root-derived C and soil temperature and moisture regimes (Allman et al., 2023; Kim et al., 2021; Ye et al., 2023). These changes, in turn, influence understory vegetation composition and soil physicochemical properties, leading to cascading effects on microbial communities (Braga et al., 2023).

Recent studies have revealed that soil fungi, particularly mycorrhizal species, are more sensitive to forest management practices than bacteria due to their dependency on plant hosts (Bastida et al., 2017; Štraus et al., 2023; Sun et al., 2017). Even subtle disturbances can trigger marked shifts in fungal functional roles, thereby altering nutrient cycling processes in boreal forest soils (Bonfante & Venice, 2020; Chen et al., 2022). For instance, in Alaskan boreal forests, ectomycorrhizal fungi such as *Suillus* and *Rhizopogon*. have been demonstrated to improve nutrient uptake and confer drought resistance, thereby facilitating the establishment and growth of black spruce seedlings (Bent et al., 2011; Rossi et al., 2015). Similarly, nitrogen-fixing bacteria, particularly those within the *Frankia* lineage, have been shown to increase soil nitrogen availability in rhizospheric soils of *Alnus nepalensis*, promoting early successional dynamics and successful seedling establishment through the seral stages of succession (Sen et al., 2022). In Scandinavian boreal ecosystems, arbuscular mycorrhizal fungi have been linked to enhanced phosphorus assimilation and stress mitigation in Scots pine (*Pinus sylvestris* L.), further underscoring their role in improving natural regeneration (Andersson & Svensson, 2017). These differential response can have profound implications for seedling establishment, nutrient acquisition, and long-term forest productivity (Heijden et al., 2016).

The impacts of silvicultural systems on rhizosphere microbial communities are not uniform and can vary depending on factors such as harvesting intensity, time since

disturbance, edaphic conditions and local climatic conditions (Goldmann et al., 2015). Moreover, the legacy effects of forest harvesting on soil microbial communities can persist for decades, influencing forest regeneration and ecosystem recovery (Hartmann et al., 2012). For example, over 36 years of forest conversion in subtropical China significantly altered rhizosphere microbial communities, particularly increasing fungal abundance and gram-negative bacteria which led to persistent shifts in soil carbon dynamics and structure, with stronger effects on rhizosphere-associated carbon than bulk soil (Zhao et al., 2021). In addition to altering biotic communities, harvesting operations can leave enduring imprints on soil physicochemical properties such as shifts in pH, nutrient availability, and organic matter content that continue to affect soil structure and function long after disturbance (Yang et al., 2015; Mushinski et al., 2018). These persistent changes in soil chemistry can constrain or enhance nutrient cycling and plant growth, thereby influencing the trajectory of ecosystem recovery (Peng & Thomas, 2006).

While soil physicochemical properties offer valuable insights into nutrient status, pH, and organic matter content, they often provide only a static snapshot of the soil environment and may not capture early or subtle shifts induced by forest disturbances. In contrast, microbial indicator species respond rapidly to changes in both biotic and abiotic conditions, serving as dynamic markers of ecosystem health and resilience (Baldrian, 2017; Lladó et al., 2017). For instance, bacterial and fungal disturbance indicators (e.g., increased *Mortierella*, and *Umbelopsis*) shifted within just 14 days of forest soil disturbance, whereas changes in soil properties were more gradual (Sukdeo et al., 2019). Moreover, microbial community traits such as substrate utilization of γ-hydroxybutyric acid were better at distinguishing between native, disturbed, and reforested soils than soil physicochemical properties (e.g., pH, Al^{3+}, base cations), which showed less consistency (Bertini et al., 2021). Their sensitivity to variations in resource availability, moisture, and nutrient fluxes means that alterations in the abundance or composition of key microbial taxa such as nitrogen-fixing bacteria or mycorrhizal fungi can signal incipient changes in nutrient cycling and plant-microbial interactions long before major shifts in soil chemistry are detectable (Philippot et al.,

2013). Therefore, these examples demonstrate that microbial indicators provide faster, more sensitive, and functionally relevant signals of forest disturbance and recovery compared to traditional soil analyses, providing an important insight on evaluating experimental silvicultural systems.

In this study, we evaluate the diversity and composition of rhizosphere soil microbial communities of black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) seedlings 19 years after clearcut and experimental partial cut in Canadian boreal forests. Our specific objectives were (i) to evaluate the mid-term impacts of clearcut and partial cut on rhizosphere soil bacterial and fungal community diversity and composition; (ii) to assess changes in soil physicochemical properties induced by silvicultural systems and determine their relationship with microbial community structure; (iii) to identify microbial taxa or functional groups as indicators of long-term silvicultural impacts. We hypothesize that 1) partial cut areas will show higher microbial diversity due to increased resource availability and environmental heterogeneity; 2) soil physicochemical properties will differ significantly among treatments, with clearcut areas showing the most pronounced changes because of the highest canopy removal and soil exposure; 3) specific microbial taxa, particularly ectomycorrhizal fungi and nitrogen-fixing bacteria, will serve as indicators of long-term silvicultural impacts due to their sensitivity to changes in soil nutrient availability (Tahovská et al., 2020; Wang et al., 2022).

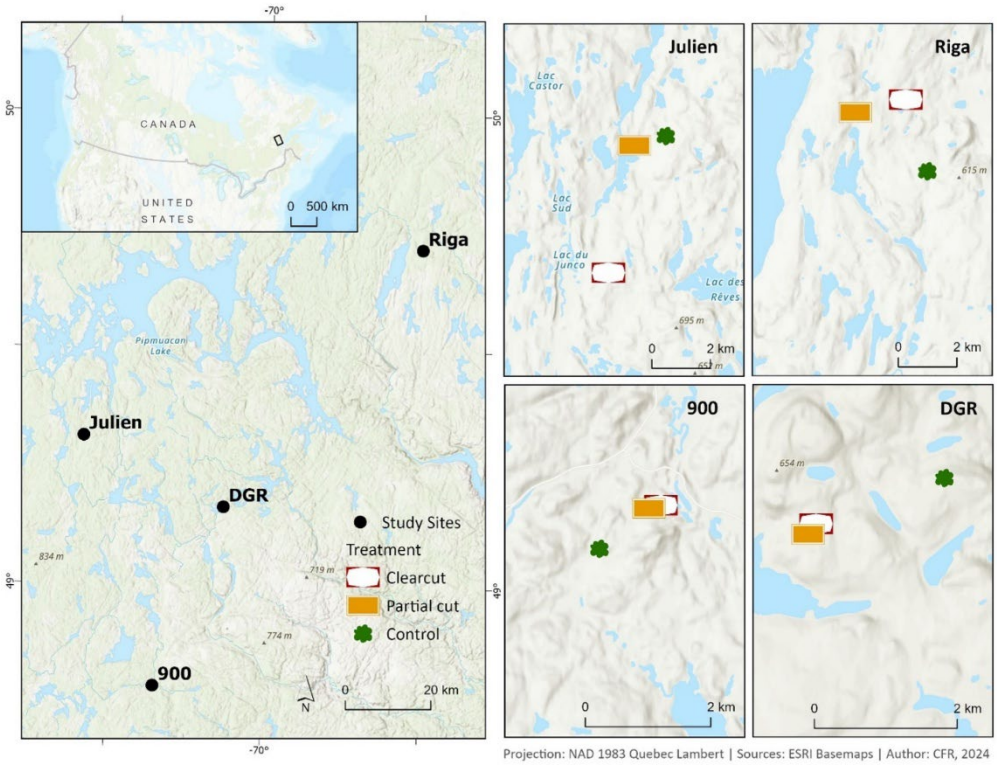
2.4 Material and Methods

2.4.1 Study Area

The study area is located within the natural even-aged black spruce forests of the northern Saguenay-Lac-Saint-Jean and North Shore regions in Quebec, Canada (Figure 3.1A and Table 3.1). The study area spans across two distinct bioclimatic regions: the balsam fir (*Abies balsamea* (L.) Mill.)-white birch (*Betula papyrifera* Marsh.) (site 900) and the black spruce-feathermosses regions (site DGR, Riga, Julien). The climate of this region is subhumid subpolar,featuring a short growing period of 140 days (Rossi et al. 2011). The average annual temperature is 2.2°C and annual precipitation averages 1 081 mm (Environment and natural resources Canada,

2022). Surface deposits consist primarily of thick glacial tills, and rocky outcrops are frequent at the top of steep slopes (Robitaille & Saucier, 1998). The soil is primarily composed of humo-ferric podzols (Montoro Girona et al., 2018).

A)



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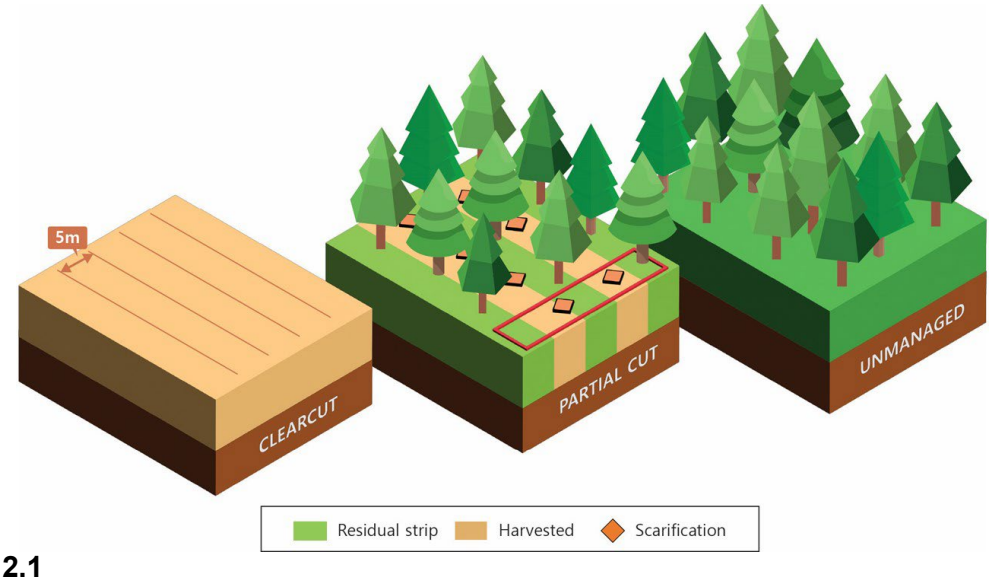


Figure 2.1
A) Location of study area, sites and experimental units; B) Illustration of the experimental silvicultural systems (a: clearcut (100% basal area removed), b: partial cut (50%), c: unmanaged control (0%)).

Table 2.1
Pre- and post-harvest stand characteristics of study sites. CC: Clearcut; PC: Partial cut; UF: Unmanaged forest; TSL: terminal shoot length

			1 year before harvesting			1 year after harvesting			18 years after harvesting				
		Elevation	Stand age	Density	Basal area	Volume	Density	Basal area	Volume	Density	Height	Diameter	TSL
Site	Treatment	m	years	stems/ha	m^2/ha	m^3/ha	stems/ha	m^2/ha	m^3/ha	seedlings/ha	cm	mm	cm
900	CC	627	NS	2,283	49	286	-	-	-	22,494	194.0	28.9	13.9
	PC	623	80-100	2,417	43	228	1,567	28	140	84,023	89.9	13.6	5.4
	UF	644	80-100	1,417	36	220	1,417	36	216	15,789	33.4	5.6	2.4
DGR	CC	568	NS	2,783	48	392	-	-	-	6,579	171.9	29.8	15.0
	PC	585	80-100	2,683	41	352	1,567	17	63	34,586	71.8	13.0	4.3
	UF	577	80-100	2,567	37	177	2,567	37	163	8,333	36.9	6.6	2.6
Riga	CC	467	NS	2,517	35	163	-	-	-	4,825	124.5	19.9	10.8
	PC	538	80-100	1,967	37	204	1,150	19	97	33,647	47.6	7.8	5.3
	UF	542	80-100	2,967	44	211	2,967	44	200	1,942	0.0	0.0	0.0
Julien	CC	620	NS	1,433	33	199	-	-	-	21,930	125.4	25.8	8.7
	PC	508	120-150	2,883	50	267	1,500	27	135	36,048	128.7	19.6	7.9
	UF	577	120-150	2,067	35	185	2,067	35	174	22,556	119.4	19.0	2.4

2.4.2 Experimental design

The MISA (managing innovative silvicultural alternatives) experiment was selected to develop silvicultural alternatives to clearcutting in boreal forest management. The experimental design for the project employs a randomized block factorial design, incorporating four replicated study sites (Figure 3.1). Each of these replicated areas consists of three experimental units corresponding with a clearcut, partial cut and control forests as control, covering 3 hectares each. The study sites are mature forests aged between 80 to 150 years, with an average tree density of 1 500 to 2 600 trees per hectare. Black spruce was the predominant species in all sites, comprising at least 90% of the stand's basal area. The experimental units were strategically placed in areas showcasing relatively uniform species composition and stand density across each block. Each experimental unit was established with permanent sampling plots (600 m^2) for the growth, mortality and natural regeneration study following partial harvest system (Girona et al., 2017; Montoro Girona et al., 2018, 2019).

2.4.3 Silvicultural systems

The Canadian Forest Service designed experimental silvicultural systems in 2003, focusing on the implementation of a uniform shelterwood system to improve our silvicultural understanding of partial harvest in boreal forests. In our study, a tailored version of the uniform shelterwood system was adopted, incorporating adjustments to the spatial pattern and site preparation techniques: through mini-strip harvesting (MS)

that creates narrow corridors (5 m wide harvest trails). In comparison, the study also examines clearcut (CC) with protection of advanced regeneration, which consisted of the complete removal of all merchantable-size trees from the stand using spaced skidtrails and uses an unmanaged forest (UF) as a control without cutting (Figure 3.1B). The harvested basal area percentages were set at 50% for the mini-strip harvesting (partial cut), and 100% for clearcut treatment. The following year, in 2004, targeted scarification was carried out within 2 m^2 rectangular plots in mini-strip shelterwood. This scarification process was conducted with a 10-ton excavator equipped with a 1 m^3 bucket, preparing the ground for subsequent regeneration efforts.

2.4.4 Soil sampling

In July, 2022, we collected bulk and rhizosphere soil samples to assess the soil physicochemical properties (bulk soil) and rhizo-microbiome (rhizosphere soil) in circular microplots of 4 m^2 (4 microplots × 12 experimental units = 48 microplots). For the bulk soil properties, sampling took place in the organic layer, ranging from 5 to 30 cm beneath the surface after the removal of litter, closely situated to the focal plant (black spruce) within each microplot. This approach yielded one composite sample per microplot, yielding a total of 48 soil samples. The distance from the bulk soil sampling spot to the focal plant was calibrated based on the height of the focal seedling (up to 1 m range), maintaining a distance equivalent to the seedling height, or extending it by one meter for seedlings over one meter in height. Following collection, the composite bulk soil samples were sieved on-site using a 6 mm mesh, then stored in an ice-packed cooler, transported in plastic bags, and subsequently stored at -25°C in the GREMA lab at Amos Campus of UQAT. For further refinement, the samples underwent an additional sieving process through a 4 mm mesh employing an automatic vibrating sieve AS 200 Control (ATS Care Retsch, Haan, Germany) after an 8-day air-drying period at ambient temperature to assist the sieving operation.

For rhizosphere soil collection, a methodical approach was adopted, tracing the lateral roots from the trunk to the fine roots, ensuring the samples originated from the targeted black spruce. The fragmented roots were then preserved in sterile 50 ml plastic tubes,

kept cool with ice until transported to the GREMA lab, where they were stored at -20°C. To isolate the rhizosphere soil and avoid extracting endophytic microbes, roots were submerged in 50 ml tubes containing 25 ml of a PBS 1X + Tween 20 (0.1%) solution, followed by vigorous vortexing for 5 minutes at maximum velocity. After removing the roots, the rhizosphere soil was separated by centrifuging the tubes at 4500 g for 20 minutes at 4°C. The supernatant was discarded, and the rhizosphere soil was then laid out on absorbent paper to eliminate any remaining PBS solution before proceeding with DNA extraction.

2.4.5 Soil physicochemical properties

We sent composite soil samples (> 50g) to the organic/inorganic chemistry lab of the Direction de la recherche forestière (Quebec City, Canada) for physicochemical analysis. Determination of nitrogen and carbon concentrations was performed by using a CN 928 elemental analyzer (Leco Corp., St Joseph, MI, USA) by combustion, in which the products of combustion were quantified by thermal conductivity detection for nitrogen and non-dispersive infra-red (NDIR) cell detection for carbon. Organic matter content and the percentage of humidity were ascertained by the method of incineration more popularly known as the loss on ignition (LOI) method. Soil pH was determined by mixing 10 g of the soil sample with 20 mL of distilled water, and pH was determined with an Orion VersaStar Pro pH meter (Thermo Fisher Scientific Inc., Pittsburgh, PA, USA). The Mehlich-III method was used to extract elements (P, K, Ca, Mg, Mn, Zn, Al, Fe), and finally, these elements were measured by plasma atomic emission spectroscopy (Optima 8300 model, ICP-OES, Perkin Elmer, Waltham, MA, USA). Samples of soil by horizon were collected in triplicate and analyzed for particle size distribution and textural class as given by the Bouyoucos method.

2.4.6 DNA Extraction, amplification, and library preparation

We extracted the DNA from 0.25 g of rhizosphere soil, using the DNeasy Powersoil Pro kit with the QIAcube system following the manufacturer's instructions (QIAGEN, Valencia, CA, USA). DNA was quantified with the Qubit™ dsDNA BR Assay Kit (Thermo Fisher Scientific Inc, Wilmington, USA). Bacterial communities were amplified using primers 515F-Y and 926R targeting the V4–V5 regions of the 16S

rRNA gene of bacteria and archaea (Parada et al., 2016). The ITS2 region of the fungal DNA was amplified using the primer set ITS9F and ITS4R (White et al., 1990; Menkis et al., 2012). Negative controls in the DNA extraction and PCR amplification were used to control potential contaminants during the process. Bacterial and fungal DNA amplicon libraries were prepared and sequenced on an Illumina Miseq platform using the sequencing kit MiSeq v3 600-cycle Reagent Kit. The 16S rRNA (bacteria) and ITS (fungi) amplicon pools were sequenced on an Illumina MiSeq instrument using the sequencing kit MiSeq Reagent Kit v3 (2x300 bp) at the Centre d'expertise et de services Génome Québec.

2.4.7 Rhizosphere soil microbial diversity analysis

We carried out bioinformatic analyses using QIIME2 software (Bolyen et al., 2019) for the 16S rRNA gene and ITS2 region sequences. The DADA2 pipeline in QIIME2 was used to process Illumina-sequenced paired-end fastq files, creating a table of amplicon sequence variants (ASVs), which offer a higher resolution compared to traditional OTUs (Callahan et al., 2016). Initially, primers were removed from ITS2 using CutAdapt and from 16S through position trimming within DADA2 (B. J. Callahan et al., 2016). We then combined the forward and reverse reads, eliminating low-quality sequences, chimeras, and rare ASVs (those with a frequency less than 0.05% of the average ASV frequency). Taxonomy was assigned with the Silva 138 database (Quast et al., 2012) for bacteria and the UNITE 8.0 database for fungi (Abarenkov et al., 2010; Nilsson et al., 2019). ASVs not matching the target taxonomy were filtered out, which come from non-bacteria and non-fungi sequences. The remaining ASVs were adjusted to a uniform feature count (rarefying), resulting in ASV tables with 14,547 bacteria and 2,911 fungi ASVs. For analyzing fungal functional groups in the soil, we used FUNGuild, taking into account only highly probable and probable confidence levels for assigned functional categories, with unidentifiable communities or those with complex nutrition modes classified as "others" (Nguyen et al., 2016).

