

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

EFFET DE LA DENSITÉ DE PLANTATION ET DE LA PRÉPARATION
MÉCANIQUE DU SOL SUR LA DIVERSITÉ ET LA COMPOSITION DU SOUS-
BOIS ET LA CROISSANCE DES ÉPINETTES NOIRES PLANTÉES DANS LA
FORÊT BORÉALE

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AVANT-PROPOS

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RÉSUMÉ

La densité de plantation est un facteur important qui influence la croissance et le rendement des forêts. Dans la forêt boréale, la préparation mécanique des sols est par ailleurs nécessaire avant la plantation pour créer des microsites favorables et assurer le succès d'établissement des plants. Cependant, nous ignorons s'il existe des interactions entre la densité de plantation et la préparation mécanique des sols. Notre objectif était donc de comprendre, neuf ans après traitement, les effets interactifs entre la densité de plantation et la préparation mécanique du sol sur la composition du sous-bois et la croissance des épinettes noires (*Picea mariana*) plantées sur des sites forestiers sujets à la paludification. L'étude a été réalisée dans la région de la ceinture d'argile du nord-ouest du Québec. En 2011, sur un site récemment coupé, nous avons établi neuf parcelles qui ont été traitées par hersage, scarifiage à disques, ou laissées comme témoins non traités. En 2012, chaque parcelle a été divisée en deux sous-parcelles soumises à une densité faible (1100 plants/ha) ou élevée (2500 plants/ha) de plantation d'épinette noire. Un total de 216 quadrats répartis dans les 9 parcelles ont été sélectionnés pour la mesure de la croissance en hauteur et en diamètre des arbres plantés et, parmi ces quadrats, 108 ont été sélectionnés pour l'inventaire botanique et l'échantillonnage du sol. Nos résultats montrent, neuf ans après traitement, qu'une régénération importante de conifère s'est établie. Nous avons également observé une augmentation importante de la diversité des bryophytes par rapport aux plantes vasculaires en réponse à l'interaction entre la densité de plantation et la préparation du sol, ainsi qu'un effet significatif sur la composition floristique; nous avons documenté un passage des espèces typiques de milieux pauvres et résineux vers des espèces caractéristiques de milieux plus riches et dominés par les feuillus. La croissance des épinettes noires plantées s'est avérée être la plus élevée dans les parcelles soumises au hersage et à la densité de plantation élevée. Nos résultats contribuent aux connaissances concernant les effets de la densité de plantation en interaction avec la préparation des sols paludifiés sur le développement des arbres et du sous-bois. Ils seront utiles aux sylviculteurs dans l'identification de traitements permettant d'atteindre de multiples objectifs d'aménagement.

Mots clés : densité de plantation, *Picea mariana* (Mill.) B.S.P, bryophytes, plantes vasculaires, sylviculture, aménagement forestier, paludification.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Mise en contexte et problématique

La forêt boréale est un biome important à l'échelle mondiale, avec une importance écologique et économique considérable au Québec. Notamment, la forêt boréale du Nord-Ouest du Québec est une zone caractérisée par la dominance de l'épinette noire (*Picea mariana* (Mill.) B.S.P.). L'industrie forestière y réalise des activités importantes de récolte et d'aménagement forestier. La récolte des peuplements s'y réalise selon les modalités de coupe avec protection de la régénération et des sols (CPRS) (Canadian Forest Service, 2016), un traitement qui vise à protéger et à utiliser la régénération préétablie pour renouveler les peuplements coupés (Harvey et Brais, 2002). Lorsque la régénération préétablie est insuffisante, la plantation devient alors le principal outil d'aménagement pour assurer le renouvellement de la forêt (Ministère des Ressources naturelles, 2002).

La forêt boréale du Nord-Ouest du Québec est une zone qui comprend la ceinture d'argile. La ceinture d'argile est une large bande de 125 000 km², caractérisée par un

sol minéral argileux, avec un faible drainage dû au relief plat et un climat froid (Lavoie et al., 2005). Ces conditions font en sorte qu'une grande proportion des peuplements d'épinettes noires est sujette à la paludification (Boucher *et al.*, 2003). La paludification est le phénomène naturel qui consiste en l'accumulation de matière organique sur le sol (Payette et Rochefort, 2013) en raison d'une prolifération de sphaignes (Fenton et Bergeron, 2007; Fenton *et al.*, 2005)

La végétation du sous-bois exerce une compétition sur les épinettes noires pour les éléments nutritifs du sol et la lumière en forêt (Inderjit et Mallik, 2002). En conséquence, les espèces du sous-bois peuvent réduire significativement la croissance des semis naturels et plantés (Balandier *et al.*, 2006). Pour pallier ce problème, la perturbation mécanique du sol est proposée comme méthode qui favorise la croissance des semis (Henneb *et al.*, 2015 ; Thiffault *et al.*, 2013). La préparation mécanique du sol (PMS) aide à diminuer efficacement le recouvrement des éricacées pendant au moins les trois premières années suivant son application, tout en améliorant les conditions d'installation des semis (Thiffault *et al.*, 2013 ; Prévost, 1996). Ceci contribue à restaurer la productivité des sites paludifiés suite à la récolte (Henneb *et al.*, 2019).