2.4.8 Statistical analysis

The effects of silvicultural systems (clearcut, partial cut, and control) on rhizosphere microbial communities were examined by assessing variations in bacterial and fungal

diversity, community composition, relative abundance, and fungal functional groups. Alpha diversity metrics, including observed ASVs (richness), Shannon's diversity index, and Inverse Simpson diversity index, were calculated using the estimate_richness function in phyloseq package (McMurdie & Holmes, 2013). These calculations were based on rarefied ASV relative abundance data to ensure comparability across samples.

Analysis of variance (ANOVA) was used to test for significant differences in alpha diversity among treatments, followed by post-hoc tests when ANOVA results were significant ($p < 0.05$). The relative abundances of the top 20 most abundant bacterial and fungal genera were compared across treatments using ANOVA. For genera showing significant differences, post-hoc comparisons were performed to identify specific treatment effects. Fungal ASVs were assigned to trophic modes and functional guilds using FUNGuild, and their relative abundances were compared across treatments using ANOVA. Soil physicochemical properties in both organic and mineral layers were also analyzed using ANOVA to detect significant differences among treatments, followed by post-hoc tests for properties showing significant effects.

Beta diversity patterns were visualized using non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis dissimilarities, computed from rarefied ASV relative abundance data using the vegan package (Oksanen et al., 2001). The envfit function was used to overlay microbial phyla and abiotic soil factors on the ordination ($p < 0.05$). Significant differences in beta diversity between treatments were determined by permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarities with 999 permutations (adonis2 function). The model included treatment, site, and their interaction as factors. The proportion of variation explained by each factor was calculated using R-squared (R2) values. Post-hoc pairwise PERMANOVAs (999 permutations, "pairwise.adonis" function) with Benjamini-Hochberg correction for multiple comparisons were also conducted.

Pearson's correlation analysis was performed to examine relationships between soil properties and microbial communities in response to silvicultural systems.

ANCOMBC2 (Analysis of compositions of microbiomes with bias correction 2) was used to identify significant differences in bacterial and fungal taxa abundance across silvicultural systems, with results reported as log fold changes (lfc) and associated p-values (Lin, 2020).

All the statistical analyses were conducted using R software (R Core Team, 2024) in conjunction with RStudio 4.2.2. The phyloseq package (McMurdie and Holmes, 2013) was employed to analyze the taxonomically annotated Amplicon Sequence Variant (ASV) table.

2.5 Results

2.5.1 Alpha diversity of rhizosphere soil microbial communities

Bacterial community alpha diversity among silvicultural systems 18 years after harvest had subtle variations, though these differences were not statistically significant. Clearcut showed a trend towards higher diversity across all metrics, with mean observed richness of 623.5, Shannon's diversity index of 5.4, and Inverse Simpson diversity index of 103.7. Partial cut and control followed with progressively lower values, but the differences were not substantial enough to be statistically significant.

Soil fungal communities displayed a more complex pattern, although no differences were statistically significant. The control treatment exhibited a slightly higher mean observed richness (239.9) compared to clearcut (235.1) and partial cut areas (211.3) and marginally higher values for Shannon's diversity index (3.8). However, the Inverse Simpson diversity index in control was lowest (14.9) compared to the other treatments.

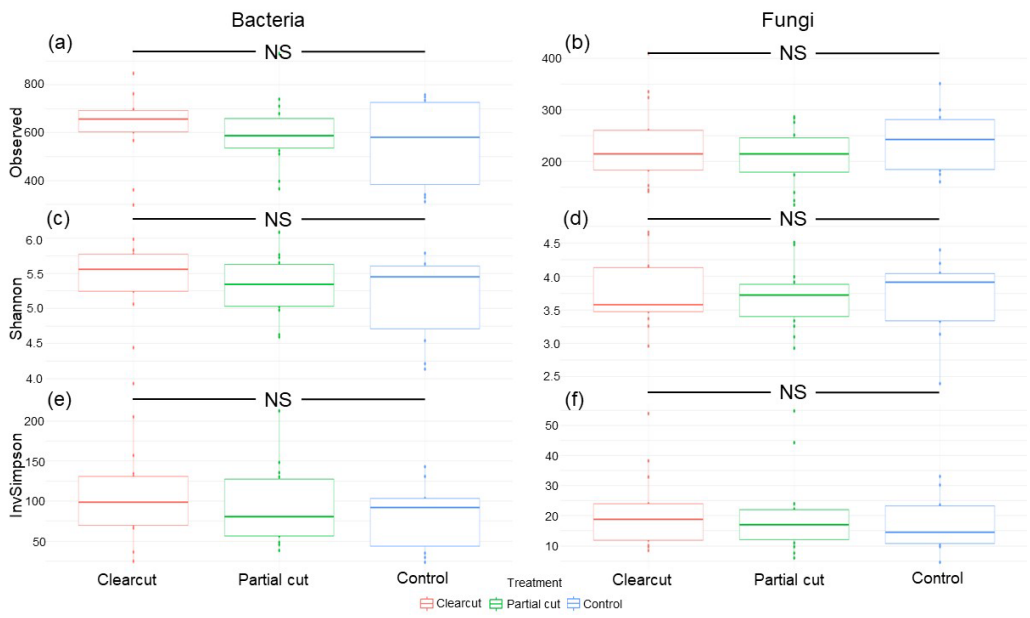


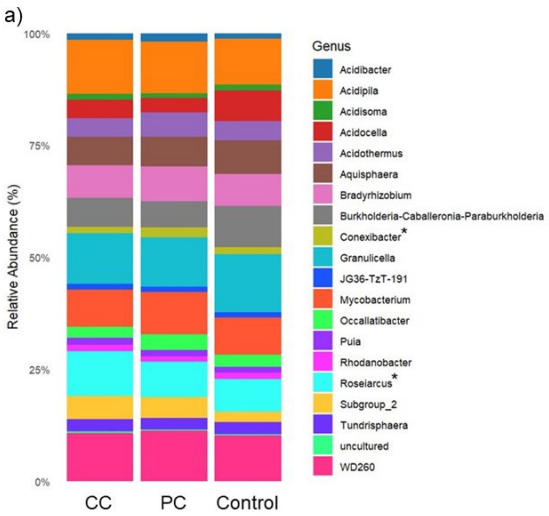
Figure 2.2
Bacterial and fungal alpha diversity among silvicultural systems in rhizosphere soil of naturally regenerated black spruce seedlings. Experimental units dominated by clearcut, partial cut and control. Significant differences between silvicultural systems (p-values) were evaluated by ANOVA using Tukey's honestly significant difference test (α = 0.05). The horizontal line in each box is the median value. NS: non-significant

2.5.2 Relative abundance of rhizosphere soil microbial genera and fungal functional groups

The analysis of the top 20 most abundant bacterial genera in the rhizosphere soil revealed distinct patterns of relative abundance across the three silvicultural systems 18 years after harvest (Figure 3.3). Across all treatments, *Acidipila, Granulicella*, WD260, *Mycobacterium*, and *Bradyrhizobium* were consistently among the most abundant genera. In clearcut areas, *Acidipila* (8.4%), *Granulicella* (7.86%), WD260 (7.5%), *Roseiarcus* (6.9%) and *Mycobacterium* (5.7%) were the most abundant genera. Partial cut areas were dominated by *Acidipila* (8%), WD260 (7.8%), *Granulicella* (7.7%), *Mycobacterium* (6.6%) and *Roseiarcus* (5.5%). Control forest displayed a slightly different pattern with *Granulicella* (9.43%) showing the highest abundance, followed by WD260 (7.5%) and *Acidipila* (7.4%). Among all the bacterial genera, only *Roseiarcus* and *Conexibacter* showed significant differences between

treatments. *Roseiarcus* showed significantly higher abundance in clearcut areas (6.9%) compared to partial cut (5.5%) and control (5.3%) (ANOVA, F= 3.7; p<0.05). For *Conexibacter*, partial cut (1.6%) had significantly higher abundance than clearcut (1%) and control (1.1%) (F= 3.3; p<0.05).

The top 20 most abundant fungal genera showed more distinct patterns in their relative abundances among silvicultural systems 18 years after harvest than bacteria genera (Figure X). *Oidiodendron*, *Cenococcum*, *Piloderma*, *Hyaloscypha*, and *Penicillium* were among the most abundant genera across all treatments. In clearcut areas, *Oidiodendron* (11.5%), *Cenococcum* (11.2%), *Piloderma* (11.4%), *Penicillium* (6.9%) and *Podila* (6.4%) were the most abundant genera. Partial cut areas were dominated by *Piloderma* (20.2%), followed by *Oidiodendron* (12.8%), *Penicillium* (11.2%) and *Hyaloscypha* (9.6%). Control plots displayed a different pattern with *Cortinarius* (11.1%) showing the highest abundance, followed closely by *Cenococcum* (10.9%), *Hyaloscypha* (10%), *Oidiodendron* (9.5%) and *Penicillium* (9.6%). In the top 20 most abundant genera, only *Piloderma* and *Mortierella* showed significant differences among treatments. *Mortierella* showed higher abundance in clearcut areas (3.4%) compared to partial cut (1.1%) and control (1.9%) (F= 3.7; p<0.05). For *Piloderma*, partial cut (20.2%) had significantly higher abundance than clearcut (11.4%) and control (4.3%) (F= 5.1; p<0.05).



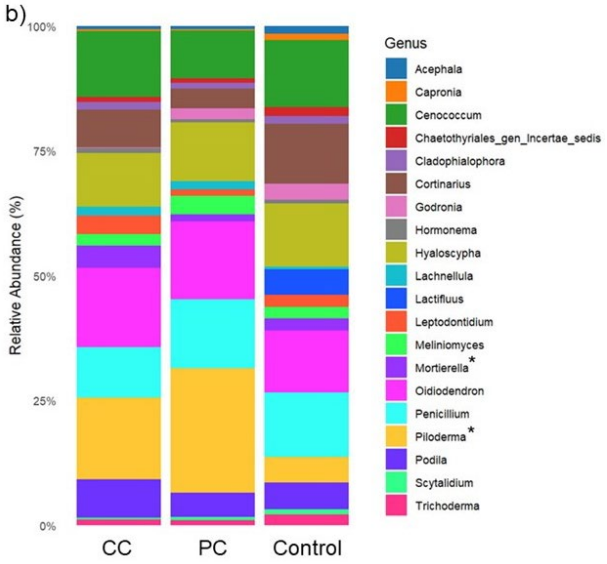


Figure 2.3
Relative abundance (%) of ASVs assigned to Top 20 most relatively abundant a) bacterial and b) fungal genera for rhizosphere soil among the silvicultural systems. CC: Clearcut (100% basal area removed); PC: Partial cut (50%); Control: Unharvested control. Stars correspond to significant differences in the relative abundance of a genus among silvicultural systems ($p < 0.001$*, $p < 0.01$**, $p < 0.05$*).**

The relative abundances of fungal functional groups did not differ significantly among silvicultural systems 18 years after harvest (Figure 3.4). However, some trends were observed: Ectomycorrhizal fungi were the most abundant group across all treatments, with the highest proportion in partial cut areas (41.6%), followed by clearcut (37.4%), and control stands (34.3%). Ericoid mycorrhizal fungi showed a similar pattern. Undefined saprotrophs were the second most abundant group, with the highest proportion in control stands (22.1%), followed closely by partial cut (21.2%) and clearcut (18.7%). Other functional groups, including wood saprotrophs, plant saprotrophs, leaf saprotrophs, animal pathogens, plant pathogens, fungal parasites, and endophytes, showed varying trends among treatments but without statistical

significance. Several functional groups, such as algal parasites, animal endosymbionts, bryophyte parasites, dung saprotrophs, epiphytes, lichen parasites, lichenized fungi, and soil saprotrophs, had very low abundances (< 1%) across all treatments.

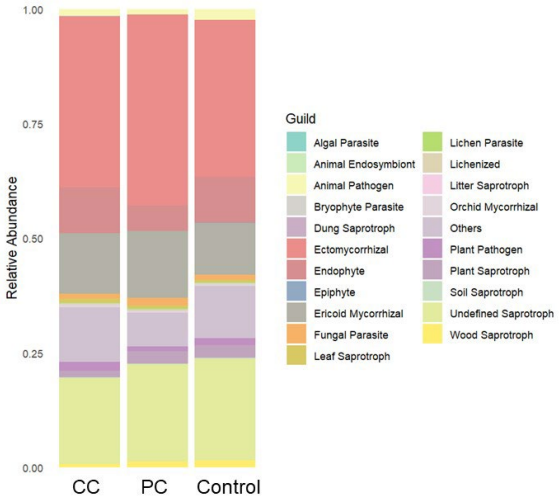


Figure 2.4
Compositions of main fungal functional guild inferred by FUNGuild. ASVs assigned to a guild with the confidence ranking of "Highly probable" and "Probable" were retained for further use, whereas those with the "possible" confidence ranking were classified as 'Others'. CC: Cleatcut (100% basal area removed); PC: Partial cut (50%); Control: Unharvested control

2.5.3 Soil physicochemical properties

The analysis of soil physicochemical properties revealed significant differences among clearcut, partial cut, and control treatments 19 years after harvesting, primarily in the organic layer (Table 3.2). Clearcut plots showed notably higher total carbon (TC) (+30% relative to partial cut), total nitrogen (TN) (+32%), and organic matter (OM) (+28%) compared to partial cut treatments, with values similar to or slightly lower than controls. Base saturation (BS) was also 59.2% higher in clearcut areas compared to partial cut and 53% higher than control ($p < 0.05$). Calcium (Ca) concentration was 115% higher in clearcut areas compared to partial cut and 124% higher than control

($p < 0.05$). Cation exchange capacity (CEC) was 30% higher in clearcut and 24% higher in control compared to partial cut ($p < 0.05$). Iron (Fe) content was 61% higher in partial cut compared to clearcut ($p < 0.05$). Soil humidity was 19% lower in partial cut compared to clearcut and 20% lower than control ($p < 0.05$). Potassium (K) content was 48% higher in control compared to clearcut and 73% higher than partial cut ($p < 0.05$). Finally, total metals (TM) were 96% higher in clearcut compared to partial cut and 66% higher than control ($p < 0.05$).

The mineral layer showed no significant differences, indicating that silvicultural systems had pronounced effects on the organic layer mostly.

Table 2.2

Soil physicochemical properties in organic layers among silvicultural systems. Values are mean ± SE (n = X). Different letters indicate significant differences among silvicultural systems within each layer (Tukey HSD, p < 0.05). Units are mg/kg unless otherwise noted. BS (base saturation, %); CEC (cation exchange capacity, cmol(+)/kg); MC (moisture content, %); OM (organic matter, g/kg); TC (total carbon, g/kg); TH (total hydrogen, g/kg); TM (total metals, mg/kg)*; TN (total nitrogen, g/kg); pH (soil acidity, unitless); BS (Base Saturation (%)

	Organic layer		
Soil	Clearcut	Partial cut	Control
Al	724.26 ± 110.07 a	1201.30 ± 176.16 a	830.56 ± 121.84 a
BS	**10.95 ± 1.44 b**	**6.88 ± 0.94 a**	**7.18 ± 0.97 a**
Ca	**2364.54 ± 314.76 b**	**1096.23 ± 142.18 a**	**1054.12 ± 136.73 a**
CEC	**142.71 ± 11.90 b**	**109.72 ± 8.98 a**	**136.35 ± 11.14 b**
Cu	14.19 ± 4.41 a	12.58 ± 3.87 a	22.36 ± 6.67 a
Fe	**257.44 ± 33.80 a**	**414.59 ± 52.47 b**	**290.41 ± 36.79 ab**
MC	**9.55 ± 0.57 b**	**7.75 ± 0.47 a**	**9.69 ± 0.57 b**
K	**367.01 ± 42.1 a**	**313.30 ± 35.29 a**	**541.30 ± 60.89 b**
Mg	**283.30 ± 42.91 b**	**165.56 ± 24.77 a**	**280.85 ± 41.92 b**
Mn	**88.59 ± 14.32 b**	**63.50 ± 13.85 ab**	**27.56 ± 13.85 a**
Na	**24.64 ± 3.53 ab**	**23.38 ± 3.31 a**	**31.17 ± 4.37 b**
OM	**850.77 ± 64.88a**	**663.07 ± 49.31b**	**901.56 ± 67.02a**
P	81.55 ± 13.52 a	87.79 ± 14.39 a	96.67 ± 15.82 a
pH	4.74 ± 0.11 a	4.77 ± 0.10 a	4.66 ± 0.10 a
S	19.62 ± 1.95 a	23.65 ± 2.27 ab	27.17 ± 2.59 b
TC	**449.20 ± 33.18 b**	**345.12 ± 24.86 a**	**452.78 ± 32.59 b**
TH	126.05 ± 11.40 a	101.33 ± 9.01 a	126.54 ± 11.23 a
TM	**15.53 ± 1.72 b**	**7.92 ± 0.90 a**	**9.37 ± 1.05 a**
TN	**10.41 ± 0.91 b**	**7.88 ± 0.70 a**	**9.81 ± 0.85 b**
Zn	40.31 ± 7.66 a	28.76 ± 5.44 a	32.22 ± 6.07 a

Table 2.3
Soil physicochemical properties in mineral layers among silvicultural systems. Values are mean ± SE (n = X). Different letters indicate significant differences among silvicultural systems within each layer (Tukey HSD, p < 0.05). Units are mg/kg unless otherwise noted. BS (base saturation, %); CEC (cation exchange capacity, cmol(+)/kg); MC (moisture content, %); OM (organic matter, g/kg); TC (total carbon, g/kg); TH (total hydrogen, g/kg); TM (total metals, mg/kg)*; TN (total nitrogen, g/kg); pH (soil acidity, unitless); BS (Base Saturation (%)

	Mineral layer		
Soil	Clearcut	Partial cut	Control
Al	982.89 ± 209.16 a	1474.06 ± 313.57 a	1198.70 ± 255.01 a
BS	2.34 ± 0.59 a	4.06 ± 0.89 a	2.35 ± 0.59 a
Ca	97.85 ± 24.04 a	67.35 ± 16.62 a	53.18 ± 13.18 a
CEC	22.10 ± 3.85 a	27.53 ± 4.76 a	23.34 ± 4.06 a
Cu	4.94 ± 1.71 a	2.27 ± 0.94 a	3.50 ± 1.30 a
Fe	383.95 ± 54.72 a	436.17 ± 62.14 a	355.29 ± 50.64 a
MC	1.70 ± 0.47 a	2.44 ± 0.60 a	2.02 ± 0.53 a
K	26.12 ± 3.95 a	35.07 ± 5.25 a	35.91 ± 5.37 a
Mg	19.71 ± 3.59 a	16.03 ± 2.96 a	13.81 ± 2.57 a
Mn	2.67 ± 0.75 a	1.67 ± 0.75 a	0.60 ± 0.75 a
Na	5.79 ± 0.44 a	6.44 ± 0.48 a	6.27 ± 0.47 a
OM	72.63 ± 16.00	95.94 ± 21.06	86.31 ± 18.97
P	23.70 ± 6.16 a	27.93 ± 7.22 a	16.06 ± 4.26 a
pH	5.22 ± 0.07 a	5.37 ± 0.07 a	5.28 ± 0.07 a
S	10.10 ± 1.66 a	14.48 ± 2.32 a	11.65 ± 1.90 a
TC	39.04 ± 8.08 a	52.74 ± 10.84 a	46.05 ± 9.49 a
TH	20.44 ± 3.78 a	26.78 ± 4.90 a	22.75 ± 4.19 a
TM	0.98 ± 0.16 a	0.67 ± 0.13 a	0.57 ± 0.12 a
TN	1.26 ± 0.32 a	1.70 ± 0.38 a	1.62 ± 0.37 a
Zn	3.69 ± 0.84 a	2.48 ± 0.62 a	2.24 ± 0.58 a

2.5.4 Soil microbial community composition

The PERMANOVA results revealed that neither the silvicultural systems nor the site had a statistically significant effect on soil bacterial community composition at the chosen significance level ($p < 0.05$). The site factor explained 9.96% of the variation in bacterial communities ($R^2 = 0.1$, $F = 1.34$, $p = 0.17$), while the silvicultural systems accounted for 6.71% of the variation ($R^2 = 0.07$, $F = 1.3548$, $p = 0.18$). The interaction between site and treatment explained the largest proportion of variation at 16% ($R^2 =$

0.16, F = 1.33, p = 0.13), although this effect was also not statistically significant. A substantial portion of the variation (66.85%) in bacterial communities remained unexplained by the model (Residual R^2 = 0.67).

For soil fungal community composition, the PERMANOVA results revealed that the site factor had a marginally significant effect (F = 2.2, R^2 = 0.17, p = 0.052). Site explained 17% of the variation in fungal communities. In contrast, silvicultural systems did not show a statistically significant effect on fungal community composition (F = 1.49, R^2 = 0.08, p = 0.22). The treatments accounted for 7.69% of the variation in fungal communities. The interaction between site and treatment explained 5.51% of the variation (R^2 = 0.06) but was not statistically significant (F = 0.42, p = 0.92). The effect of silvicultural systems on fungal communities did not vary significantly across different sites.

Non-metric multidimensional scaling (NMDS) and Pearson's correlation analysis revealed intricate relationships between soil properties and microbial communities in response to silvicultural systems (Figure 4). For bacterial community responses, soil properties significantly influenced bacterial phylum abundance. Proteobacteria exhibited positive correlations with both potassium (K) (r = 0.4, p < 0.05) and magnesium (Mg) (r = 0.36, p < 0.05). Conversely, Acidobacteriota showed negative correlations with K (r = -0.42, p < 0.01) and Mg (r = -0.44, p < 0.01). Planctomycetota abundance was negatively correlated with sulfur (S) (r = -0.4, p < 0.05), while Bacteroidota showed a positive correlation with K (r = 0.35, p < 0.05). Myxococcota had positive correlations with both total nitrogen (N) (r = 0.37, p < 0.05) and manganese (Mn) (r = 0.32, p < 0.05). Bdellovibrionota exhibited strong positive correlations with phosphorus (P) (r = 0.47, p < 0.01), K (r = 0.33, p < 0.05), and S (r = 0.32, p < 0.05). Firmicutes showed a positive correlation with copper (Cu) (r = 0.36, p < 0.05). Gemmatimonadota displayed contrasting correlations, with a positive association with total N (r = 0.36, p < 0.05) and a negative correlation with K (r = -0.35, p < 0.05). Abditibacteriota abundance was positively correlated with K (r = 0.36, p < 0.05).

The analysis of fungal phyla abundance revealed significant correlations with soil properties, particularly for Mucoromycota. This phylum showed negative correlations with soil moisture ($r = -0.35$, $p < 0.05$), soil organic matter (SOM) ($r = -0.31$, $p < 0.05$), total carbon (C) ($r = -0.33$, $p < 0.05$), phosphorus (P) ($r = -0.33$, $p < 0.05$), and potassium (K) ($r = -0.41$, $p < 0.05$). Interestingly, no significant correlations were observed between soil properties and the other fungal phyla examined (Ascomycota, Basidiomycota, and Mortierellomycota).

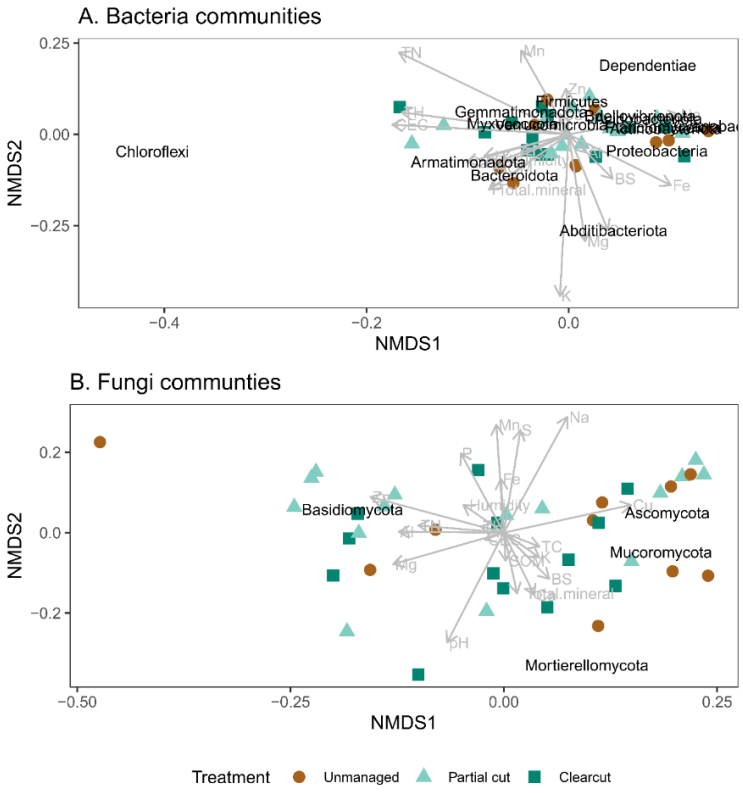


Figure 2.5
Two-dimensional non-metric multidimensional scaling (NMDS) of the rhizosphere soil A) bacterial and B) fungal community from the silvicultural systems. Grey arrows indicate the correlation between sample level and ordination axes scores for microbial phyla and soil physicochemical properties, respectively, added a posteriori in the ordination (displayed phyla of maximum estimated P < 0.05). Ordination based on Bray-Curtis dissimilarities of the rarefied ASV relative abundances.

2.5.5 Soil bacterial and fungal indicators on silvicultural systems

The analysis of soil bacterial communities using ANCOMBC2 (Analysis of compositions of microbiomes with bias correction 2) revealed significant differences in the abundance of several bacterial taxa across silvicultural systems. The control sites generally showed the most distinct bacterial community composition, with many taxa exhibiting significant differences in abundance compared to the clearcut treatment. The partial cut generally resulted in intermediate abundance levels between clearcut and control treatments. Some bacterial taxa, such as *Granulicella*, *Acidibacter*, and *Burkholderia-Caballeronia-Paraburkholderia*, showed no significant differences across treatments.

The five most abundant bacterial genera showed the significant differences on bacterial abundance between treatments. *Caulobacter* were more abundant in the control treatment compared to clearcut (log fold change [lfc] = 1.61, p = 0.0095). *Candidatus Koribacter* showed a significant negative response to both partial cut (lfc = -0.83, p = 0.067) and control treatments (lfc = -1.40, p = 0.0054) compared to clearcut. *Ferruginibacter* displayed a positive response to the control treatment compared to clearcut (lfc = 1.03, p = 0.017). *Lacunisphaera* showed significant negative responses to both partial cut (lfc = -1.05, p = 0.0067) and control treatments (lfc = -0.80, p = 0.056) compared to clearcut. *Rickettsiella* exhibited significant negative responses to both partial cut (lfc = -0.97, p = 0.028) and control treatments (lfc = -0.85, p = 0.078) compared to clearcut.

The analysis of soil fungal communities revealed several significant differences in the abundance and composition of individual fungal taxa. While the overall fungal community did not differ significantly among treatments, specific fungal taxa showed significant responses to treatments.

Some of the six most abundant fungal genera and families showed significant differences in abundance between treatments. *Humicolopsis* exhibited the most pronounced response to silvicultural systems. It was significantly more abundant in the partial cut compared to control (lfc = 2.72, p = 0.004) or clearcut areas (LFC = -

2.78, p = 0.007). *Mortierellaceae* were significantly less abundant in partial cut areas relative to the control (LFC = -2.06, p = 0.005) or clearcut areas (LFC = 2.10, p = 0.008). *Scytalidium* was significantly more abundant in partial cut compared to control (LFC = 1.49, p = 0.010). *Pseudopenidiella* was significantly more abundant in both partial cut (LFC = 1.61, p = 0.009) and clearcut (LFC = 1.79, p = 0.014) areas compared to control. Both *Coniochaeta* (LFC = -1.39, p = 0.011) and *Cladosporium* (LFC = -1.37, p = 0.005) were less abundant in partial cut areas compared to control.

2.6 Discussion

Studying the rhizosphere of regenerated seedlings following silvicultural systems may help us understand forest ecosystem resilience, as this narrow soil zone governs essential plant–microbe interactions that drive nutrient cycling, seedling establishment, and organic matter decomposition (Kohout et al., 2018b; Mohanram & Kumar, 2019). Our results provide valuable insights into the long-term effects of silvicultural systems on rhizosphere soil microbial communities in Canadian boreal forests. After 19 years of recovery time, our findings suggest that the rhizosphere microbial community composition has largely stabilized across different silvicultural systems in Canadian boreal forests. However, notable differences in the abundance of specific genera and microbial indicators were observed among treatments, which may have important implications for forest ecosystem functioning and regeneration processes. Notably, to our knowledge, this study represents the first comprehensive evaluation of the long-term effects of partial harvest on rhizosphere microbiome diversity in boreal ecosystem, filling a significant gap in our understanding of how moderate silvicultural disturbances shape belowground ecosystem processes.

2.6.1 Rhizosphere Soil Microbial Diversity, Abundance, and Functional Groups

Our study reveals that after nearly two decades, the rhizosphere soil microbial community structure might have largely recovered from silvicultural interventions. This finding aligns with the previous studies that bacterial communities underwent a rapid shift in first decade and after that, slower transition until stabilizing 50 years post conversion to agricultural systems from boreal forest in Canada (Benalcazar et al., 2024). These findings indicate that even land conversion treatments, which impose

more severe disturbances than clearcutting, can exhibit considerable resilience in soil microbial communities within 10 years. A reason of the observed stabilization of microbial communities may be associated with restoration of forest biomass after harvesting because the regrowth of vegetation over time provides a more stable environment for microbial communities (Zhou et al., 2020). Additionally, because our sampling targeted only the rhizosphere of black spruce seedlings, the host-driven recruitment of specific microbial assemblages may have further contributed to the convergence of community composition (Uroz et al., 2016). Studies have demonstrated that the recovery of microbial communities post-disturbance is closely linked to vegetation regrowth and the gradual accumulation of organic matter, factors that collectively bolster soil resilience and structural stability (Duret et al., 2024; Mushinski et al., 2018). Another study has shown that soil microenvironment and respiration can return to pre-disturbance states within 5-6 years after low-level interventions like thinning (Peng & Thomas, 2006). Additionally, fine root biomass as an important driver of microbial activity also recovers to its pre-thinning state in about six years(Asaye & Zewdie, 2013; Cheng et al., 2015). However, since the harvesting intensities in our study (100% for clearcut and 50% for partial cut) are substantially higher than the 30% typical of thinning, the recovery period is expected to extend beyond 5 years, potentially reaching up to 20 years.

However, the inherent sensitivity of key microbial taxa to even subtle disturbances make it challenging for soil microbial diversity to fully recover, as these species often fail to re-establish their pre-disturbance community structures (Baldrian, 2017). Moreover, naturally regenerated seedlings growing in soil may stimulate dormant microorganisms that react in response (Baldrian, 2017). Our study also revealed some specific microbial responses to the silvicultural systems, which is significantly different in this case. Nitrogen-fixing bacteria *Roseiarcus* spp. showed higher abundance in clearcut areas, where the level of disturbance was the highest. It could be explained because nitrogen-fixing bacteria play a crucial role in nitrogen supply to forest ecosystems, particularly in boreal forests, which can significantly influence nutrient availability and consequently may contribute to the stabilized composition of

the rhizosphere bacterial community (Lladó et al., 2017). Moreover, this may be related to the higher seedling growth observed in our study areas with clearcut treatment, as nitrogen-fixing bacteria can enhance soil fertility and promote plant growth (Hayat et al., 2010).

For fungi, the high abundance of ectomycorrhizal fungi (EMF), particularly *Piloderma* spp., in partial cut areas may be attributed to the increased density of black spruce seedlings combined with scarification treatments, which expose mineral soil surfaces and create favorable conditions for more abundant EMF. This aligns with an ectomycorrhizal study in boreal forest, showing that EMF species richness and composition varied significantly among seedlings regenerating in three distinct microhabitats: forest floor, decaying stumps, and moss-covered erratic boulders (Iwański & Rudawska, 2007). Scarification enhances root-soil contact and nutrient exchange, thus promoting the recruitment of symbiotic fungi, while the greater density of host trees in partial cut stands further increases the available niche for these fungi to establish (Otsing et al., 2021). These findings suggest that the overall microbial community structure appears to stabilize over time in post-harvest stands of natural boreal forests with minor shifts in specific microbial taxa, reflecting both resilience and legacy effects of moderate silvicultural interventions on belowground ecosystem processes.

2.6.2 Relationship between Soil Physicochemical Properties and Microbial Communities

The similarity in bacterial and fungal community structures in post-harvest stands appears to be closely associated with soil physicochemical properties. Our results revealed intricate relationships between soil properties and microbial communities, highlighting the complex interplay between abiotic and biotic factors in the rhizosphere.

Soil pH emerged as a critical factor influencing soil microbial community composition in several studies (Bahram et al., 2018; Kim et al., 2021; Rousk et al., 2009). However, our study found that pH was not significantly different among treatments after 19 years. The stabilization of soil pH across treatments likely reflects the resilience of these ecosystems and their capacity to recover from silvicultural interventions over extended

periods. This pH stability may also contribute to the observed similarities in microbial community composition across treatments. In a previous meta-analysis of soil chemistry in major forest ecosystems in China, the 20-year period between soil samplings provided sufficient time for forest ecosystems to respond to and potentially recover from initial disturbances or changes in soil pH (Yang et al., 2015).

The gradual accumulation of organic matter over the 19-year recovery period could play a crucial role in shaping the observed microbial communities. The accumulation of organic matter from decaying plant material may contribute to improved soil structure and stability, creating a more favorable environment for microbial activity (Mushinski et al., 2018). In our study, 19 years post-clearcut area showed similar organic matter contents with untreated area, which may drive increased abundance of specific microbial species (e.g., *Curvibasidium* spp.) in the clearcut area. In contrast, the partial cut areas underwent scarification, leading to greater exposure of mineral soil and reduced organic matter accumulation, which may partly explain the observed differences in soil organic matter between treatments.

Conversely, K and Mg can influence the composition and activity of microbial communities in the rhizosphere soils (Li et al., 2018). They are essential macronutrients for plant growth and development: K is crucial for osmotic regulation, enzyme activation, and photosynthesis (Jan et al., 2017). Mg is a central component of chlorophyll and is involved in various enzymatic reactions (Zhou et al., 2024). In our study, they also showed strong correlation with Proteobacteria (positive) and Acidobacteriota (negative), indicating that K and Mg could be one of main diving factors of these two bacterial phyla and shape most of the bacterial community structure in the rhizosphere (Xie et al., 2022). Another study examining rhizosphere microbial communities in contaminated soils found that Mg levels were positively correlated with the abundance of Proteobacteria. This suggests that Mg could play a significant role in stabilizing bacterial membrane structures and regulating enzyme functions, thereby potentially influencing the prevalence of Proteobacteria in the rhizosphere. Research on tobacco plants revealed that lower levels of exchangeable and water-soluble K in the rhizosphere were associated with reduced abundance of

beneficial bacterial genera, many of which belong to the Proteobacteria phylum (Yang et al., 2024). This indicates that adequate K availability may promote the growth of Proteobacteria, and thereby contributes to shaping the overall bacterial community structure in the rhizosphere.

Our analysis of fungal community composition revealed that Mucoromycota could uniquely be sensitive to soil properties compared to other fungal phyla. Specifically, Mucoromycota exhibited significant negative correlations with soil humidity, organic matter content, total C, P, and K, indicating that this phylum is particularly responsive to changes in soil nutrient and moisture status. These results suggest that shifts in nutrient availability following silvicultural systems may have pronounced effects on the abundance of Mucoromycota, which in turn could impact nutrient cycling and organic matter turnover. This observation aligns with findings from Chen et al. (2022), who reported that Mucoromycota in *Cinnamomum camphora* forests was significantly influenced by soil physical properties such as bulk density, porosity, and water content. Similarly, Bonfante and Venice (2020) underscored the dual role of Mucoromycota as both a plant-associated symbiont and an ecosystem degrader, which reflects its capacity to form mutualistic associations (often colonizing root epidermal cells to facilitate nutrient exchange with host plants) while also producing a suite of extracellular enzymes (e.g., cellulases, ligninases) that break down complex organic polymers in soil. Fluctuations in soil moisture and nutrient levels directly affect both its symbiotic efficiency and its saprotrophic activity, making Mucoromycota a sensitive indicator of changes in soil health and organic matter turnover (Bonfante & Venice, 2020). However, the study in *Cinnamomum camphora* forests did not find a direct positive correlation between Mucoromycota and potassium levels. Instead, it reported that Mortierellomycetes, a prevalent fungal class, was positively correlated with total phosphorus and available and total potassium but negatively with alkaline-hydrolyzable nitrogen (Chen et al., 2022). These findings underscore the importance of considering fungal phyla-specific responses when evaluating the long-term impacts of silvicultural systems on soil microbial communities, and they point to the need for

future research to further elucidate the functional roles of Mucoromycota under varying environmental conditions.

2.6.3 Microbial Indicators of Silvicultural systems

Studying microbial indicator species in the rhizosphere of target tree species is invaluable for revealing subtle, treatment-specific shifts in ecosystem functioning that are often overlooked by conventional soil analyses. Our findings demonstrate that specific bacterial and fungal genera respond differentially to silvicultural practices such as clearcutting and partial cutting, thus providing early signals of changes in nutrient cycling, seedling establishment, and overall forest regeneration. These microbial indicators not only reflect the immediate impacts of forest management but also offer predictive insights into long-term ecological resilience, enabling more targeted and adaptive management strategies in boreal forests.

The bacterial genera *Caulobacter* and *Ferruginibacter*, being more abundant in control compared to clearcut plots, indicate a preference for undisturbed forest conditions. *Caulobacter* is a biofilm-forming bacterium often associated with surface colonization and nutrient cycling in stable environments (Berrios, 2022). Its abundance in control plots suggests it plays a role in maintaining soil structure and organic matter decomposition in mature forests. *Ferruginibacter*, part of the Chitinophagaceae family, is often associated with the degradation of complex organic compounds (Rosenberg, 2014). The control plots likely provide a more diverse and stable supply of organic matter (although having no significant differences with other plots at the sampling time), supporting metabolic preferences of *Ferruginibacter*. Conversely, *Candidatus Koribacter*, being less abundant in both partial cut and control compared to clearcut, suggests that C. *Koribacter* thrives in more disturbed environments, possibly due to its adaptability to changing soil conditions or competitive advantage in early successional stages. The genus belongs to the Acidobacteria phylum, known for its versatility and abundance in various soil types, which may explain its resilience in clearcut areas (Bandopadhyay & Shade, 2024).