Par ailleurs, selon le contexte, la densité de plantation (le nombre de plants mis en terre par unité de surface) varie d'environ 1100 à 2500 plants/ha au Québec (McClain *et al.*, 1994). La gestion de la densité de plantation limite les besoins d'éclaircie en bas âge. En conséquence, la compétition intraspécifique et interspécifique devient des enjeux seulement aux stades du perchis ou de la futaie. La densité de plantation a le potentiel d'influencer les espèces de sous-bois, notamment les espèces qui compétitionnent avec la régénération forestière. En effet, la fermeture rapide du couvert forestier pourrait limiter la croissance des plantes concurrentes et ainsi

diminuer leur effet négatif sur la productivité forestière (Moroni *et al.*, 2009 ; Titus *et al.*, 1995). Bien que plusieurs connaissances existent sur les effets de la densité de plantation et de la préparation mécanique du sol sur la croissance des arbres, leurs interactions potentielles sur la croissance, le développement du sous-bois et les relations sol-plante demeurent inexplorées.

1.2 État des connaissances

1.2.1 La densité des peuplements forestiers

Depuis quelques décennies, les stratégies de production de bois migrent graduellement des forêts naturelles aux forêts de plantation. Les forêts plantées jouent en effet un rôle de plus en plus important dans les économies mondiales pour sécuriser les sources de bois industriel. On considère que les forêts plantées fournissent environ un tiers de la production mondiale de bois industriel (Jürgensen *et al.*, 2014). Les vastes étendues de forêts naturelles sont susceptibles de présenter un avantage de production à court terme, mais cette allocation finira par diminuer en raison des meilleurs résultats de rendement offerts par les plantations (FAO, 2001). Cependant, le succès de cette stratégie repose sur le contrôle de la croissance et la densité des peuplements, lesquels régulent l'accroissement des arbres et de la qualité du bois (Kenk, 1990).

La densité des peuplements est contrôlée au stade de l'initiation de la plantation en variant la distance entre les arbres plantés. Des densités faibles augmentent la taille des arbres individuels en raison de la réduction de la concurrence intraspécifique (Boyden *et al.*, 2008). L'effet global de la densité sur le volume des peuplements

demeure toutefois mitigé (Thiffault *et al.*, 2021). La densité de plantation, en plus d'influencer le volume du peuplement et la taille des arbres, influence aussi plusieurs paramètres dans le système sol-plante (p. ex. la quantité de la lumière transmise au sous-bois, l'humidité et la température du sol), ainsi que la composition et la biomasse de la végétation du sous-bois (Messier *et al.*, 1998 ; Anderson *et al.*, 1969 ; Voigt, 1960). Dans un contexte d'aménagement durable des ressources forestières, il est important de comprendre les interactions entre la densité des arbres, la végétation du sous-bois et le cycle des éléments nutritifs.

1.2.2 Relation sol-plante

Dans les écosystèmes forestiers, il existe une relation étroite entre la flore et le sol. La flore influence la structure du sol et la dynamique des nutriments, alors que le sol agit comme un support physique et sert de réserve pour les éléments nutritifs (Brady et Weil, 2008). Ce rapport entre le sol et la flore est contrôlé par certaines conditions abiotiques, tels que le climat (Hlásny *et al.*, 2017), les propriétés du sol (Yuan *et al.*, 2018) et des conditions biotiques comme la diversité des plantes (Tilman *et al.*, 2014 ; Paquette et Messier, 2011).

Afin de soutenir la productivité végétale, le sol doit répondre aux besoins du système racinaire en regard de l'alimentation en eau, en oxygène et en nutriments, en plus d'être un support pour la partie aérienne des plantes. Une structure du sol bien développée permet une bonne aération en évitant les conditions asphyxiantes pour les racines (Franzluebbers, 2002 ; Brais *et al.*, 1995). En retour, les plantes influencent les propriétés du sol en affectant le microclimat et, par conséquence, les communautés microbiennes édaphiques (Moussavou Boussougou *et al.*, 2010 ; Scott,

1998 ; Harris *et al.*, 1966). Notamment, les arbres ont des effets spécifiques sur les propriétés du sol; lors de la décomposition de la matière organique, la quantité des nutriments libérés dépend directement du type de litière (Gartner et Cardon, 2004 ; Facelli et Pickett, 1991). Le stockage du carbone (C) et de l'azote (N) inorganique dans le sol, ainsi que l'acidification, sont affectés par les différentes espèces d'arbres (Mueller *et al.*, 2012).

La forêt boréale est reconnue comme l'un des écosystèmes les plus limités en N (Tamm, 1991). L'azote est un élément essentiel pour la croissance des espèces végétales; il permet d'augmenter la capacité photosynthétique et la surface foliaire, ce qui stimule la croissance (Lupi, 2013). Les contraintes nutritionnelles induisent des diminutions de la productivité dans la forêt, particulièrement dans les peuplements paludifiés d'épinette noire (Lafleur *et al.*, 2011 ; Simard *et al.*, 2007 ; Fenton *et al.*, 2005).