The fungal genus *Humicolopsis* was more abundant in partial cuts compared to control or clearcuts. This pattern suggests that *Humicolopsis* benefitted from the unique conditions created by partial cut treatments, which involve scarification that reduces the organic matter layer and exposes more mineral soil. Although partial harvesting reduces the organic layer, the remaining woody debris and root fragments still supply enough substrate to support saprotrophic fungi adapted to breaking down tough lignocellulosic materials. This pattern is consistent with Mushinski et al. (2018), who showed that scarification and moderate disturbance create unique soil microhabitats that favor the proliferation of saprophytic fungal taxa (Mushinski et al., 2018). Mortierellaceae, known for their role in decomposing labile organic matter, may exploit the rapid nutrient turnover in clearcut soils (Li et al., 2023) and their decline in partial cuts could reflect competition with ectomycorrhizal fungi (e.g., *Piloderma* spp.) that dominate in less disturbed soils (Ozimek & Hanaka, 2021; Telagathoti et al., 2022). As a fungal indicator, fluctuations in Mortierellaceae abundance provide valuable insights into nutrient cycling dynamics and substrate quality following silvicultural systems. Their elevated presence in clearcut soils suggests these environments favor rapid decomposition and nutrient mobilization, whereas their reduced abundance in scarified, partially harvested stands underscores the influence of altered organic matter content and competitive interactions on fungal community composition.

Pseudopenidiella showed increased relative abundance in both partial cuts and clearcuts than control, potentially indicating its opportunistic nature in post-disturbance environments. Its elevated presence may suggest that this genus functions as a pioneer taxon, rapidly colonizing soils following silvicultural interventions where competitive pressures are reduced and stress factors prevail (Trofymow et al., 2023). The resilience and adaptability of *Pseudopenidiella* enable it to exploit transient niches created by disturbance, making it a potential bioindicator for assessing the immediate impacts of forest management practices on soil microbial communities, as well as the subsequent trajectory of ecosystem restoration and succession.

2.6.4 Implications for Forest Management and Ecosystem Functioning

While the overall microbial community structure appears broadly similar among treatments 19 years after harvest, some microbial groups still show persistent differences that may influence forest structure and ecosystem functioning. These enduring microbial signatures, such as the increased abundance of nitrogen-fixing bacteria in clearcut areas and the distinct responses of ectomycorrhizal fungi in partially harvested stands, have the potential to alter nutrient cycling dynamics and soil organic matter turnover (Hayat et al., 2010; Nash et al., 2020). In turn, such changes may affect nutrient availability for tree growth and seedling establishment in later successional stages, ultimately shaping the successional trajectory of forest stands (Baldrian et al., 2023). Moreover, shifts in microbial processes can influence rates of carbon sequestration and decomposition, thereby impacting overall ecosystem productivity and resilience (Bowd et al., 2019). These observations can underscore the critical interconnectedness of belowground microbial processes with aboveground forest structure, emphasizing the importance of integrating microbial insights into long-term forest management strategies.

In response, recent advances in soil microbiology have highlighted the potential of microbial inoculants and targeted soil amendments as tools to modify and enhance soil microbial communities, ultimately supporting forest restoration and productivity (Asmara et al., 2023; Gomes et al., 2025). By introducing beneficial microorganisms such as specific ectomycorrhizal fungi, plant growth-promoting bacteria, or even customized microbial consortia, forest managers can actively steer the rhizosphere towards a composition that favors nutrient acquisition, stress tolerance, and seedling establishment. Concurrently, soil amendments such as organic compost, biochar, or customized mineral additives can improve soil structure and nutrient availability, creating a more hospitable environment for these beneficial microbes. This dual approach not only accelerates the recovery of disturbed sites but also promotes long-term ecosystem resilience by fostering synergistic plant–microbe interactions that underpin successional dynamics in boreal forests. Such strategies may be particularly valuable in areas affected by intensive silvicultural systems, where natural microbial recovery is slow or incomplete. Future research should continue to refine these

inoculant formulations and amendment protocols, integrating them with adaptive forest management practices to enhance natural regeneration processes and sustain soil biodiversity in managed ecosystems.

2.7 Conclusion

Our study reveals that 19 years after silvicultural systems in Canadian boreal forests, the overall rhizosphere microbial community has largely stabilized, yet minor treatment-specific shifts persist. We observed a subtle increase in certain bacterial and fungal taxa such as a higher abundance of nitrogen-fixing bacteria in clearcut areas and distinct ectomycorrhizal fungal profiles in partially harvested stands that may indicate the lasting ecological legacy of these management practices. These findings shows the potential role of microbial indicator such as *Roseiarcus* and *Piloderma* in influencing nutrient cycling and plant–microbe interactions, which may in turn affect carbon sequestration and forest regeneration over successional stages. Future research should focus on elucidating the functional roles of these key taxa and on long-term monitoring to better understand their impacts on forest productivity and ecosystem resilience. With more microbial studies, we could consider applying microbial inoculants or soil amendments to promote soil restoration, provided that we have a comprehensive understanding of the ecosystem in which they are deployed.

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3. LA RÉCOLTE PARTIELLE RÉDUIT LE STRESS HYDRIQUE CHEZ LES SEMIS DE CONIFÈRES : UNE ANALYSE $\delta^{13}C$ SUR 18 ANS DANS LES FORÊTS BORÉALES CANADIENNES

Partial Harvest Reduces Water Stress in Conifer Seedlings: An 18-Year δ^{13} C Analysis in Canadian Boreal Forests

(Manuscript)

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3.1 Résumé

Les pratiques sylvicoles pourraient induire un stress hydrique chez les semis de conifères en régénération naturelle. Il est essentiel de comprendre leurs impacts physiologiques à long terme pour élaborer des stratégies de gestion forestière résilientes et durables dans un contexte de changement climatique. Nous avons évalué les effets de méthodes de régénération représentant un gradient d'intensité de récolte sur le stress hydrique chez des semis de l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et du sapin baumier (*Abies balsamea* (L.) Mill) régénérés naturellement, 18 ans après la récolte dans les forêts boréales canadiennes. Comme indicateur du stress hydrique, nous avons analysé la composition isotopique du carbone foliaire ($\delta^{13}C$), une mesure intégrative de l'efficacité intrinsèque de l'utilisation de l'eau, à partir de 180 semis prélevés selon quatre méthodes de régénération (coupe totale, coupe avec réserve de semenciers, coupe progressive régulière par mini-bandes, témoin non coupé). Les traitements avec les intensités de récolte les plus élevées (coupe à blanc et arbre semeur) ont présenté des valeurs de $\delta^{13}C$ significativement plus élevées que celles des témoins non coupés, indiquant un stress physiologique plus important lié à la sécheresse dans des conditions à découvert. En revanche, la récolte partielle a maintenu des niveaux de $\delta^{13}C$ similaires à ceux des témoins non coupés, soulignant leur potentiel pour atténuer le stress lié à la sécheresse en préservant des conditions microclimatiques favorables. Le diamètre des semis était le facteur prédictif de croissance le plus fort du $\delta^{13}C$, indiquant un stress hydrique plus important chez les semis plus grands. La couverture de bryophytes, notamment les mousses hypnacées, a également réduit le stress en tempérant les conditions microclimatiques et en conservant l'humidité du sol. Compte tenu de l'augmentation des épisodes de sécheresse prévue en raison du changement climatique, ces résultats plaident en faveur de stratégies de récolte partielle afin d'améliorer la régénération naturelle et la résilience des forêts, en mettant l'accent sur des approches de gestion intégrée qui combinent des mesures de croissance et des mesures physiologiques afin d'éclairer les pratiques sylvicoles adaptatives dans les écosystèmes boréaux.

Mots-clés : épinette noire, sapin baumier, composition isotopique stable, adaptation au changement climatique, aménagement forestier, sylviculture, procédé de régénération par coupe progressive uniforme

3.2 Abstract

Silvicultural practices could induce water stress in naturally regenerating conifer seedlings. Understanding their long-term physiological impacts is essential for developing resilient and sustainable forest management strategies under a changing climate. We evaluated the effects of regeneration methods representing a gradient of harvest intensity on water stress in naturally regenerated black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill) seedlings, 18 years after harvest in Canadian boreal forests. As a proxy for drought stress, we analyzed foliar carbon isotope composition ($\delta^{13}C$), an integrative measure of intrinsic water-use efficiency, from 180 seedlings sampled across four regeneration methods (clearcut, seed-tree, mini-strip shelterwood, unmanaged control). Treatments with the highest harvest intensities (clearcut and seed-tree) had significantly enriched $\delta^{13}C$ values compared to unmanaged forests, indicating greater physiological drought stress under open-canopy conditions. In contrast, partial harvesting maintained $\delta^{13}C$ levels similar to unmanaged forests, highlighting their potential in mitigating drought stress by preserving favorable microclimatic conditions. Seedling diameter was the strongest growth-related predictor of $\delta^{13}C$, indicating greater drought stress in larger seedlings. Bryophyte cover, notably feathermosses also reduced stress by buffering microclimatic conditions and conserving soil moisture. Given increasing drought events expected due to climate change, these findings may advocate for partial harvesting strategies to enhance natural regeneration and forest resilience, emphasizing integrated management approaches that combine growth and physiological metrics to inform adaptive silvicultural practices in boreal ecosystems.

Keywords: balsam fir, black spruce, climate change adaptation, forest management, shelterwood system, silviculture, stable isotope

3.3 Introduction

Natural regeneration can be a cornerstone of sustainable forest management in boreal ecosystems, particularly given the inherently low productivity and slow growth rates characteristics of these ecosystems (Kim et al., 2025; Marty et al., 2023). By promoting the establishment of native species, natural regeneration may support habitat preservation and enhances the resilience of boreal forest landscapes (Girona et al., 2023; Niemelä, 1999). The success of natural regeneration is shaped by both silvicultural practices and environmental stressors (Canuel et al., 2024; Montoro Girona et al., 2018). Understanding how these factors interact is increasingly important as climate change intensifies drought conditions in terms of severity and frequency, posing greater challenges to seedling survival and growth, as well as to adaptive silvicultural systems (D'Amato et al., 2023).

Clearcut and partial harvest (e.g. shelterwood) are the main silvicultural options to promote natural regeneration in boreal forests although clearcut is the most dominant (Kim et al., 2025; Kuuluvainen et al., 2012). Traditional clearcut methods increasingly lead to regeneration challenges by causing high soil disturbance, simplifying stand structure (Girona et al., 2023; Kim et al., 2021). The loss of vertical and spatial heterogeneity reduces seed sources, alters light and microclimate conditions, and limits the variety of microsites available for germination (Barrette et al., 2022; Kim et al., 2025; Lafleur et al., 2016). By entirely opening the canopy, clearcuts increase incoming solar radiation and wind speed, raising near-surface soil and air temperatures by 3–5 °C and reducing volumetric soil moisture by 10–30 % compared to intact stands, thereby exacerbating evaporative demand and seedling water stress (LeDuc & Rothstein, 2007). On the Clay Belt of Ontario–Québec, removing the transpiring canopy through clearcutting frequently raises the water table, promoting waterlogged organic layers and paludification that hinder black spruce regeneration (Renard et al., 2016). In contrast, silvicultural systems using partial harvest has emerged as a promising approach that seeks to emulate intermediate severity of natural disturbances such as insect outbreaks or windthrows occurring between stand-replacing fires (Aakala et al., 2023; Sylvie Gauthier, Kuuluvainen, Macdonald,

Shorohova, Shvidenko, Bélilse, et al., 2023; Subedi et al., 2023). Partial harvest limits water table rise and promotes growth response in residual trees, enhancing structural diversity and facilitating the regeneration of shade-tolerant species (Bose et al., 2023; Girona et al., 2016; Kim et al., 2025; Maleki et al., 2020; Moussaoui et al., 2020a; Noualhaguet et al., 2023; Pothier et al., 2003). Partial harvest retains sufficient overstory cover to buffer microclimatic extremes, reducing temperature fluctuations and conserving soil moisture (Pavlović et al., 2024).

Assessing drought stress in naturally regenerated seedlings after harvesting will be essential in the adaptation of silvicultural systems to face climate change, especially in boreal forests where frequent drought risks is expected (Chagnon et al., 2023; Seidl et al., 2017). From 1970-2020, about 43% of Canada's boreal forests have experienced a statistically significant rise in drought-induced tree mortality with trends accelerating since 2002 (Liu et al. 2023). Silvicultural treatments modify the forest structure providing major changes in the microclimatic conditions, potentially leading to increased water evapotranspiration in regenerated seedlings (Kerhoulas et al., 2020). For instance, studies in black spruce forests have shown that partial harvest on sites with deep organic layers has been associated with poor regeneration and post-harvest volume losses due to increased tree mortality, likely linked to increased water table and drought susceptibility (Bourgeois et al., 2004). On the other hand, redwood, typically confined to moist coastal environments, has demonstrated successful establishment in dry inland areas when planted following partial harvest, even under drought conditions (Kerhoulas et al., 2020). In Canada's red pine plantation, different canopy retention strategies significantly affected below-canopy evapotranspiration. Dispersed retention patterns increased evapotranspiration from understory vegetation and soil more than aggregated patterns, highlighting how altered structure changes microclimate and water fluxes (Bodo et al., 2022). However, none of these regeneration studies employed a large-scale experimental design (>400 m^2) or evaluated long-term effects (>5 years) across multiple silvicultural treatments.

To assess drought stress in plants, stable carbon isotope analysis has proven to be a valuable tool (Zhang et al., 2023). By measuring $^{13}C/^{12}C$ ratio in plant leaves,

researchers can infer intrinsic water-use efficiency and detect historical water stress experienced by plants (DesRochers et al., 2007). Under water-limited conditions, plants tend to exhibit reduced discrimination against the heavier carbon isotope (^{13}C) during photosynthesis, resulting in enriched foliar $\delta^{13}C$ values in plant leaves compared to the atmosphere (Ma et al., 2021). This method offers an integrative assessment of a plant's physiological responses to water availability over time (Namvar et al., 2024). Recent studies across diverse forest ecosystems including boreal, temperate, and tropical biomes have demonstrated that $\delta^{13}C$ can effectively capture physiological responses to both environmental stress and forest management practices (Brienen et al., 2011; Matteo et al., 2017; Namvar et al., 2024). Despite these new advances, there is a notable gap in understanding the long-term effects of silvicultural treatments on water stress in naturally regenerated conifer seedlings, particularly within boreal forests (Trouvé et al., 2021).

Our study aims to evaluate the impact of a gradient of silvicultural treatments ranging from uncut control to clearcut on water stress in naturally regenerated seedlings of black spruce and balsam fir, 18 years after treatment in even-aged black spruce stands. We hypothesized that silvicultural treatments will be positively correlated with water stress in seedlings through stomatal regulation. We predict that the silvicultural treatments with high harvest intensity, such as clearcutting and seed-tree, will result in more enriched $\delta^{13}C$ values, indicative of altered photosynthetic discrimination and enhanced water-use efficiency compared to partial harvest. Additionally, we predicted that black spruce would exhibit a stronger response in $\delta^{13}C$ relative to balsam fir due to more conservative stomatal regulation. Our study will be helpful for evaluating silvicultural options that not only promote natural regeneration but also enhance the adaptive capacity of boreal forests in the face of ongoing environmental and climate change.

3.4 Material and Methods

3.4.1 Study Area

Our study area is located in the natural, even-aged black spruce forests of the northern Saguenay-Lac-Saint-Jean and North Shore regions in Quebec, Canada, across two

distinct bioclimatic domains: the balsam fir-paper birch and the black spruce-feathermosses domains (Figure 4.1). The climate is subhumid subpolar, with a short growing period of 140 days (Rossi et al. 2011). The average yearly temperature hovers at 2.2°C and precipitation averages at 1 081 mm (Environment and Natural Resources Canada, 2022). The surface deposits consist in thick glacial tills, with rock outcrops becoming prominent on the crests of steep inclines (Robitaille & Saucier, 1998). The soil is primarily composed of humo-ferric podzols (Girona et al., 2017).

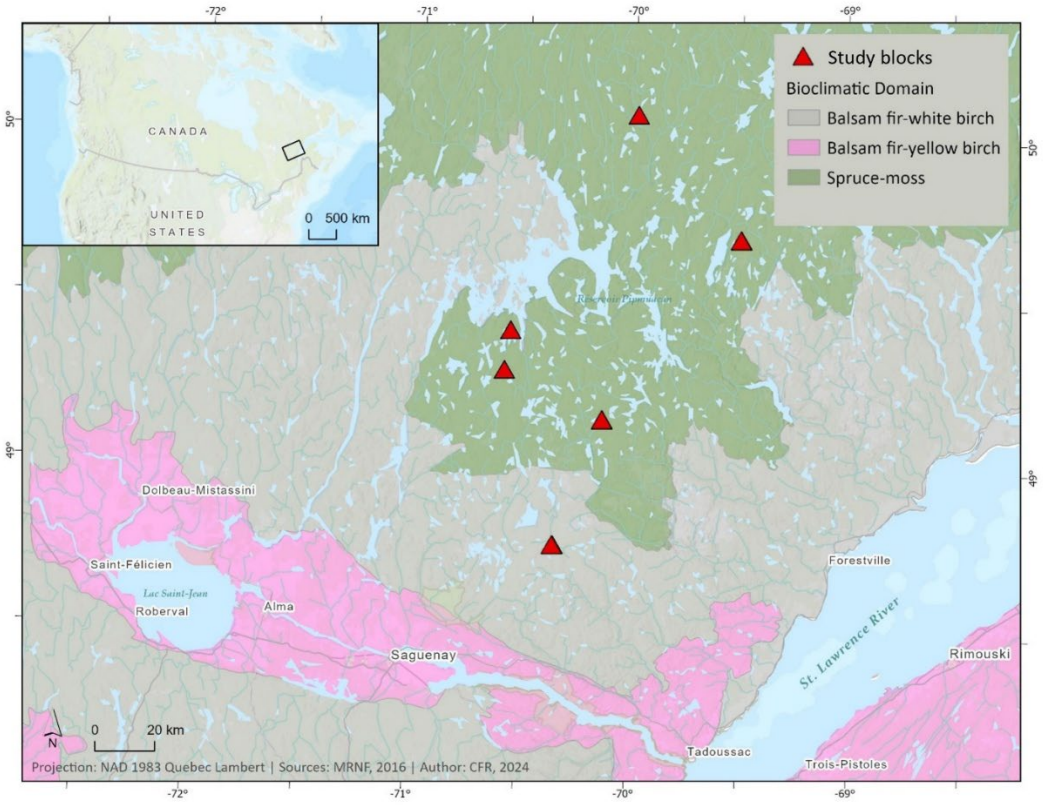

Figure 3.1
Location of the study blocks in the northern Saguenay-Lac-Saint-Jean and North Shore regions of Quebec, Canada.

3.4.2 Experimental design and sampling

The MISA experiment (Managing Innovative Silvicultural Alternatives) was established in 2003 by the Canadian Forest Service to investigate alternative silvicultural practices

to clearcutting in boreal forest management. The experimental design followed a fully randomized block design across six blocks (replicates), each located within mature, even-aged black spruce stands on upland sites in Eastern Canada (Figure 2). Each block contained four randomly assigned silvicultural systems associated to regeneration methods (clearcut, seed-tree, mini-strip shelterwood, and unmanaged). The mini-strip shelterwood treatment was further divided into two distinct microsite environments (harvest trails and residual strips) to capture within-treatment variability. This design resulted in a total of 30 experimental units:

(6 blocks × 4 treatments = 24 units) + (6 additional units from residual strips within mini-strip shelterwood).

To evaluate water stress in naturally regenerated seedlings, we established 180 circular microplots (4 m² each), systematically arranged to include three individuals of each species (black spruce and balsam fir) per environment in every block. Specifically, each experimental unit (3 hectares) contained six microplots (three per species), placed around individual seedling samples. Sampling for foliar carbon isotope analysis ($\delta^{13}C$), serving as a proxy for water stress, was conducted 18 years post-treatment, coinciding with a complementary regeneration survey (Kim et al., 2025; Larchevêque et al., 2011).

The black spruce stands were relatively homogeneous prior to silvicultural systems because of their shared fire history, a condition verified through dendrochronological dating (Girona et al., 2016). Study blocks were dominated by black spruce (96% in terms of stem count), with balsam fir (3%), trembling aspen (*Populus tremuloides* Michx; 1%), and paper birch (0.3%) as secondary species one year before cutting. Eighteen years after treatments, natural regeneration remained dominated by black spruce (present in 81% of plots, 28,376 seedlings/ha), though with notable shifts in species composition, followed by balsam fir (31% presence in our study plots, 8,091 seedlings/ha) and white birch (21% , 2,066 seedlings/ha), while other species such as *Larix laricina*, *Salix* spp., *Prunus pensylvanica*, *Sorbus americana*, *Populus*

tremuloides, *Amelanchier* spp., and *Alnus* spp. were minor species in terms of density and stocking (Kim et al., 2025).

3.4.3 Silvicultural systems

In our experimental design, three regeneration methods (clearcut, seed-tree, uniform shelterwood) were compared to an unmanaged forest as control were established in each study block (Figure 2). The clearcut treatment involved the complete removal of all merchantable trees that are above 9 cm of diameter at breast height (DBH) while protecting advanced regeneration, and no scarification was conducted. The seed-tree method had 15 m wider cut strips with 5 m wide intact residual strips (75% of removal). The uniform shelterwood method tested a novel variant termed mini-strip shelterwood with a harvest intensity of 50% of removal (Montoro-Girona, 2017). Mini-strip shelterwood was implemented by creating narrow residual strips of 5 m and harvested trails of 5 m wide. Unmanaged forests served as control areas with no harvesting. In 2004, spot scarification was applied to both the seed-tree and mini-strip treatments by creating 2 m² rectangular spots using a 10-ton excavator equipped with a 1 m³ bucket, following a spatial pattern adapted to each treatment, with an average scarified area of 1 296 $m^2\ ha^{-1}$ and 848 $m^2\ ha^{-1}$ for mini-strip and seed-tree respectively.

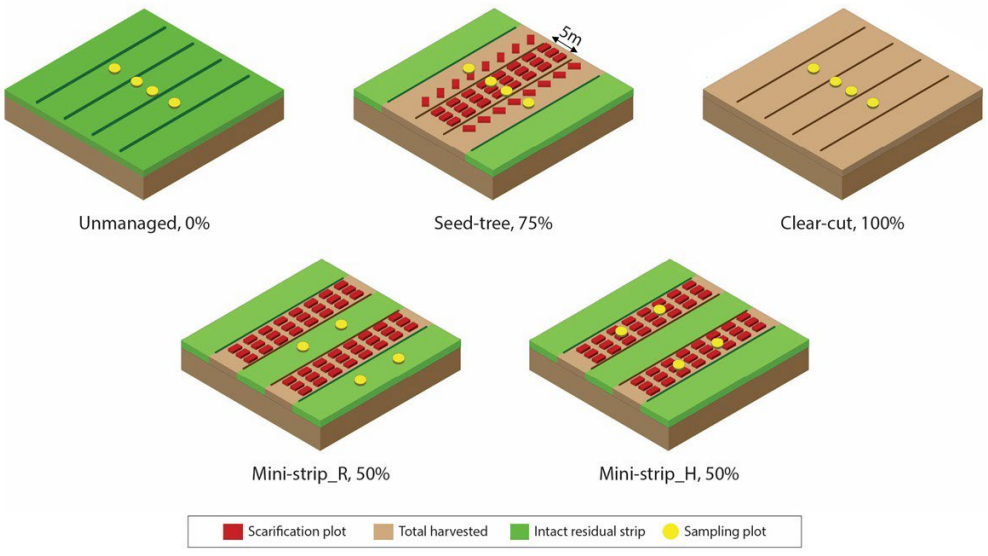

Figure 3.2
Spatial patterns of silvicultural systems and sampling plot distribution. Fully harvested areas and skid trails are depicted in brown, whereas intact residual strips are shown in dark green. Red rectangles indicate scarification spots (each 2 m²). Ministrip_R: Ministrip Residual strip; Ministrip_H: ministrip harvesting trail

3.4.4 Carbon isotope analyses ($\delta^{13}C$)

For the study of drought stress using ^{13}C discrimination, we collected fresh branch cuttings from black spruce and balsam fir seedlings across all sites. Shoots were collected from naturally regenerated seedlings growing in the harvested areas of three treatments (clearcut, seed-tree, mini-strip) and in the uncut areas of two treatments (residual strip of mini-strip and unmanaged forest), totaling 180 samples. To inhibit microbial activity and changes in stable isotope composition, the collected samples were promptly placed and preserved in a Styrofoam icebox cooled with ice packs. Samples were then freeze-dried, finely ground with a Brinkmann MM2 ball grinder (Brinkmann Instruments Ltd, Mississauga, ON, Canada), and homogenized before encapsulation in the GREMA lab (University of Québec in Abitibi-Témiscamingue) (Grosbois et al., 2017). The $^{13}C/^{12}C$ isotopic ratio was quantified using a Costech ECS 4010 Elemental Combustion System (Costech Analytical Technologies, Inc., Valencia, CA, USA), interfaced with a continuous flow Finnigan Delta Plus Avantage IRMS (ThermoFinnigan, Bremen, Germany) in the GEOTOP lab (University of Québec in Montréal). The relative abundance of ^{13}C in the foliage of seedlings was expressed as the carbon isotope composition ($\delta^{13}C$), in accordance with the equation 1:

$$\delta^{13}C=\frac{R1-Rs}{Rs} \; x \; 1000$$

where *R*1 and *Rs* denote the ratios of $^{13}C/^{12}C$ in the foliage sample and in the standard references, respectively. For calibration purposes, BMO, CS, and NBS 1575N were used as reference standards, and red clover served as the working standard. These standards exhibited carbon isotope compositions of −23.91‰, −12.5‰, −26.3‰, and −27.42‰, respectively, in relation to Pee Dee Belemnite.

We also conducted two inventories to assess seedling density, growth, and competitive interactions among shrubs (e.g., *Ericaceous* spp.), coniferous trees (e.g., *A. balsamea*), and deciduous trees (e.g., *Betula papyrifera* Marsh, *Salix* spp., *Prunus pensylvanica* L.f., *Sorbus americana* Marshall, *Populus tremuloides* Michx, *Amelanchier* spp., and *Alnus* spp.) using the same methodology as described in our previous study (Kim et al., 2025).

3.4.5 Microclimate monitoring and time-series analysis

In order to assess microclimatic effects, we deployed WatchDog® Series 1000 data loggers equipped with SMEC 300 soil moisture sensors from July 2021 to July 2022. Watchdog devices recorded hourly soil and air temperatures and volumetric soil moisture at 10 cm depth and air-temperature probes mounted 1 m above the forest floor. Logger data were downloaded monthly via HOBOware™ Connect and imported into R for processing. Although sensor inconsistencies and device damages (e.g., rodent browsing cords) precluded robust statistical comparisons among treatments, we identified and removed them. After filtering, treatment-specific time-series graphs were produced to illustrate the general trajectories of soil moisture depletion and thermal variation under differing harvest intensities.

3.4.6 Data analysis

Harvesting intensity effects on carbon isotope discrimination ($\delta^{13}C$) were assessed separately for black spruce and balsam fir as well as on the combined dataset (due to insignificant difference between the two species). For the combined dataset, differences among treatments were examined using one-way Welch's ANOVA, which does not assume homogeneity of variances. Pairwise comparisons were conducted with the Games–Howell post hoc test (Tukey adjustment) to account for unequal variances and sample sizes. For both conifer species, separate analyses were performed and estimated marginal means (± SE; standard error) were calculated for each treatment. Tukey's HSD groupings were used to identify statistically similar groups. To minimize site-related bias and improve the accuracy of treatment effect estimates, we excluded site 900 from the analysis, as this site was unusually wet (bog-type) and located in a different bioclimatic domain compared to the other five sites.

Univariate relationships between $\delta^{13}C$ and potential predictors including harvesting intensity (modeled as a categorical variable with control as the reference), seedling position (harvest trail vs. residual strip in minis-strip shelterwood), height, diameter (ground-level), terminal shoot length in the sampling year (Growth 2021), and age were evaluated using simple linear regression models. Model fit was assessed using adjusted R^2, and significance of individual predictors was determined based on p-values. A stepwise variable selection procedure was used to identify the most informative predictors for carbon isotope discrimination. This process resulted in a final multiple linear regression model in which $\delta^{13}C$ was regressed on harvesting intensity and diameter. Model adequacy was evaluated by examining the F-statistic, residual standard error, and adjusted R^2.

A principal component analysis (PCA) was performed on the 180 conifer seedlings using six variables (height, diameter, age, G2021 (growth in 2021: terminal shoot length), PTC (*Ptilium crista-castrensis*), and $\delta^{13}C$) to explore the multivariate structure of seedling performance. PCA was conducted using the FactoMineR package, which automatically scales continuous variables (with PTC, a binary variable, being treated in the same standardized framework). PCA results, including eigenvalues, variable loadings, and squared cosines (cos^2), were visualized using the factoextra package.

All statistical analyses were performed using R software version 3.6.0 (R Core Development Team, 2024). All tests were conducted at a significance level of $\alpha = 0.05$. Prior to analysis, assumptions of normality and homoscedasticity were verified using diagnostic plots.

3.5 Results

3.5.1 Effects of silvicultural systems on carbon isotope discrimination of conifer seedlings

Values of $\delta^{13}C$ differed significantly among silvicultural systems for both black spruce ($F = 3.9$, $p < 0.05$) and balsam fir ($F = 3.3$, $p < 0.05$). For black spruce, estimated marginal means ranged from -30.6 ± 0.3‰ in the control to -28.9 ± 0.3‰ in the clearcut (Figure 3). Pairwise comparisons for black spruce identified three groups: the control (–30.6‰), the intermediate residual strip of ministrip (–30.1‰) and harvested

trails in ministrip (–29.9‰), and the seed-tree (–29.3‰) and clearcut (–28.9‰). Both seed-tree (+1.2‰, $p < 0.001$) and clearcut (+1.5‰, $p < 0.001$) treatments produced significantly less negative $\delta^{13}C$ values relative to the control, whereas residual strips and harvested trails in mini-strip did not differ significantly from the control. In balsam fir, mean $\delta^{13}C$ values ranged from –30.7 ± 0.3‰ (Control) to –29.6 ± 0.4‰ (clearcut), indicating a 1.1‰ increase in $\delta^{13}C$ under the clearcut compared to the control.

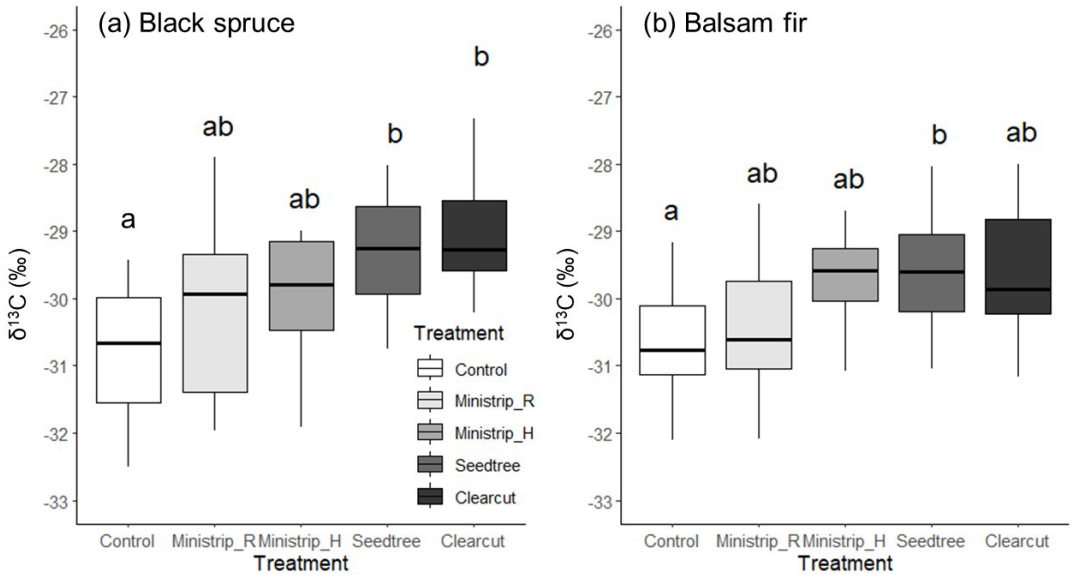

Figure 3.3
Foliar carbon isotopic composition ($\delta^{13}C$) for a) black spruce and b) balsam fir seedlings, 18 years after silvicultural systems. Box plots show the median, interquartile range (IQR), and whiskers indicating the range or 1.5×IQR. Means that differ significantly are noted with the different letter (a < b < c < d). Ministrip_R: Ministrip Residual strip; Ministrip_H: Ministrip Harvest trail.

For both conifer species combined, post-hoc tests revealed that the seed-tree (–29.6‰) and the clearcut (–28.9‰) exhibited significantly higher $\delta^{13}C$ values compared to the control (–30.6‰), with differences of +1.2‰ ($p < 0.001$) and +1.5‰ ($p = 0.001$), respectively (Table 4.1). Both position types in mini-strip shelterwood were statistically similar to the control. The interaction between tree species and harvesting intensity was not significant for $\delta^{13}C$, indicating black spruce and balsam fir responded similarly to our study treatments.

Table 3.1
Pairwise Games–Howell test results for carbon isotope discrimination ($\delta^{13}C$) of conifer seedlings (black spruce and balsam fir) among silvicultural systems. Ministrip_R: Residual strip of ministrip; Ministrip_H: Harvested trail in mini-strip.

Comparison	Estimate (‰)	95% CI	p-adj	Significance
Control vs. Ministrip_R	0.37	–0.62 to 1.37	0.821	ns
Control vs. Ministrip_H	0.78	–0.05 to 1.61	0.077	ns
Control vs. Seed-tree	1.2	0.43 to 1.96	<0.001	***
Control vs. Clearcut	1.45	0.47 to 2.42	0.001	***
Ministrip_R vs. Ministrip_H	0.40	–0.56 to 1.36	0.744	ns
Ministrip_R vs. Seed-tree	0.82	–0.08 to 1.73	0.089	ns
Ministrip_R vs. Clearcut	1.07	–0.004 to 2.15	0.051	ns
Ministrip_H vs. Seed-tree	0.42	–0.30 to 1.14	0.459	ns
Ministrip_H vs. Clearcut	0.67	–0.27 to 1.61	0.260	ns
Seed-tree vs. Clearcut	0.25	–0.643 to 1.14	0.921	ns

3.5.2 Driving factors in water stress of the conifer seedlings

When silvicultural treatment was modeled as a categorical variable (with control as the reference), it significantly influenced $\delta^{13}C$ ($R^2 = 0.22$, $p < 0.001$) (Figure 4). Relative to the control, the seed-tree treatment increased $\delta^{13}C$ by 1.20‰ (coefficient estimate = 1.2, $p < 0.001$) and the clearcut treatment by 1.45‰ (Estimate = 1.45, $p < 0.001$). The

harvested trails in mini-strip shelterwood were associated with a moderate increase in $\delta^{13}C$ (estimate = 0.78, $p < 0.05$), whereas the effect of residual strip of mini-strip was similar to the control (estimate = 0.37, $p > 0.05$). A separate regression of $\delta^{13}C$ on the spatial position (residual strip vs harvest trail) of seedlings in the mini-strip treatment revealed a significant negative effect of harvested trails ($R^2 = 0.18$, $p < 0.001$), indicating that seedlings in the residual strips exhibited $\delta^{13}C$ values approximately 0.98‰ lower than those located in harvest trails.

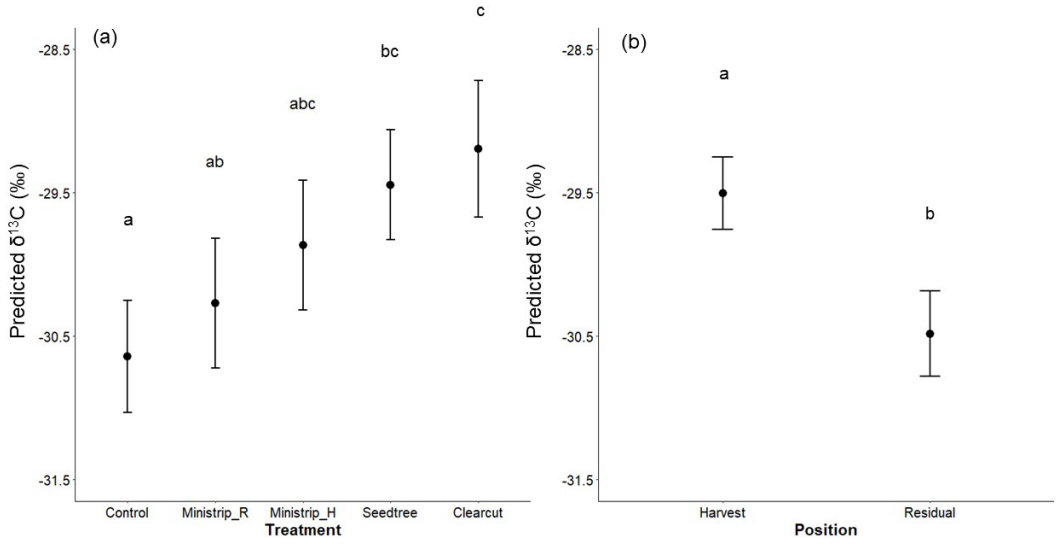

Figure 3.4
Predicted $\delta^{13}C$ values by silvicultural treatment and spatial position. Predicted mean $\delta^{13}C$ values (with 95% confidence intervals) from one-way ANOVA models are shown for (a) treatment (control, mini-strip residual strip, mini-strip harvest trail, seed-tree, clearcut) and (b) position (harvest trail, residual strip). Tukey's HSD group letters indicate statistically similar groups ($p < 0.05$).