1.2.3 La paludification

Dans plusieurs écosystèmes forestiers boréaux à travers le monde, les sols peuvent accumuler des couches organiques épaisses, ce qui peut mener à un phénomène naturel appelé la paludification (Payette et Rochefort, 2013). Ce processus s'accompagne d'une ouverture du couvert forestier et d'une perte de productivité ligneuse, d'une colonisation des sites par les espèces de sphaignes et d'une hausse de la nappe phréatique près de la surface du sol (Drobyshev *et al.*, 2010; Simard *et al.*, 2007; Fenton *et al.*, 2005).

Il existe deux types de paludification : la paludification édaphique et la paludification successienne. La paludification édaphique, également appelée paludification des dépressions humides, est un phénomène irréversible dirigé par la topographie et le drainage. Elle favorise un établissement rapide des sphaignes sur le site et une accumulation importante de matière organique, accompagnée d'une canopée ouverte dominée par les épinettes noires (Laamrani *et al.*, 2014). En contraste, la paludification successienne est un phénomène associé à la dynamique de succession forestière après feu, notamment dans la région de la ceinture d'argile (Simard *et al.*, 2009; Fenton et Bergeron, 2006). La paludification successienne est un processus réversible; par exemple, un feu sévère peut entièrement éliminer la couche organique, ce qui facilite la régénération de peuplements forestiers (Simard *et al.*, 2009, 2007). La paludification crée des conditions défavorables pour la croissance et la régénération de l'épinette noire en raison de l'humidité et de la prolifération de sphaignes et de mousses (Fenton *et al.*, 2005). Ces conditions conduisent à l'augmentation de l'épaisseur de la couche organique et à la réduction du taux de décomposition, ce qui entraîne la diminution de la productivité des pessières noires pouvant atteindre 50 à 80 % (Simard *et al.*, 2007).

En absence de feu sévère, la plupart des sites paludifiés continuent à évoluer vers un état de paludification avancé. Il importe alors d'adopter des pratiques sylvicoles qui remplacent les feux sévères, comme la préparation mécanique du sol (PMS) lors de la récolte. Ces méthodes ont le potentiel de réduire l'épaisseur de la couche organique et de limiter la paludification, ce qui favorise la remise en production des sites paludifiés (Lavoie *et al.*, 2005).

1.2.4 La préparation mécanique du sol (PMS)

La préparation du sol après coupe est une pratique courante en foresterie pour pallier les échecs de la régénération naturelle. Elle vise à enlever les déchets de coupe et réduire la végétation concurrente, pour créer un environnement favorable à l'établissement et à la croissance de la régénération forestière (Sutherland et Foreman, 2000 ; Orlander *et al.*, 1990). Elle permet également de créer des conditions de température (Man et Lieffers, 1999) et d'humidité (Fleming *et al.*, 1994) favorables pour la régénération à la surface du sol et de stimuler la minéralisation de la matière organique (Munson *et al.*, 1993).

La préparation mécanique du sol résulte en des conditions de terrain relativement homogènes facilitant les travaux de reboisement et d'entretien des plantations. Les techniques de préparation mécanique du sol peuvent être réalisées par plusieurs activités, selon les objectifs et les conditions du terrain (Bédard et Côté, 1996). Le scarifiage et le hersage forestier sont deux techniques de PMS fréquemment utilisées au Québec.

Le scarifiage mécanique est la méthode de préparation de terrain la plus fréquemment appliquée sur les sites forestiers au Québec (Prévost, 1992). Il s'agit d'une méthode qui mélange l'horizon organique au sol minéral, ou qui enlève une partie ou tout l'horizon organique. Le scarifiage influence aussi les caractéristiques du sol comme la température, la disponibilité en eau, l'environnement des organismes décomposeurs et les processus de minéralisation (Thiffault *et al.*, 2003). Le scarifiage par sillons est réalisé par un scarificateur équipé de deux disques dentés, lesquels pénètrent dans le sol, ameublissent plus ou moins les couches superficielles du sol forestier et perturbent la couche d'humus et le sous-bois (Bédard et Côté, 1996). Pour

sa part, le hersage forestier présente des meilleures croissances dans les sites faiblement à modérément paludifés (Henneb *et al.*, 2020); il permet d'ameublir et d'aérer le sol et de défaire la couche d'humus. Il est réalisé à l'aide d'une herse forestière à disques (6 à 10 disques) qui broie et incorpore la matière organique aux horizons minéraux de surface (Doucet *et al.*, 2011).

1.2.5 La diversité du sous-bois en forêt boréale

La végétation du sous-bois est une composante importante des écosystèmes forestiers. Elle influence la production primaire (Bisbee *et al.*, 2001 ; Gower *et al.*, 1997), la respiration du sol (O'Connell *et al.*, 2003) et la fertilité du site (Spies et Barnes, 1985). Les forêts boréales se distinguent notamment des forêts plus septentrionales par le rôle important que joue la végétation du sous-bois dans leur fonctionnement (Nilsson et Wardle, 2005). Dans la forêt boréale nord-américaine, la diversité végétale vasculaire du sous-bois est faible, avec moins de 300 espèces de plantes réparties en 47 familles (La Roi, 1967). En plus de contribuer à la biodiversité, les plantes vasculaires affectent la succession et la régénération des forêts, le cycle des éléments nutritifs et la disponibilité d'habitats fauniques (Hart et Chen, 2006).