Among growth metrics, $\delta^{13}C$ increased with both height and ground-level diameter (Figure 4.5). The height model ($\delta^{13}C \sim$ Height) produced an estimate of 0.01 ($R^2 = 0.21$, $p < 0.001$), while the diameter model yielded a slightly stronger association ($R^2 = 0.23$, $p < 0.001$), indicating that larger seedling diameters had higher $\delta^{13}C$ values. For instance, a seedling with a diameter of 23 mm and height of 103 cm exhibited a $\delta^{13}C$ value of –28.02‰, compared to a smaller individual with a diameter of 10 mm

and height of 49 cm, which had a much lower δ¹³C of –31.88‰. Similarly, δ¹³C increased with terminal shoot length (growth 2021) (R^2 = 0.11, $p < 0.001$), though it accounted for a more modest proportion of the variance. A notable example is a seedling with a terminal shoot length of 29.4 cm and δ¹³C of –28.39‰, versus one with a 1 cm shoot and δ¹³C of –30.12‰. Finally, seedling age was also positively related to δ¹³C (R^2 = 0.06, $p < 0.01$), potentially suggesting that older seedlings tended to exhibit higher δ¹³C values, albeit with limited explanatory power (Figure 5). For instance, a 26-year-old pre-established seedling recorded a δ¹³C value of –28.26‰, while a 4-year-old post-harvest seedling showed –31.96‰.

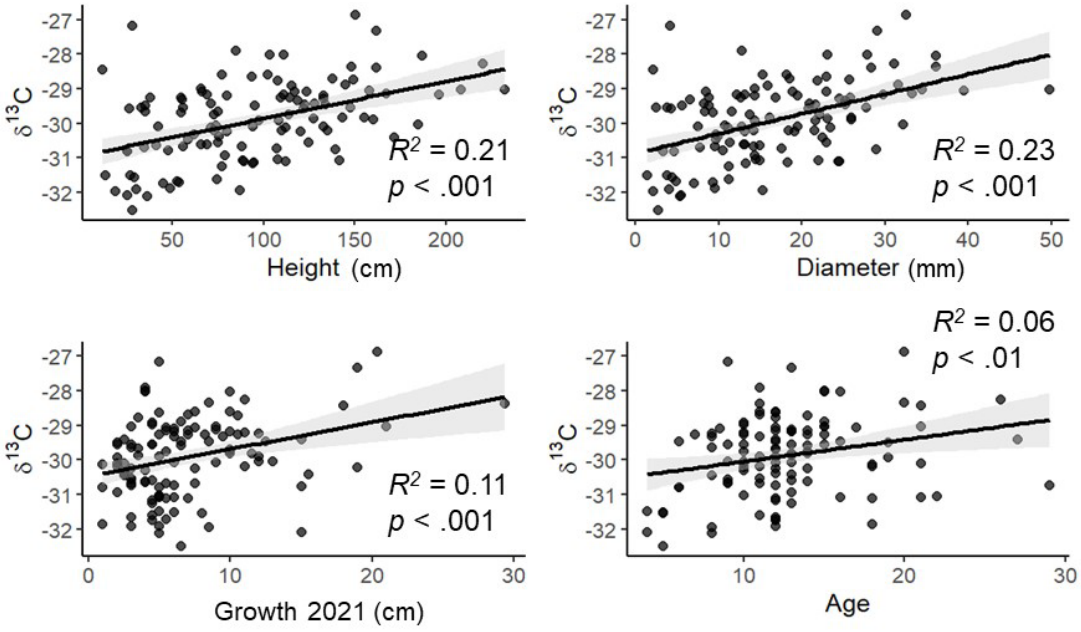

Figure 3.5
Relationships between δ¹³C and height, diameter, growth 2021 (terminal shoot length in the sampling year 2021), and age for conifers seedlings

Prior to the multiple linear regression analysis, a stepwise variable selection procedure was employed to identify the most informative predictors of carbon isotope discrimination (δ¹³C) among candidate variables. In this model, the intercept was estimated at –31.1 (SE = 0.21, $p < 0.001$), representing the baseline δ¹³C under reference conditions (Table 4.2). Harvesting intensity had a significant positive effect

on $\delta^{13}C$ (Estimate = 0.01, SE = 0.003, t = 3.6, $p < 0.001$), indicating that an increase of one unit in harvesting intensity was associated with an approximate 0.011‰ increase in $\delta^{13}C$. Similarly, diameter emerged as a significant predictor (Estimate = 0.04, SE = 0.01, t = 3.8, $p < 0.001$), suggesting that larger seedling diameters were linked to higher $\delta^{13}C$ values. Overall, the model explained 29.3% of the variation in $\delta^{13}C$ and was highly significant ($F_{2,105} = 21.7$, $p < 0.001$). Our model determined that harvest intensity and seedling diameter are stronger influencing factors of carbon isotope discrimination in naturally regenerated conifer seedlings.

Table 3.2
Multiple linear regression predicting $\delta^{13}C$ (‰) in conifer seedling.

Predictor	Estimate (‰)	Std. Error	t value	p-value
(Intercept)	−31.12	0.213	−146.33	**<0.001**
Harvesting intensity	0.01	0.003	3.6	**<0.001**
Diameter	0.04	0.011	3.78	**<0.001**

Adjusted $R^2 = 0.28$; VIF = 1.16; $F(2,105) = 21.7$; $p < 0.001$. Residual standard error = 0.97 (df = 105).

The first principal component (PC1) accounted for 45.3% of the total variance, while the second component (PC2) explained an additional 20.6%, yielding a cumulative variance of 65.9% across the two axes (Figure 6). The first three components together explained 80.5% of the variance. PC1 was dominated by seedling size, with height (loading = 0.92, $\cos^2 = 0.85$) and diameter (loading = 0.92, $\cos^2 = 0.85$) contributing strongly. The $\delta^{13}C$ also exhibited a moderate association with PC1 (loading = 0.66, $\cos^2 = 0.43$). In contrast, PC2 was primarily influenced by temporal and cover variables, with age (loading = 0.53, $\cos^2 = 0.28$), G2021 (loading = –0.59, $\cos^2 = 0.35$), and PTC (loading = 0.7, $\cos^2 = 0.49$) being the predominant contributors. PC2, which

explained an additional 14.6% of the variance, was further influenced by G2021 and PTC, although to a lesser extent than PC1 and PC2 (Figure 6).

The treatment ellipses in the PCA biplot (Figure 6) represent 95% confidence intervals around seedling group centroids, illustrating the variability in multivariate trait space. While most treatments largely overlap, clearcut and seed-tree treatments show greater dispersion, with several seedlings falling outside the central cluster. These outliers align with higher $\delta^{13}C$ values (i.e., less negative, indicating greater water-use efficiency and water stress) and greater terminal shoot length (G2021), indicating bigger physiological responses under high-intensity harvests. In contrast, seedlings from partial harvest and control treatments cluster more tightly, reflecting more uniform growth and stress conditions in buffered microclimates.

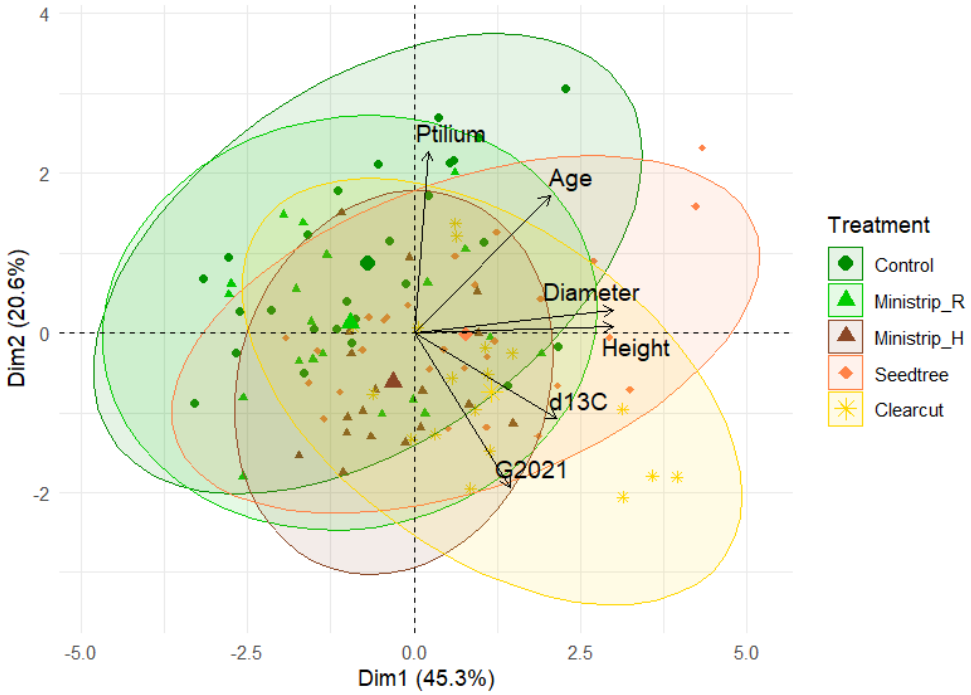

Figure 3.6
Principal component analysis (PCA) biplot of growth attributes, moss cover, and carbon isotope discrimination in naturally regenerated conifer seedlings 18 years after silvicultural systems.

In addition to these treatment and positional effects, microclimatic conditions varied markedly among harvest regimes (Figure S1). During the growing season (May to August), hourly air temperatures were broadly similar across treatments, diverging only in winter when clearcut plots exhibited slightly higher minimum temperatures. Soil temperature at 10 cm depth fluctuated more under clearcuts throughout the growing season and remained significantly warmer in winter compared to both seed-tree and shelterwood plots. Soil moisture was consistently highest in shelterwood, reflecting moisture buffering from retained canopy (lower evaporation) and reduced stand-level transpiration relative to control. Control plots tended to show lower growing-season moisture, possibly due to higher transpiration demand, while clearcuts displayed greater variability often recharged after snowmelt but prone to sharp drawdowns during warm, dry spells.

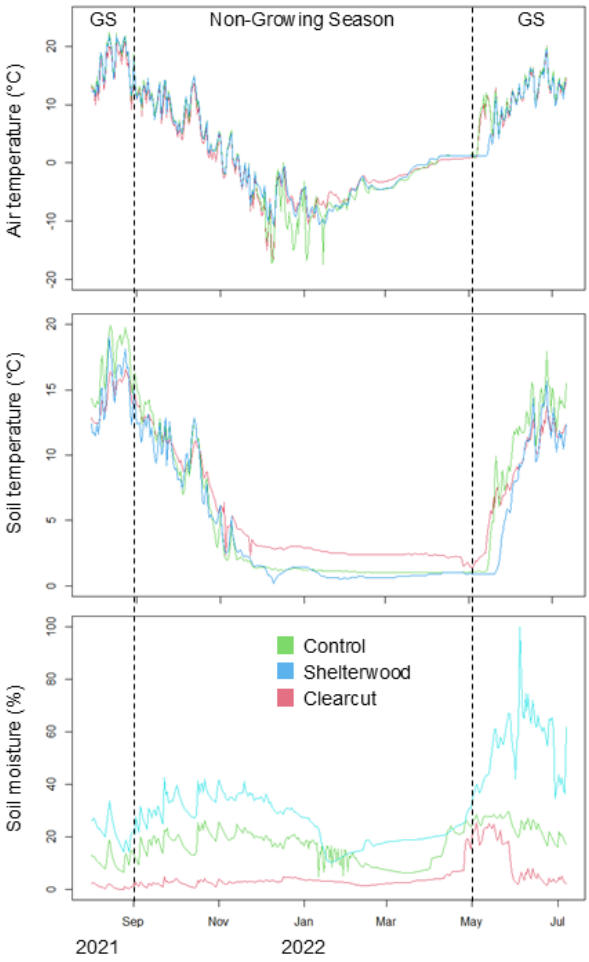

Figure 4.7.
Hourly microclimatic and soil moisture dynamics under silvicultural treatments in Canadian boreal forests from July 2021 to July 2022.

3.6 Discussion

3.6.1 Effects of Silvicultural systems on $\delta^{13}C$ and Water Stress of Conifer Seedlings

Our study highlights the potential mid-term effects along a gradient of harvest treatments on drought stress in naturally regenerated conifer seedlings using the foliar carbon isotope composition ($\delta^{13}C$). Our results evidenced how silvicultural systems still influencedwater relations in conifer seedlings after 18 years. Clearcut and seed-tree treatments increased $\delta^{13}C$ values, indicating elevated intrinsic water-use efficiency and stomatal closure indicative of physiological water stress compared to unharvested controls. This finding is consistent with previous studies in boreal forests

following clearcutting (≥50 years), that have shown that changes in microclimate, particularly near forest edges, led to greater exposure to heat and evaporative stress (Lunde et al., 2025). Higher $\delta^{13}C$ values observed in clearcut and seed-tree treatments reflect enhanced water-use efficiency driven by reduced canopy cover, increased solar radiation, and higher vapor pressure deficits (VPD), all of which exacerbate seedling water stress through augmented transpiration demands (Puchi et al., 2024; Price et al., 2013). Therefore, our findings are consistent with previous studies reporting elevated $\delta^{13}C$ values following high harvest intensity (>75% removal) in temperate and boreal forests, confirming these management approaches can significantly intensify physiological stress in seedlings under drought conditions (Brienen et al., 2011; Zhang et al., 2023).

In contrast, regeneration methods using partial harvests such as mini-strip shelterwood displayed intermediate $\delta^{13}C$ values that were not significantly different from those of unmanaged controls. This intermediate harvest intensity (50%) maintains a sufficient canopy cover that protects seedlings from microclimatic extremes (Moussaoui et al., 2020b; Parker & Dey, 2008). Partial canopy cover regulates surface temperature fluctuations, minimizes soil moisture loss, and moderates wind speed, thereby reducing evaporative stress and improving conditions for early seedling establishment of shade-tolerant species (Drössler et al., 2017; Lavoie et al., 2012; Montoro Girona et al., 2023). Previous studies in boreal forests have consistently demonstrated that partial harvesting promoted higher soil moisture retention, decreased transpiration stress, and supported better growth and physiological functioning of regenerating seedlings compared to clearcutting (Bescond et al., 2011; Maleki et al., 2020). Furthermore, partial harvest can maintain biodiversity, facilitates more balanced forest regeneration, and enhances forest resilience to drought, pests, and climate extremes, aligning with adaptive forest management objectives under anticipated climate change (D'Amato et al., 2023; Girona et al., 2023; Kim et al., 2025; Lavoie et al., 2021).

Conifer species exhibit varying degrees of drought tolerance, influenced by differences in root architecture, leaf morphology, and xylem anatomy (Boucher et al., 2020).

Previous research suggested that jack pine (*Pinus banksiana* Lamb) had a deeper root system, smaller needle area, and lower specific conductivity, allowing it to postpone dehydration and recover stomatal function better than black spruce, which suffered from higher needle leakage and incomplete stomatal recovery (Blake & Li, 2003; Pajares et al., 2025). In genus like *Picea*, *Abies*, and *Pinus*, traits such as torus thickness and pit chamber depth influence embolism resistance, indicating that greater wood density and reinforced tracheid walls were also associated with higher drought resistance (Hacke & Jansen, 2009). Finally, black spruce and balsam fir seedlings showed no significant differences in $\delta^{13}C$ responses across silvicultural systems, suggesting similar long-term response to silvicultural systems over nearly two decades contrary to our expectations. This convergence could be attributed to similar limitations in soil moisture availability and their rooting strategies (e.g., adventitious rooting), especially in canopy-opening disturbances from harvesting, which increase solar radiation and wind, leading to desiccation of the moss and litter layer (Bourgeois et al., 2004; Krause et al., 2009). Previous study showed similar result that despite ecological and structural differences, balsam fir and black spruce showed similar sap flow patterns driven mainly by vapor pressure deficit and solar radiation, with minimal influence from soil moisture, even during drought (Oogathoo et al., 2020). These findings highlight the complexity of seedling drought response in boreal conifer seedlings and suggest that similar $\delta^{13}C$ values across species may reflect convergent stomatal regulation under comparable post-harvest environmental conditions, rather than differing physiological mechanisms. However, further research is needed to disentangle the roles of rooting depth, xylem anatomy, and microclimatic adaptation in shaping species-specific drought resilience under ongoing climate change.

3.6.2 Driving factors in water stress of the conifer seedlings

Our analyses demonstrated significant correlations between growth traits (diameter and height) and foliar $\delta^{13}C$, with seedling diameter emerging as the best predictor in the multiple regression model. The stronger relationship of diameter to $\delta^{13}C$ may indicate that larger seedlings experience greater physiological water stress under conditions of limited soil moisture or increased evapotranspiration demand due to their larger leaf areas and biomasses (Ismael et al., 2022). Height and age also positively

correlated with $\delta^{13}C$, albeit with slightly weaker predictive power. In our study, seedlings in the clearcut and seed-tree treatments were notably larger and exhibited more enriched $\delta^{13}C$ values compared to those in the partial harvest and control treatments, indicating a potential interaction between growth vigor and water-use efficiency under intensive post-harvest conditions. This aligns with the previous study that black spruce had strong negative correlations between height growth and $\delta^{13}C$, suggesting that faster-growing trees had lower $\delta^{13}C$ values (Johnsen et al., 1999). In *Quercus aquifolioides*, foliar $\delta^{13}C$ values also increased with tissue age and altitude, reflecting adjustments in water-use efficiency along environmental gradients, while in *Pinus resinosa*, $\delta^{13}C$ enrichment with canopy height was primarily attributed to variations in light availability (Berry et al., 1997; Li et al., 2009). Therefore, interpreting $\delta^{13}C$ in regenerating seedlings requires careful consideration of growth stage and size, as physiological responses to drought and microclimate may vary substantially across developmental trajectories.

Accordingly, relying solely on $\delta^{13}C$ or individual growth features may not fully represent seedling water stress or water use efficiency. The $\delta^{13}C$ primarily reflects stomatal regulation over time and does not capture short-term or non-stomatal mechanisms (e.g., changes in mesophyll conductance or hydraulic conductivity), which also influence water-use efficiency (Ma et al., 2021, 2023). A study on eight tree species suggested that accurate interpretation requires an integrative approach that combines physiological metrics ($\delta^{13}C$) with growth data, such as evaluating $\delta^{13}C$ values at defined growth stages or specific size classes (Vadeboncoeur et al., 2020). Comparing $\delta^{13}C$ across seedlings at a standardized height (e.g., comparing among 30 cm height seedlings) or diameter (e.g., at 1 cm ground-level diameter seedlings) could provide clearer insights into water stress responses associated specifically with physiological maturity or resource acquisition strategies (Johnsen et al., 1999). Researchers found that $\delta^{13}C$ measured from mid-rotation trees correlated strongly with modeled water stress, emphasizing the need for size-standardized sampling for reliable interpretation (Fischer & du Toit, 2019). Deciduous seedlings (*Quercus* spp.) also displayed distinct $\delta^{13}C$ values and biomass allocation patterns under varying light and water conditions,

yet achieved comparable overall performance, underscoring the importance of standardizing seedling size when comparing water-use strategies across species (Espelta et al., 2005). This combined analysis enhances predictive accuracy by clarifying whether variations in $\delta^{13}C$ reflect genuine physiological adaptations to drought or merely differential resource acquisition and competitive interactions among seedlings.