Le sous-bois de la forêt boréale comporte également des bryophytes (des plantes non vasculaires). Les plus répandues en forêt boréale sont *Pleurozium schreberi* (Brid.) Mitt. et les sphaignes (*Sphagnum* spp). Les sphaignes constituent des tapis de mousses qui croissent en colonies qui couvrent le sol forestier (Fenton et Bergeron, 2006). Les sphaignes sont classées en deux principaux groupes. Les sphaignes de creux développent des tiges robustes, formant des tapis relativement productifs et espacés sur le sol forestier. Les sphaignes de butte se développent pour leur part en

coussins denses formant des pousses minuscules et qui leur permettent de retenir l'eau (Lang *et al.*, 2009). Les bryophytes peuvent avoir des effets importants sur les propriétés physico-chimiques du sol (Cornelissen *et al.*, 2006), dont le pH (Lavoie *et al.*, 2005), la décomposition de la matière organique (Turetsky *et al.*, 2010), l'humidité (Turetsky *et al.*, 2012) et la température (Soudzilovskaia *et al.*, 2013).

La diversité des espèces de sous-bois de la forêt boréale est contrôlée par des facteurs écologiques, tels que les caractéristiques physiques des sites, des facteurs climatiques et les interactions biologiques (Grandpré *et al.*, 2014 ; Shmida et Wilson, 1985). Par exemple, les essences comme le pin gris (*Pinus banksiana* Lambert), le bouleau à papier (*Betula papyrifera* Marshall) et le peuplier faux-tremble (*Populus tremuloides* Michaux) laissent passer une quantité importante de la lumière jusqu'à la végétation du sous-bois, créant ainsi un milieu favorable pour les plantes vasculaires. Des essences comme le sapin baumier (*Abies balsamea* (Linnaeus) Miller), l'épinette noire et le thuya (*Thuja occidentalis* Linnaeus) favorisent pour leur part les bryophytes comme les *Pleurozium* et les sphaignes (Légaré *et al.*, 2001 ; Messier *et al.*, 1998).

1.2.6 Les traits fonctionnels du sous-bois

L'utilisation des traits fonctionnels est un moyen de prédire les conséquences d'un changement environnemental dans un écosystème (Lavorel et Garnier, 2002 ; Woodward et Cramer, 1996). Il est donc possible de comprendre une partie du fonctionnement de l'écosystème en étudiant les traits fonctionnels des individus.

Il y a deux types de traits fonctionnels : les traits de réponse et les traits d'effet. Les traits de réponse (p.ex., la surface foliaire spécifique) permettent à la plante de résister et persister au sein de la communauté en répondant aux facteurs environnementaux. Les traits d'effet (p. ex., la rétention d'eau) influencent les facteurs environnementaux (Violle *et al.*, 2007 ; Lavorel et Garnier, 2002). La plupart des communautés présentent une combinaison unique de traits qui influencent l'écosystème (Eviner et Chapin III, 2003). L'utilisation de la diversité fonctionnelle des communautés serait plus appropriée que la diversité spécifique afin de comprendre l'impact des changements environnementaux sur les écosystèmes (Diaz et Cabido, 2001 ; Walker *et al.*, 1999 ; Woodward et Diament, 1991).

1.3 Objectifs de l'étude et hypothèse générale

1.3.1 Objectifs de l'étude

L'objectif général de l'étude est de comprendre, neuf ans après traitements, les effets interactifs entre la densité de plantation et la préparation mécanique du sol sur la composition du sous-bois et la croissance des épinettes noires plantées dans des sites forestiers sujets à la paludification. Afin d'atteindre cet objectif général, nous avons défini les quatre objectifs spécifiques suivants :

1. Évaluer l'effet de l'interaction de la plantation à faible et à forte densités et de la préparation mécanique du sol sur les conditions environnementales.
2. Déterminer l'effet de l'interaction entre la densité de plantation et de la préparation mécanique du sol sur la diversité et la composition du sous-bois.

3. Déterminer s'il y a des effets interactifs entre la densité de plantation et la préparation mécanique du sol sur les traits fonctionnels des plantes vasculaires et des bryophytes.
4. Déterminer s'il y a des effets interactifs entre la densité de plantation et la préparation mécanique du sol sur la croissance, la hauteur, le diamètre, l'azote et le carbone foliaires des épinettes noires plantées.

1.3.2 Hypothèse générale

Nous formulons l'hypothèse principale que sur un site coupé et préparé mécaniquement, une augmentation de la densité de reboisement induit des impacts positifs sur la fertilité du sol, modifie significativement la composition du sous-bois et stimule la croissance des conifères.

CHAPITRE II

PLANTING DENSITY AND MECHANICAL SITE PREPARATION EFFECTS ON UNDERSTORY COMPOSITION, FUNCTIONAL DIVERSITY, AND PLANTED BLACK SPRUCE GROWTH IN BOREAL QUEBEC, CANADA

2.1 Abstract

Tree density impacts the renewal of forests and the sustainability of their management, as it affects yield and wood quality. In boreal forests, mechanical site preparation is used before planting to improve soil conditions by creating microsites that ensure seedling survival and growth, which is essential to maintain ecological functions of forest ecosystems after disturbances. This is especially true for sites prone to paludification, where the rapid accumulation of organic matter significantly reduces tree growth, and hence, affects forest productivity. However, the potential effects of mechanical site preparation in interaction with planting density remain unclear. We conducted a study in the Clay Belt region of northwestern Quebec, Canada. After careful logging, the study area was divided in nine sites that were treated by plowing, disc trenching or left unprepared (harvesting only). Sites were divided in two and planted using black spruce seedlings at a density of 1100 seedlings/ha (low) or 2500 seedlings/ha (high). The composition and diversity of the

understory and the growth of the planted trees were assessed nine years after the site preparation treatments. Our results showed that there was a higher density of naturally established conifers after careful logging alone than after plowing or disc trenching. The interaction between planting density and mechanical site preparation had a significant effect on understory diversity and composition in plowed plots. Black spruce growth was significantly increased with higher planting densities in the plow treatment only. However, planting density and mechanical site preparation alone had no effect on height and diameter. In summary, our short-term results suggest that plowing with planting at a high density could be a strategy to increase stand growth and improve forest productivity. Our results provide a foundation for future studies on forest productivity and diversity of paludified forests.

2.2 Introduction

Global wood production strategies are gradually shifting from natural forests to plantation forestry. Plantation forestry offers an opportunity for increased productivity compared with natural forests. The high yields of planted forests are indeed an opportunity for achieving wood fibre production and allowing the provision of other ecosystem services (Paquette and Messier, 2010 ; Park and Wilson, 2007). Plantation success depends on interdependent decisions and actions (Thiffault *et al.*, 2020). For example, planting density is an important factor affecting forest production through its effects on survival, tree growth, wood yield, and biodiversity (e.g., Thiffault *et al.*, 2020 ; Benomar *et al.*, 2012 ; Sharma *et al.*, 2002). Planting density has the potential to influence understory species, particularly those that compete with forest regeneration. Indeed, rapid canopy closure could limit the growth of competing plants and thus reduce their negative effect on forest productivity (Moroni *et al.*, 2009; Titus *et al.*, 1995). Also, mechanical site preparation (MSP)

before planting is one of the most common practices in Canada's forests to ensure successful regeneration of harvested sites (Sutherland and Foreman, 1995). The main benefits of MSP are to reduce competition from other species colonizing regeneration areas (Mallik and Kravchenko, 2016 ; Johansson *et al.*, 2013 ; Thiffault and Jobidon, 2006) and to increase the availability of resources, which enhances seedling survival (Luoranen *et al.*, 2017 ; Heiskanen *et al.*, 2013). In boreal forests, MSP has been shown to increase the growth of planted black spruce (*Picea mariana* (Mill.) BSP) seedlings by increasing nutrient availability (Sutherland and Foreman, 2000) and N mineralization and uptake due to warmer soils and improved soil moisture (Nordborg *et al.*, 2003 ; Johansson, 1994). Therefore, MSP is a critical tool for creating a suitable planting environment for regenerating harvested sites (Wallertz *et al.*, 2018 ; Hébert *et al.*, 2014 ; Thiffault and Jobidon, 2006).

Although most planted forests are primarily managed for wood production and other economic objectives, these forests are also expected to contribute to the conservation of biodiversity (Nagaike, 2012 ; Bremer and Farley, 2010). Plantation of conifers (e.g., *Abies* and *Picea* species) offers specific habitats for understory plants by affecting resource availability such as light and physical characteristics of the litter layer in temperate and boreal forests (Barbier *et al.*, 2008 ; Saetre *et al.*, 1997). However, some MSP methods that retain more of the organic layers and downed woody material may provide a better balance between competition control, plantation establishment and site productivity, while maintaining other ecological values (Powers, 2006 ; Ramovs and Roberts, 2003 ; Bock and Van Rees, 2002). In turn, understory plants play an essential role in maintaining the structure and functions of ecosystems (Gilliam, 2007 ; Nilsson and Wardle, 2005), such as soil nutrient cycling, carbon stocks (Zhou *et al.*, 2018), and are important indicators of site quality (Wei *et al.*, 2020). Hence, it is important to understand the interactions between planted trees,

silvicultural treatments, and the understory in managed forests so that ecosystem dynamics and functions are maintained (Gilliam and Roberts, 2003). Unfortunately, few studies have investigated stand properties (i.e., growth, understory composition and function) under different planting densities and after different site preparation techniques.

In this study, we aimed to evaluate the main and interacting effects of planting density and mechanical site preparation on understory composition and functional traits and the growth of planted black spruce in forest sites prone to paludification. Our specific objectives were to evaluate the sole and combined effects of planting density and mechanical site preparation on (1) environmental conditions, (2) understory diversity and composition, (3) bryophyte and vascular plant functional traits and (4) planted sapling growth. We expected significant interactions between the treatments to influence sapling growth, understory composition, and functional traits. More specifically, we posited that higher planting density and mechanical site preparation intensity would significantly modify understory composition and functional traits, which would lead to a positive influence on sapling growth compared to control conditions.