Bryophytes regulate soil moisture and microclimatic stability by buffering temperature extremes and reducing evaporative loss, thereby indirectly supporting seedling establishment and growth under stressful conditions (Glime, 2024). Our results revealed that the presence of the feathermosses exhibited a moderate relationship with $\delta^{13}C$. This could be explained because *feathermosses* play a dominant role in nitrogen input among forest mosses, supporting seedlings indirectly through nitrogen cycling, which may correlate with increased photosynthesis resulting in enriched $\delta^{13}C$ in plant tissues (Darnajoux et al., 2024; DesRochers et al., 2006). More actively, a 10-year experiment demonstrated that moss transplantation significantly enhanced soil properties, foliar nutrients, and jack pine growth, indicating its effectiveness in facilitating the transition from open-canopy lichen woodland to a more productive forest ecosystem. Therefore, integrating moss covers and surveys, particularly *feathermosses* in black spruce stands, into assessments of seedling water stress can enhance our understanding of how bryophyte-mediated microclimate buffering and nitrogen inputs influence seedling physiology.

3.6.3 Management Implications

Our findings carry relevant implications for boreal forest management, especially under future climate scenarios characterized by more frequent and severe droughts. Clearcut and seed-tree harvesting significantly altered forest structure and microclimate with broadly opened canopy, affecting water stress in regenerating seedlings. These findings align with existing literature demonstrating long-term effects of clearcutting include reduced structural diversity, which can lead to lower moisture retention and habitat buffering, making ecosystems more susceptible to drought and temperature extremes (Thompson et al., 2003). Prolonged drought periods can lead

to substantial reductions in forest productivity and increased tree mortality rates, particularly among drought-sensitive species, for instance, studies have shown that drought-induced water stress has been a major contributor to widespread tree mortality and growth decline in the western Canadian boreal forests (Cardoso et al., 2025). Thus, despite the operational efficiency of clearcutting, this method may pose vulnerability for natural regeneration under projected climatic conditions (Girona et al., 2023). This underscores the necessity for adaptive silvicultural strategies that enhance forest resilience to water stress in the face of climate change (Achim et al., 2021; D'Amato et al., 2023) as well as a better integration of water resources into forest management (Grosbois et al., 2023).

Accordingly, our results support partial harvest, such as the mini-strip shelterwood system, as a strategy to mitigate drought stress. These methods preserved 50% of the canopy to buffer microclimatic extremes, thereby maintaining soil moisture, reducing wind and temperature fluctuations, and moderating overall evaporative stress (Gao et al., 2024; Lavoie et al., 2012). Such outcomes align with findings that seedlings such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and coast redwood in inland northern California exhibit higher water potential, greater stomatal conductance, faster growth, and lower drought mortality after partial harvesting compared to unmanaged forests (Kerhoulas et al., 2020). Uniform shelterwood systems in sub-boreal British Columbia also moderated minimum temperatures and reduced frost frequency compared to clearcuts, enhancing regeneration success in Douglas-fir (Sagar et al., 2010). Partial harvest on moisture-limited sites provides immediate and medium-term benefits for remaining trees in terms of drought resilience (Montwé et al., 2022). Similarly, in European boreal forests, partial harvest has been associated with reduced canopy mortality and improved stand stability during drought events (Lindner et al., 2010). Thus, partial harvest systems can enable successful establishment of species typically limited by drought, by creating favorable microsites through moderated environmental conditions.

In practice, forest managers can use easily observed stand and seedling attributes as proxies for the $\delta^{13}C$ signal. Foresters can use small soil cores to assess organic-layer

thickness, color and texture (Jia et al., 2017; Roudier et al., 2015). For example, darker, fine-textured humus indicates higher moisture retention (Stutter & Richards, 2012). Simple field tests such as pH strips in the mineral horizon and portable sodium-selective electrodes or colorimetric kits in the organic layer can distinguish well-buffered, moist patches (characterized by darker, fibric moss layers, neutral pH and elevated Na^+) from drier, high-stress microsites (lighter, coarser litter, lower Na^+ and more acidic mineral soil) (Anthony Federer & Hornbeck, 1985; Caldwell et al., 2005).

Because our July-August fresh branch samples integrate only the spring to mid-summer window, managers should complement these proxies with periodic soil-moisture monitoring and visual checks for seedling wilting later in the season, especially along clearcut edges and south-facing slopes where evaporative demand peaks. Protecting partial feathermoss mats and the intact organic layer during harvest will also preserve natural moisture reservoirs and support consistent stomatal function. By weaving together canopy-retention guidelines, seedling-size thresholds, targeted soil testing, and seasonal field observations, silvicultural prescriptions may shift from reacting to drought impacts toward proactively fostering seedling vigor and long-term resilience in boreal forests.

3.7 Conclusion

Our assessment demonstrated that clearcut and seed-tree harvesting significantly elevate physiological water stress in naturally regenerated boreal conifer seedlings even 18 years after harvest while partial harvest significantly showed less enriched water stress. In our study, harvest intensity and seedling diameter emerged as strong predictors of water stress, with high harvest intensities and larger seedlings experiencing greater stress. Partial harvest buffered understory microclimates by retaining canopy cover that reduces soil temperature extremes and conserves soil moisture through shading and moss retention. These moderated conditions could help maintain more stable water availability at the rooting zone, preventing the chronic stomatal closure and elevated $\delta^{13}C$ values observed under open-canopy treatments. Ultimately, our research underscores that regeneration methods using partial harvesting such as uniform shelterwood provides a promising, silvicultural alternative

to conventional clearcutting, significantly enhancing long-term boreal forest resilience under anticipated climate stressors.

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4. GENERAL CONCLUSION

The three chapters of this thesis together reveal a multifaceted portrait of boreal forest regeneration under a gradient of silvicultural regimes, weaving above- and below-ground processes to offer actionable insights to adapt partial harvest as silvicultural option for ecosystem-based management.

Integrating seedlings, soil, and physiological insights reveals the complex, multi-scale processes by which silvicultural systems shape boreal forest regeneration. Across chapters (II, III, IV), shelterwood systems consistently showed contrasting differences with clearcutting and these results may help us to find sustaining conifer regeneration, soil health, and seedling resilience under drought. Furthermore, the efficacy of silvicultural systems hinges on natural regeneration success, legacy effects in soil microbiomes, and the modulation of water stress through canopy and ground-cover interactions.

Natural Regeneration Responses. The natural regeneration chapter revealed obvious contrasts between clearcut and shelterwood systems in regenerating black spruce and balsam fir seedlings. Clearcutting created an open microsite environment favoring pioneer species such as white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and ericaceous shrubs, but presenting obstacles for shade-tolerant conifers. The fluctuations in soil temperature, reduced moisture retention, and greater evapotranspiration rates could contribute to poor seedling survival and uneven regeneration in clearcut area (Hynes & Germida, 2012; Kohout et al., 2018b). In contrast, silvicultural systems using partial harvest maintained residual stands that buffered microclimatic extremes, moderated light conditions, and promote seed dispersal. These residual canopy elements produced more diverse understory microclimate, supporting seedling densities nearly threefold higher than that of clearcuts. This aligns with the previous study in temperate mixedwood stands that the irregular shelterwood system was also suggested as an alternative to clearcutting to achieve compositional and structural objectives stands by favoring late-successional conifers (e.g., red spruce and balsam fir) with the three times greater seedling densities than clearcut (Raymond & Bédard, 2017). In another study, retention of

overstory trees also created a heterogeneous canopy mosaic that buffered microclimatic extremes, thereby enhancing conifer seedling recruitment (Messier et al., 1999; Ruel et al., 2013). However, regeneration outcomes varied by treatment type and site conditions: harvested trails with spot scarification in partial cuts frequently exhibited higher seedling densities than residual strips, underscoring the importance of spatial configuration and gap size in managing regeneration microsites (Bose et al. 2014).

Key drivers behind these regeneration patterns included seedbed quality (mineral soil exposure vs. organic layer), ground cover type (e.g., feathermosses vs lichen), and competition from ericaceous shrubs (e.g., *Kalmia angustifolia*, *Rhododendron groenlandicum*;). In another study in Eastern Canada, scarification and experimental moss transplantation improved seedbed conditions, seedling establishment markedly increased, suggesting that active microsite control can enhance natural regeneration after partial harvests (Gao et al., 2023; Simard et al., 2021). These findings underscore that while partial harvest and microsite enhancements can significantly improve conifer regeneration, site-specific limitations such as intact organic layers and competing vegetation still constrain recruitment, highlighting the need for tailored silvicultural interventions to optimize natural regeneration outcomes.

Soil Ecosystem Legacies and Microbial Dynamics. After nearly two decades of recovery, rhizosphere microbial communities beneath black spruce in both clearcut and partial cut (mini-strip shelterwood only in soil microbial chapter) stands showed remarkable stability, contrary to our first hypothesis that partial cuts would foster greater microbial diversity through increased resource heterogeneity. In general, partial harvest maintains soil physicochemical integrity and microbial networks critical to nutrient cycling (Thacker & Quideau, 2021). Partial harvest also preserves litter inputs and moderate soil compaction, enabling ectomycorrhizal taxa and nitrogen-fixing bacteria to persist at levels comparable to unharvested controls (Hartmann et al., 2012). These symbionts enhance seedling nutrient uptake and drought tolerance, effectively linking soil biodiversity to regenerative success (Policelli et al., 2020; Sanhueza et al., 2024). On the other hand, clearcuts often provoke declines in soil

organic carbon and pH shifts that favor fast-growing saprotrophs while eroding ectomycorrhizal richness (Bell-Doyon et al., 2022). However, long-term studies do not always confirm these divergent trajectories. Our study's unexpected resilience likely may reflect the site's unique history of no prior harvesting disturbances (natural forests), as well as the time after silvicultural treatment (18-19 years). Similar patterns have been documented in the northeastern Canadian boreal forests. In 156 conventionally clearcut stands of the Eastern Canadian boreal forest, maintained high bacterial richness and strong microbial activity even under low soil organic matter, supporting key ecosystem functions despite stand-replacing anthropogenic disturbances (Giguère-Tremblay et al., 2020). Furthermore, in northern Alberta, neither partial nor clearcut harvesting produced lasting changes in microbial biomass or community structure within the forest floor five years after harvest, highlighting a testament to microbial resilience driven by minimal soil disruption and rapid natural vegetation recovery after silvicultural intervention (Hannam et al., 2006).

Despite overall recovery trends in soil health, both microbial communities and soil physicochemical properties retain clear footprints of past harvest. Two decades after treatment, the rhizosphere continues to reflect whether a stand was clearcut or partially harvested, particularly in the balance of symbiotic fungi and nitrogen-fixing bacteria that underpin nutrient uptake and growth. These indicator groups may contribute to explain why seedlings in different treatments diverge in size and vigor. Sites with higher populations of N-fixers often show boosted fertility and growth rates (Hayat et al., 2010), even in more exposed clearcut areas. Similarly, subtle shifts in the organic horizon's chemistry such as variations in base saturation, calcium, potassium, and magnesium track closely with changes in dominant bacterial phyla, reinforcing that soil nutrients and microbe assemblages co-evolve. For example, reduced potassium and magnesium levels correspond with declines in Acidobacteriota but favor Proteobacteria, shaping the broader bacterial landscape in the seedling rhizosphere (Xie et al., 2022). Enzyme activity profiles further attest to these legacies, as patterns of cellulase, phosphatase, and protease activity align with zones of high microbial diversity and healthier seedling growth.

Taken together, these persistent soil signatures demonstrate that silvicultural systems leave lasting impacts beyond soil disturbances such as skid trails. They affect the belowground microbial networks essential for forest recovery. Understanding and managing these microbial indicators is crucial for developing silvicultural systems in order to promote long-term ecosystem resilience, rather than resetting the trajectory of natural regeneration (Policelli et al., 2020).

Water Stress on Conifer Seedlings. Water availability is a critical factor shaping seedling establishment and survival in post-harvest environments, particularly under increasing climatic variability (Kerhoulas et al., 2020). Assessing physiological responses to water stress can therefore offer valuable insights into how different silvicultural systems affect regeneration dynamics over the long term. In our study, seedlings from clearcut plots consistently exhibited enriched $\delta^{13}C$ values, reflecting chronic stomatal closure in response to elevated evaporative demand (Namvar et al., 2024). Notably, $\delta^{13}C$ enrichment was positively correlated with harvesting intensity, indicating that greater canopy removal led to higher $\delta^{13}C$ values. This pattern aligns with previous findings showing that $\delta^{13}C$ increases with canopy height and light availability, conditions typically associated with reduced stomatal conductance and enhanced water-use efficiency (Li & Zhu, 2011). Such responses have been observed across both conifer and deciduous species (e.g., Korean pine and Mongolian oak) in a temperate forest, suggesting that canopy-opening disturbances like harvesting may indirectly drive $\delta^{13}C$ enrichment in regenerating vegetation (Li & Zhu, 2011).

Partial harvest, by retaining 50% basal area in the mini-strip shelterwood, effectively recreated the shading and wind-break functions of intact stands (Montoro Girona et al., 2019). This canopy retention intercepted solar radiation and attenuated wind, leading to lower daytime soil temperatures and reduced direct evaporation (Wolken et al., 2016). The result was a microclimate that allowed seedlings to keep stomata more open, sustaining gas exchange and carbon assimilation without incurring excessive water loss (Powers et al., 2009).

Beyond broad treatment effects, two key microsite factors modulated seedling water use strategies. First, seedling size correlated positively with $\delta^{13}C$ (larger saplings exhibited higher isotopic enrichment), reflecting their greater transpiration demand and hydraulic challenges in all treatments. Second, ground-cover composition, specifically feathermoss mats dominated by *Ptilium crista-castrensis* maintained microsite moisture. Seedlings rooted in thick bryophyte layers showed $\delta^{13}C$ values lowered compared to adjacent mineral-soil patches, highlighting the role of moss in dampening drought stress. Previous study also shows that soils under *Ptilium crista-castrensis* have higher moisture content and greater intensity of podzolization compared to those under other moss species, evidenced by thicker Ae horizons and higher Fe and Al accumulation in the Bf horizon (Carter & Arocena, 2000). This supports the role of bryphyte in retaining water and moderating soil conditions, potentially benefiting seedlings rooted in these mats.

These physiological patterns could be compatible with Chapters II and III findings on regeneration dynamics and soil biology. For instance, the same partial harvest stands that fostered richer ectomycorrhizal networks (which enhance water uptake) may exhibit the most favorable $\delta^{13}C$ profiles. Conversely, microsites with depleted mycorrhizal abundance and poorer soil properties could correspond to the highest drought stress in seedlings. These integrative studies can underscore a holistic feedback loop: retention forestry can preserve both the soil biological infrastructure and microclimatic conditions necessary to ameliorate drought stress.

Implications for Ecosystem-Based Management. The combined findings from regeneration dynamics (Chapter II), soil–microbial indicators (Chapter III), and water stress on seedlings (Chapter IV) strengthens the rationale for incorporating partial harvest into an ecosystem-based management (EBM) framework in Canada's vast boreal landscapes. By retaining 45–60 % of stand basal area in structured patterns such as uniform shelterwood systems, forest managers can emulate intermediate-severity natural disturbances, maintain essential overstory elements, and support advance regeneration of shade-tolerant conifers (Bose et al., 2023; Gauthier et al., 2023). This structural retention moderates microclimates, preserves soil moisture, and

sustains coarse woody debris and litter layers that uphold ectomycorrhizal and nitrogen-fixing communities, critical for nutrient uptake and drought tolerance (Simard et al., 2021; Urbanová et al., 2015). Furthermore, foliar $\delta^{13}C$ analysis could be a cost-effective, integrative indicator tool for seedling water stress, enabling EBM practitioners to diagnose microclimatic buffering efficacy and adapt prescriptions accordingly (Namvar et al., 2024).

The study of uniform shelterwood in even-aged black spruce stands (younger stands: 80–100; older stands: 120–150 years old) demonstrates that mini-strip shelterwood variant can substantially enhance natural regeneration compared to conventional clearcutting. Moreover, their spatial pattern is the simplest among the shelterwood variants and loggers will have no difficulty to follow 5 m intervals between strip cuts. In particular, managers may integrate scarification (2 m^2 circular spots) within harvest corridors to break through thick organic mats and suppress ericaceous shrubs, thereby improving seed–soil contact and reducing vegetative competition in early growth of conifer seedlings (Löf et al., 2012; Rosenvald et al., 2020). Exposing mineral soil through scarification not only promotes better seed anchorage and moisture–nutrient exchange but also reduces damping-off pathogens associated with the organic layer, further increasing the likelihood of successful germination (Prévost, 1997). Leaving small retention islands (≥ 5 % of merchantable volume) on well-drained hummocks can further concentrate seed rain and preserve microsite conditions favorable to shade-tolerant conifers without reducing timber yield.

Two decades after treatment, overall bacterial and fungal diversity tends to converge between clearcut and partial harvest stands, reflecting the resilience of Canadian boreal forest soil communities (Giguère-Tremblay et al., 2020). Yet critical mutualists such as ectomycorrhizal fungi and nitrogen-fixing bacteria show persistent treatment-specific differences. According to our study, a healthy black spruce rhizosphere may host abundant ectomycorrhizal fungi (e.g., *Piloderma* spp.) alongside diverse Proteobacteria and Actinobacteria (Tahovská et al., 2020; Wang et al., 2022). It can also include nitrogen-fixers like *Roseiarcus* spp. and active saprotrophs that together balance nutrient cycling (Hayat et al., 2010). For practitioners aiming to sustain plant

health, it may therefore be prudent to preserve coarse woody debris and litter in retention patches, limit skid-trail compaction to designated corridors, and avoid extensive soil disturbance, all of which may support seedling nutrient uptake and long-term soil fertility.

Under projected warming and more frequent summer droughts, intermediate-intensity retention harvests (30 %–50 % basal area removal) can serve as an effective strategy to moderate vapor-pressure deficits and buffer soil moisture relative to full clearcuts (Puchi et al., 2024). Beyond regulating water availability, partial harvest helps retain nutrients on land, reducing leaching into aquatic systems and mitigating the risks of both soil desiccation and aquatic eutrophication through cyanobacterial blooms (Grosbois et al., 2024). Foliar $\delta^{13}C$ studies indicate that seedlings in such partial harvest environments maintain more open stomata and robust growth, whereas clearcut-regenerated trees exhibit chronic water stress. In the context of a changing climate, scaling up these retention systems paired with targeted ground-cover enhancements such as preservation of mosses through closure of canopy may offer a viable adaptation strategy to bolster seedling hydraulic resilience and secure the long-term stability of Canadian boreal forests (D'Amato et al., 2023).

Finally, the adoption of partial harvesting within EBM must be supported by an economic valuation of ecosystem services (Kuuluvainen et al., 2012; Nieminen et al., 2018; Pukkala, 2016). Although retention systems may entail higher initial costs and operational complexity compared to clear-cutting, these investments are offset by reduced replanting requirements, enhanced growth in residual trees, and the sustained provision of key services such as carbon sequestration, hydrological regulation, aquatic ecosystem restoration, and biodiversity conservation and biodiversity values (Díaz-Yáñez et al., 2021; Elliott et al., 2020). Since terrestrial disturbances such as harvesting propagate into aquatic environments and food webs (Grosbois et al., 2020), partial harvest plays a pivotal role in preserving the multifunctionality of boreal landscape. Policy instruments such as performance-based certification standards or payment-for-ecosystem-services schemes (PES) could further incentivize the uptake of retention forestry, ensuring that boreal landscapes

remain both productive and resilient in the face of accelerating climate change (Brnkalakova et al., 2021; Paluš et al., 2021).