2.3 Materials and Methods

2.3.1 Study area

The study was conducted in the black spruce–feather moss bioclimatic domain (Saucier *et al.*, 2009) located in the Clay Belt region of north-western Quebec,

Canada, which is covered by a fine-textured clay deposit left by the proglacial lakes Barlow and Ojibway (Vincent and Hardy, 2011). The soil of the region is dominated by compacted clay and is subdivided by sand and gravel deposits of the Harricana moraine (Veillette, 1994). The study site, called Valrennes, is located approximately 200 km north-east of Rouyn-Noranda (49° 27' N, 78° 31' W) (Figure 2.1). The site is prone to paludification with imperfect drainage, low topographic relief, and a wet, cold climate (Fenton *et al.*, 2005; Lavoie *et al.*, 2005). The average annual temperature is 1 °C and the average annual precipitation is 32.5 mm (Environment Canada, 2021).

Before harvest, the Valrennes site was dominated by mature black spruce, followed by trembling aspen (*Populus tremuloides* Michx), tamarack (*Larix laricina* [Du Roi] K. Koch), balsam fir (*Abies balsamea* [L.] Miller), and white birch (*Betula papyrifera* Marshall). The shrub cover was dominated by Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) and sheep laurel (*Kalmia angustifolia* L.). The forest floor was covered by Sphagnum mosses (including *Sphagnum magellanicum* Brid.; *S. russowii* Wamst.; and *S. capillifolium* (Ehrh.)) and feather mosses (*Pleurozium schreberi* (Brid.) Mitt) (Laamrani, 2014).

2.3.2 Study design and treatments

The field experiment was established on nine sites averaging 32 ha each (Henneb *et al.*, 2019). In summer 2010 (before harvest), 15 circular sampling plots of 400 m² each were established in each site for forest stand measurements. In each sampling plot, four quadrats of 1 m² were established to survey understory vegetation. In the fall of 2010, all sites were harvested using careful logging around advanced growth

(CLAAG). In 2011, six sites out of the nine were randomly selected to be subjected to one of two mechanical site preparation treatments: three were treated using a forest plow (Plow), and three were treated by disc trenching using a T26 scarifier (Bracke Forest AB, Bräcke, Sweden) (Figures 2.1 & 2). The three-remaining sites were kept as controls (harvested without mechanical site preparation). In early summer 2012, each site was divided into two sub-sites that were planted with black spruce seedlings at a low (1100 stems per ha) or high (2500 stems per ha) planting density (Figure 2.1 & 2). Seedlings were produced from a local seed source in containers of 45 cells of 110 cm³ each; seedlings averaged 20 cm in height at the time of planting.

After planting in 2012, we selected and tagged a planted seedling in each quadrat (or the seedling closest to the quadrat if none were available within the quadrat) for initial height measurement. Tagged seedlings were remeasured for height in 2016.

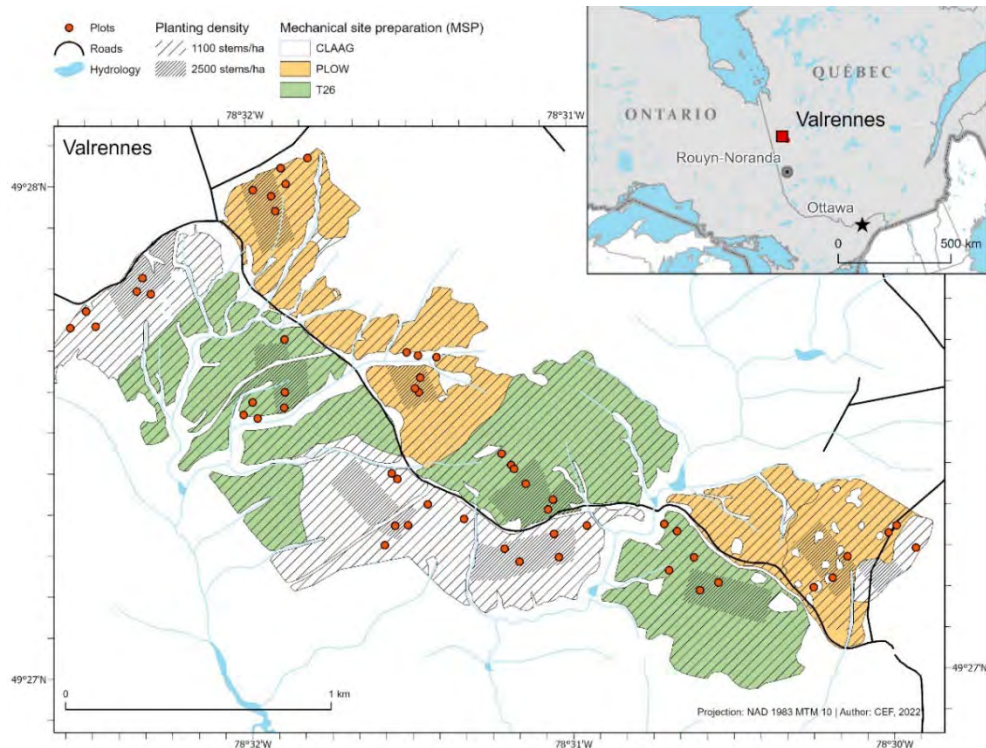


Figure 2.2 Location of the study region and experimental site, showing the distribution of the silvicultural treatments (careful logging around advanced growth (CLAAG), plowing and T26 scarification) with location of the low (1100 stem per ha) and high (2500 stem per ha) planting density areas within each site.