Consequently, the evidence presented across regeneration dynamics (Chapter II), soil–microbial legacies (Chapter III), and water stress on seedlings (Chapter IV) converges to potentially endorse silvicultural systems using partial harvest as a keystone practice of ecosystem-based management. By harmonizing canopy structure, soil biodiversity, and plant water-use strategies, shelterwood systems enable boreal forests to sustain timber yields while maintaining ecosystem functions essential for long-term resilience.

Research limitations. While this thesis provides robust research evidence for natural regeneration, soil microbiome and seedling ecology after partial harvest, certain limitations constrain the broader applicability of results. First, study sites were geographically restricted to two bioclimatic zones, limiting extrapolation to other boreal regions with distinct disturbance regimes or species assemblages. Second, experimental treatments focused on specific silvicultural systems (shelterwood and seed-tree); other retention levels or hybrid systems (e.g., variable retention) warrant evaluation. It should be noted, however, that these findings pertain to even-aged stands and do not directly inform irregular partial harvest commonly used in old-growth forest management. Third, functional redundancy among microbial taxa may mask shifts in ecosystem processes, underscoring a gap in linking community composition to *in situ* soil function. In addition, the reliance on DNA metabarcoding characterized microbial composition but lacked direct functional assays, necessitating future metatranscriptomic analyses. Fourth, we attempted to augment our physiological assessments with on-site environmental monitoring, measuring PAR transmittance (400–700 nm) via a fixed quantum sensor and recording soil moisture, temperature, and EC with WatchDog 1000 loggers over one year. However, we found PAR highly variable at the microsite scale, and many loggers failed during severe winter freezes or animal interference, resulting in patchy data that could not be robustly analyzed. Consequently, our water-stress evaluation relied primarily on foliar $\delta^{13}C$. Future work should integrate complementary hydraulic (e.g., sap flow, leaf water potential), growth,

and more reliable microclimate measurements to fully characterize seedling performance. Finally, our study represents a single snapshot at approximately 18 years post-harvest; future work should implement repeated sampling, ideally every 5 years to better understand the dynamics in regeneration, thereby improving predictions of full stand maturation and long-term carbon trajectories.

Contributions. This thesis yields three principal advances that collectively deepen our understanding of silvicultural effects on boreal forest regeneration and offer concrete tools for ecosystem-based management.

The regeneration study establishes that partial harvests a specifically uniform shelterwood variants retaining 50% of basal area sustain robust natural regeneration trajectories over nearly two decades. Seedling densities of shade-tolerant conifers in these treatments consistently approached those of unharvested controls and were nearly threefold greater than in clearcuts. By extending the temporal scope beyond the typical 5–10 year window of silvicultural experiments, this work confirms that partial harvest alone can secure self-maintaining conifer populations without artificial planting, thereby validating its role as a keystone practice for reconciling biodiversity conservation with timber production in the black stands (Gauthier, 2009).

Nearly two decades post-harvest, boreal soils still reflect past treatments effects through subtle shifts in microbial functional groups and soil physicochemical properties. While overall microbial relative abundance and diversity remain resilient in both clearcut and partial cut stands, mirroring findings from other Canadian boreal sites (Giguère-Tremblay et al., 2020; Hannam et al., 2006). The relative abundances of ectomycorrhizal fungi and nitrogen-fixers vary with gradients of base saturation, calcium, potassium, and magnesium. These chemical–microbial correlations, alongside enzyme-activity hotspots, align closely with seedling growth patterns, confirming that harvest intensity leaves enduring imprints on the biogeochemical networks that underpin regeneration. Managing for these below-ground legacies through retention of organic inputs, minimal soil compaction, and targeted microsite treatments will be critical to sustaining nutrient cycling and long-term forest resilience.

Our study confirms foliar $\delta^{13}C$ as a powerful integrative metric for assessing water stress in regenerating seedlings. Regenerated seedlings in clearcut exhibit consistently enriched $\delta^{13}C$ signatures, indicating sustained stomatal closure while seedlings in partial harvest and unharvested treatments maintain values congruent with healthy photosynthetic function. These microsite linkages also highlight actionable management strategies: preserving or translocating bryophyte carpets and controlling competing shrubs can measurably reduce water stress, thus enhancing drought resilience in regenerating stands.

Together, those thesis contributions are helpful to better understand the response of natural regeneration, soil biota, and plant physiology after partial harvest in order to adapt and to optimize those silvicultural systems to boreal forest conditions and evaluating ecosystem-based silviculture in Eastern Canadian boreal forests. To our knowledge, this is the first boreal forest study to simultaneously assess mid-term natural regeneration, enduring soil microbial legacies, and integrative water stress physiology, thereby establishing a unified framework for long-term ecosystem-based management.

Future Research Directions. To adopt partial harvest approaches in Canadian boreal forests, future work should develop comprehensive, cradle-to-grave economic models that capture all costs and benefits over a full rotation. Such analyses would incorporate harvesting expenses, road and trail construction, post-harvest site preparation (e.g., scarification, moss/microbial inoculation), projected timber yields under variable retention regimes, and the avoided costs of artificial reforestation. By demonstrating that partial harvest with 40-60 percent basal-area retention can reduce long-term expenditures on planting and site maintenance while delivering comparable timber volumes, these studies will furnish the hard economic evidence needed to persuade provincial agencies, industry partners, and local communities to scale up partial harvests across boreal landscapes.

Although shelterwood systems provide the structural framework for successful regeneration, seedling establishment ultimately depends on microsite quality (Nagati et al., 2020). Building on evidence that spot scarification, microbial inoculation (e.g., *Piloderma* spp.), and favouring feathermoss can each improve seedbed conditions, factorial field trials should systematically test all combinations of these treatments. Trials must span a minimum of three growing seasons and be replicated across uniform shelterwoods, seed-tree method, and clearcut blocks to capture interactions between canopy retention and ground-cover treatments. Key response variables such as seedling density and height, soil moisture, organic-horizon depth, and rhizosphere community composition will allow managers to identify the most cost-effective packages of microsite treatments for different stand types.

To understand how soil biology and plant water relations jointly influence regeneration success, future research should combine microclimate monitoring, stable-isotope diagnostics, seedling physiological measurements, and rhizosphere microbiome analyses. A three-year study in permanent experimental plots could combine mid-season foliar $\delta^{13}C$ sampling (to capture cumulative water-use efficiency) with predawn leaf water-potential measurements (to pinpoint acute stress), while biannual rhizosphere DNA metabarcoding and targeted enzyme assays (e.g., phosphatase, cellulase) track microbial functional shifts. By overlaying these datasets on microclimatic records (soil moisture, temperature) and canopy-structure maps, researchers and practitioners will gain a mechanistic understanding of stress hotspots and be able to refine retention levels and microsite prescriptions in an adaptive, feedback-driven management framework.

APPENDICE A – FOR CHAPTER 1

Table S1.1.
Post-hoc pairwise comparisons of black spruce seedling density across silvicultural systems within younger and older stands.

Black spruce density - Older stand

contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	2593	4683	983	0.554	0.9938
Unmanaged - (Distant-sel.)	-7731	5141	983	-1.504	0.6619
Unmanaged - (Mini-strip)	-8752	4814	983	-1.818	0.4546
Unmanaged - (Seed-tree)	1813	4659	983	0.389	0.9988
Unmanaged - Clearcut	3775	4501	983	0.839	0.9602
(Close-sel.) - (Distant-sel.)	-10324	4974	983	-2.076	0.3009
(Close-sel.) - (Mini-strip)	-11345	4636	983	-2.447	0.1413
(Close-sel.) - (Seed-tree)	-780	4475	983	-0.174	1
(Close-sel.) - Clearcut	1182	4309	983	0.274	0.9998
(Distant-sel.) - (Mini-strip)	-1021	5098	983	-0.2	1
(Distant-sel.) - (Seed-tree)	9544	4952	983	1.927	0.3859
(Distant-sel.) - Clearcut	11506	4803	983	2.396	0.1587
(Mini-strip) - (Seed-tree)	10565	4612	983	2.291	0.1987
(Mini-strip) - Clearcut	12527	4452	983	2.814	0.0561
(Seed-tree) - Clearcut	1962	4284	983	0.458	0.9975

Black spruce density - Younger stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	-3277	5661	983	-0.579	0.9924
Unmanaged - (Distant-sel.)	-12259	5877	983	-2.086	0.2955
Unmanaged - (Mini-strip)	-30614	5671	983	-5.398	<.0001
Unmanaged - (Seed-tree)	1340	5681	983	0.236	0.9999
Unmanaged - Clearcut	12031	5623	983	2.14	0.2678
(Close-sel.) - (Distant-sel.)	-8982	4768	983	-1.884	0.4128
(Close-sel.) - (Mini-strip)	-27337	4511	983	-6.059	<.0001
(Close-sel.) - (Seed-tree)	4618	4524	983	1.021	0.9111
(Close-sel.) - Clearcut	15309	4451	983	3.439	0.008
(Distant-sel.) - (Mini-strip)	-18355	4780	983	-3.84	0.0018
(Distant-sel.) - (Seed-tree)	13599	4792	983	2.838	0.0525
(Distant-sel.) - Clearcut	24290	4723	983	5.143	<.0001
(Mini-strip) - (Seed-tree)	31954	4537	983	7.044	<.0001
(Mini-strip) - Clearcut	42645	4464	983	9.553	<.0001
(Seed-tree) - Clearcut	10691	4477	983	2.388	0.1613

Table S.1.2.
Post-hoc pairwise comparisons of balsam fir seedling density across silvicultural systems within younger and older stands.

Balsam fir seedling density - Older stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	4286	2036	416	2.105	0.2868
Unmanaged - (Distant-sel.)	1102	1785	416	0.617	0.9897
Unmanaged - (Mini-strip)	5425	1942	416	2.794	0.0603
Unmanaged - (Seed-tree)	7054	2050	416	3.442	0.0083
Unmanaged - Clearcut	-815	2024	416	-0.402	0.9986
(Close-sel.) - (Distant-sel.)	-3184	1651	416	-1.928	0.3864
(Close-sel.) - (Mini-strip)	1140	1819	416	0.627	0.989
(Close-sel.) - (Seed-tree)	2769	1934	416	1.432	0.7077
(Close-sel.) - Clearcut	-5100	1906	416	-2.675	0.0824
(Distant-sel.) - (Mini-strip)	4323	1533	416	2.821	0.0562
(Distant-sel.) - (Seed-tree)	5952	1668	416	3.569	0.0053
(Distant-sel.) - Clearcut	-1917	1636	416	-1.172	0.8501
(Mini-strip) - (Seed-tree)	1629	1834	416	0.888	0.9492
(Mini-strip) - Clearcut	-6240	1805	416	-3.457	0.0079
(Seed-tree) - Clearcut	-7869	1921	416	-4.097	0.0007

Balsam fir seedling density - Younger stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	1429	1906	416	0.749	0.9755
Unmanaged - (Distant-sel.)	1226	2609	416	0.47	0.9971
Unmanaged - (Mini-strip)	-3683	1756	416	-2.097	0.2907
Unmanaged - (Seed-tree)	495	1981	416	0.25	0.9999
Unmanaged - Clearcut	3103	2776	416	1.118	0.8739
(Close-sel.) - (Distant-sel.)	-202	2599	416	-0.078	1
(Close-sel.) - (Mini-strip)	-5111	1741	416	-2.935	0.0408
(Close-sel.) - (Seed-tree)	-934	1968	416	-0.475	0.997
(Close-sel.) - Clearcut	1675	2767	416	0.605	0.9906
(Distant-sel.) - (Mini-strip)	-4909	2490	416	-1.971	0.3608
(Distant-sel.) - (Seed-tree)	-731	2654	416	-0.276	0.9998
(Distant-sel.) - Clearcut	1877	3290	416	0.57	0.9929
(Mini-strip) - (Seed-tree)	4178	1822	416	2.292	0.1995
(Mini-strip) - Clearcut	6786	2665	416	2.546	0.1134
(Seed-tree) - Clearcut	2608	2819	416	0.925	0.9399

Table S.2.1.
Post-hoc pairwise comparisons of black spruce seedling growth (terminal shoot length) across silvicultural systems within younger and older stands

Black spruce growth - Older stand

contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	-2.5299	0.857	681	-2.952	0.0383
Unmanaged - (Distant-sel.)	-2.4302	0.956	681	-2.543	0.1133
Unmanaged - (Mini-strip)	-5.9834	0.908	681	-6.588	<.0001
Unmanaged - (Seed-tree)	-5.2527	0.889	681	-5.908	<.0001
Unmanaged - Clearcut	-7.203	0.791	681	-9.107	<.0001
(Close-sel.) - (Distant-sel.)	0.0997	0.973	681	0.103	1
(Close-sel.) - (Mini-strip)	-3.4535	0.926	681	-3.727	0.0029
(Close-sel.) - (Seed-tree)	-2.7228	0.908	681	-3	0.0333
(Close-sel.) - Clearcut	-4.6731	0.812	681	-5.757	<.0001
(Distant-sel.) - (Mini-strip)	-3.5532	1.018	681	-3.489	0.0068
(Distant-sel.) - (Seed-tree)	-2.8225	1.001	681	-2.819	0.0557
(Distant-sel.) - Clearcut	-4.7729	0.915	681	-5.215	<.0001
(Mini-strip) - (Seed-tree)	0.7307	0.956	681	0.764	0.9733
(Mini-strip) - Clearcut	-1.2197	0.866	681	-1.409	0.7216
(Seed-tree) - Clearcut	-1.9504	0.845	681	-2.307	0.1926

Black spruce growth - Younger stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	-3.9405	1.161	681	-3.393	0.0095
Unmanaged - (Distant-sel.)	-4.2402	1.172	681	-3.617	0.0043
Unmanaged - (Mini-strip)	-2.2007	1.191	681	-1.848	0.4355
Unmanaged - (Seed-tree)	-7.4908	1.276	681	-5.87	<.0001
Unmanaged - Clearcut	-10.8178	1.175	681	-9.208	<.0001
(Close-sel.) - (Distant-sel.)	-0.2997	0.841	681	-0.356	0.9992
(Close-sel.) - (Mini-strip)	1.7398	0.866	681	2.008	0.3388
(Close-sel.) - (Seed-tree)	-3.5503	0.98	681	-3.621	0.0042
(Close-sel.) - Clearcut	-6.8773	0.844	681	-8.145	<.0001
(Distant-sel.) - (Mini-strip)	2.0394	0.881	681	2.314	0.1896
(Distant-sel.) - (Seed-tree)	-3.2507	0.993	681	-3.272	0.0142
(Distant-sel.) - Clearcut	-6.5777	0.86	681	-7.653	<.0001
(Mini-strip) - (Seed-tree)	-5.2901	1.015	681	-5.212	<.0001
(Mini-strip) - Clearcut	-8.6171	0.884	681	-9.743	<.0001
(Seed-tree) - Clearcut	-3.327	0.996	681	-3.34	0.0114

Table S.2.2.
Post-hoc pairwise comparisons of balsam fir seedling growth (terminal shoot length) across silvicultural systems within younger and older stands.

Balsam fir growth - Older stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	0.0469	1.51	157	0.031	1
Unmanaged - (Distant-sel.)	-0.7734	1.2	157	-0.646	0.9872
Unmanaged - (Mini-strip)	-3.721	1.51	157	-2.46	0.1426
Unmanaged - (Seed-tree)	-0.362	1.51	157	-0.239	0.9999
Unmanaged - Clearcut	-0.0765	1.31	157	-0.058	1
(Close-sel.) - (Distant-sel.)	-0.8204	1.4	157	-0.585	0.9919
(Close-sel.) - (Mini-strip)	-3.7679	1.68	157	-2.241	0.225
(Close-sel.) - (Seed-tree)	-0.409	1.68	157	-0.243	0.9999
(Close-sel.) - Clearcut	-0.1234	1.5	157	-0.082	1
(Distant-sel.) - (Mini-strip)	-2.9476	1.4	157	-2.1	0.2926
(Distant-sel.) - (Seed-tree)	0.4114	1.4	157	0.293	0.9997
(Distant-sel.) - Clearcut	0.697	1.18	157	0.591	0.9915
(Mini-strip) - (Seed-tree)	3.359	1.68	157	1.998	0.3481
(Mini-strip) - Clearcut	3.6445	1.5	157	2.431	0.1521
(Seed-tree) - Clearcut	0.2855	1.5	157	0.19	1

Balsam fir growth - Younger stand					
contrast	estimate	SE	df	t.ratio	p.value
Unmanaged - (Close-sel.)	-4.6792	1.77	157	-2.644	0.0929
Unmanaged - (Distant-sel.)	-1.3208	2.62	157	-0.503	0.996
Unmanaged - (Mini-strip)	-6.3514	1.96	157	-3.247	0.0176
Unmanaged - (Seed-tree)	-8.8158	2.44	157	-3.608	0.0055
Unmanaged - Clearcut	-7.0958	2.9	157	-2.446	0.1473
(Close-sel.) - (Distant-sel.)	3.3583	2.33	157	1.442	0.7016
(Close-sel.) - (Mini-strip)	-1.6722	1.54	157	-1.087	0.8859
(Close-sel.) - (Seed-tree)	-4.1367	2.12	157	-1.948	0.3771
(Close-sel.) - Clearcut	-2.4167	2.64	157	-0.916	0.9419
(Distant-sel.) - (Mini-strip)	-5.0306	2.47	157	-2.033	0.3285
(Distant-sel.) - (Seed-tree)	-7.495	2.88	157	-2.607	0.1016
(Distant-sel.) - Clearcut	-5.775	3.27	157	-1.764	0.4918
(Mini-strip) - (Seed-tree)	-2.4644	2.28	157	-1.08	0.8886
(Mini-strip) - Clearcut	-0.7444	2.77	157	-0.269	0.9998
(Seed-tree) - Clearcut	1.72	3.13	157	0.55	0.9939

Table S3.
Frequency of bryophyte and vegetation cover associated with regenerated black spruce seedlings across different microsite positions (residual strip, edge, and skid trail).

Frequency (%)	Residual strip	Edge	Skid trail
Pleurozium sp.	80.9	77.6	82.3
Polytrichum sp.	6.7	23.7	35.3
Ptilium sp.	35.1	35.5	30.9
Sphagnum sp.	26.7	27.6	23.3
Hylocomium sp.	9.3	15.1	7.3
Gaultheria sp.	80.0	75.7	62.8
Cladina spp.	5.8	8.6	12.9

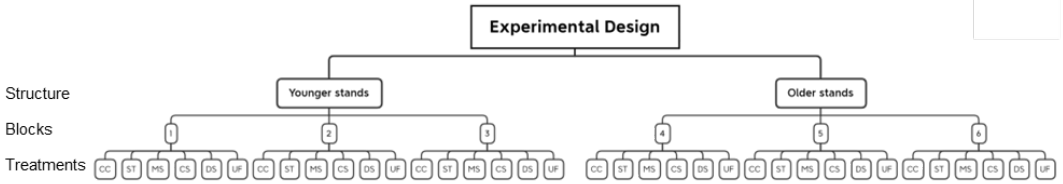

Figure S1.
Schematic representation of experimental design. Stand structures (younger and older) are indicated as supra-variable in the design. The blocks are numbered (1 to 6), the experimental units are control plots (UF: unmanaged forest) and study treatments (CC: clearcut, ST: seed-trees, CS: close-selection shelterwood, DS: distant-selection shelterwood, MS: mini-strip shelterwood).

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