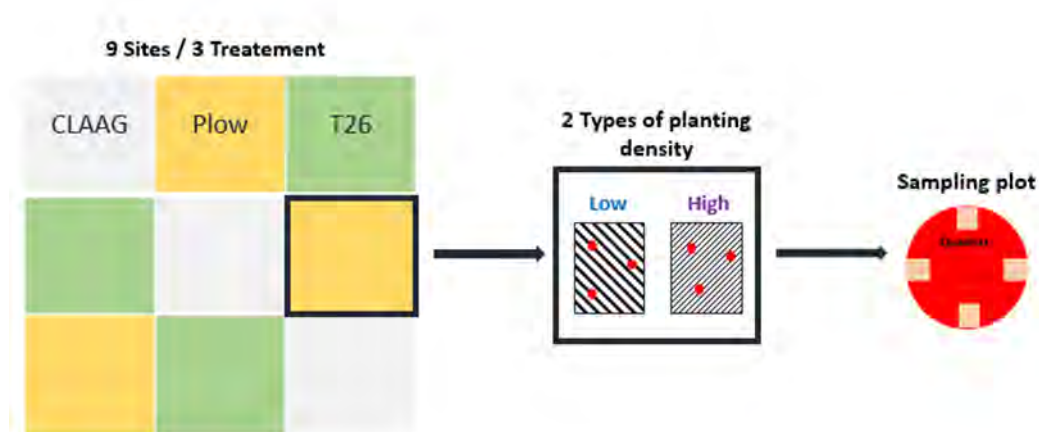


Figure 2.1 Schematic representation of the experimental design showing the 9 sites with the 3 treatments (CLAAG, plowing and T26 scarification), and the 3 sampling plots in each subsite with 2 types of planting density in each site and 4 quadrats in each sampling plot.

2.3.3 Data collection

In 2020 (the ninth growing season after planting), we revisited three sampling plots (n=54) randomly selected in each planting density subsite. During the summer and autumn, we collected data related to understory vegetation diversity and function in two 1 m² quadrats (n=108) in each selected sampling plot. All vascular plants and macro bryophyte species were identified in the field, except for *Sphagnum* spp., which were identified in the lab.

To determine the functional traits of vascular plants and bryophytes separately, percent cover was used as a proxy for biomass, and we added together the most abundant species in the quadrats until they represented at least 80% of the biomass of each of these layers (Garnier *et al.*, 2004). For bryophytes, we measured the functional “effect” traits related to the roles that bryophytes may have on ecosystem functioning (Lavorel et Garnier, 2002). We selected four effect traits: colony density (mg.cm⁻³), water content at field capacity (%), absorption capacity (ml.cm⁻³), and water percolation (%.cm⁻³). Traits were measured on 10 cm diameter colonies taken from each quadrat. In every sampled colony, all individuals were carefully removed to keep the colony structure intact. In the lab, colony samples were re-humidified before measurements by watering, and then left for 12 h in a container with water for full rehydration and weighed. Colony density was calculated using water-saturated bryophyte mass and volume. After 5 days of drying, the bryophyte colony-samples were placed in pots that contained 300 ml of water. To measure water content at field capacity, excess water was collected in a 500 ml graduated container after 12 h of soaking. The colony samples were then turned 10 times in a salad spinner. Mass was recorded and the procedure was repeated until a stable weight (+/- 0.1g) was reached.

Samples were then weighed to obtain mass at field capacity. For percolation, water that percolated through the colony was collected and measured. The percentage of water percolated was calculated and standardized by the volume of the colonies to obtain water percolation through bryophytes. Finally, the water was then added to the 500 ml graduated container. By subtracting this new volume from the initial 300 ml, we obtained the water absorption capacity of the samples.

For vascular plants, we used the Traits of Plants in Canada (TOPIC) database (Aubin *et al.*, 2020, 2012) to obtain values for three functional traits: morphology type (MOR) (abundance of herbaceous and small shrubs), maximum height (HT) (cm), and specific leaf area (SLA) ($\text{m}^2\cdot\text{kg}^{-1}$). These traits can be used to assess the impact of community changes on ecosystem properties (Garnier *et al.*, 2004).

To measure environmental conditions and planted trees, 4 quadrats were selected for measurement in each of the same plots ($n=54$), thus visiting 216 quadrats in total. Quadrats with dead trees were removed from the analysis; a total of 180 quadrats remained. We collected three soil samples at a 20 cm depth and combined them into one composite soil sample per quadrat for chemical analyses. Soil samples were transported to the lab, air-dried, sieved, and analyzed for determination of total carbon and nitrogen concentrations by dry combustion (LECO CNS-2000, LECO Corporation, TruMac CNS). We measured canopy openness at 0.3 m height in the centre of each quadrat in the four cardinal points with a spherical crown densiometer (Forestry Suppliers, Convex Model A). We also inventoried coniferous, deciduous, and shrub species taller than 1 m in height in a 40 m^2 circular sampling plot centered on the tagged planted black spruce sapling of each quadrat.

We measured the ground-level diameter and height of the tagged trees and calculated 4-year height growth using 2016 and 2020 data. In the fall 2020, needles were harvested from the top third of the planted trees; six current year twigs were collected from each tree. The needles from collected twigs were oven-dried at 50 °C for 24 h. Samples from each quadrat were combined into one composite sample and analyzed for foliar N and C concentrations.

2.3.4 Statistical analysis

All analyses were conducted in the R statistical environment v.4.1.0 (R Core Team, 2020). First, we used linear mixed models (lmer function from the *lme4* package), the sites and sampling plots were included as random factors, to evaluate the effects of planting density, mechanical site preparation (MSP), and their interaction on conifer density (natural and planted), deciduous species density, shrub density, vegetation cover and soil C/N ratio (Objective 1). We calculated estimated marginal means and conducted Tukey's honestly significant difference (HSD) pairwise comparisons with the *emmeans* package (Lenth *et al.*, 2022). We used $\alpha \leq 0.05$ as a threshold for significance when comparing treatments. Using the same approach, we evaluated treatment effects on bryophyte and vascular plant functional trait values (Objective 3), and on sapling height growth, diameter, and foliar N and C concentrations (Objective 4). Linear correlation was used to examine the relationship between functional traits and growth with the package *ggpubr* (Objective 3).

Second, in each plot, we calculated % cover (for bryophytes), Simpson's dominance index (for vascular plants) and Shannon-Wiener diversity index using the *vegan* package. We used linear mixed models followed by multiple means comparisons

using *emmeans* (Objective 2, a). Permutational multivariate analysis of variance with 999 permutations (Permanova, “adonis” function from the *vegan* package, Oksanen *et al.*, 2020) were run to test the effects of planting density, mechanical site preparation, and their interaction on understory composition vascular plants and bryophytes (Objective 2, b). The plot term nested in site was used in the “Strata” function to take into account the spatial structure in the data in the Permanova analysis and non-significant interaction terms were removed in final analysis. Results were visualized using principal coordinates analysis (PCoA, “PCOA” function in the *vegan* package) with Bray–Curtis dissimilarity distance and the Cailliez correction (package *ape*; Paradis and Schliep, 2019). Convex hulls were used to highlight the plots from different treatments in each planting density type. The “envfit” function in *vegan* was then used to fit vectors of environmental conditions (conifer density, deciduous density, shrub density, vegetation cover and soil C/N ratio) onto the ordinations to illustrate how environmental conditions in the understory relate to community composition.

2.4 Results

2.4.1 Environmental conditions

Planting density and mechanical site preparation affected all variables we measured to describe the understory environment, independently or in interaction (Table 2.1). Coniferous and deciduous density, and vegetation cover were only affected by mechanical site preparation. There was a higher density of naturally regenerated conifers in CLAAG than Plow, but there was no difference with the T26 treatment. The density of deciduous trees was higher also in CLAAG than T26 but there was no

difference with the treatment Plow. Vegetation cover was higher in CLAAG than in the other treatments. There was no significant effect of planting density on conifer density, deciduous density, and vegetation cover (Figure 2.3A, B, C, D, E & F).

The soil C/N ratio was influenced by planting density and MSP independently, with lower values measured in low planting density and CLAAG plots. Plowed plots had significantly higher values than the CLAAG treatment, and T26 was intermediate (Table 2.1, Figure. 2.3G, H). The interaction between planting density and MSP was significant for shrub density (Table 2.1), with higher shrub density in plots that received the T26 treatment and high planting density than in CLAAG with high planting density, and no difference with the other treatments (Figure. 2.3I).

Table 2.1 Results from linear mixed model for the main and interacting effects of planting density and mechanical site preparation on environmental conditions and understory diversity. Bold indicates significance at $\alpha \leq 0.05$.

Response variable	Treatment effects					
	Planting density		Mechanical site preparation		Planting density \times MSP	
	Df	<i>p</i> -value	Df	<i>p</i> -value	Df	<i>p</i> -value
Environmental conditions						
Conifer density (stems/ha)	1	0.28	2	<0.001	2	0.87
Deciduous species density (stems/ha)	1	0.56	2	0.036	2	0.3
Shrub density (stems/ha)	1	0.55	2	0.65	2	0.05
Vegetation cover (%)	1	0.5	2	0.01	2	0.96
C/N ratio	1	0.003	2	<0.001	2	0.3
Understory diversity						
Vascular plant dominance (Simpson index)	1	0.3	2	0.9	2	0.65
Vascular plant diversity (Shannon index)	1	0.07	2	0.91	2	0.09
Bryophyte cover (%)	1	0.002	2	0.11	2	<0.001
Bryophyte diversity (Shannon-Wiener index)	1	0.15	2	0.2	2	0.46

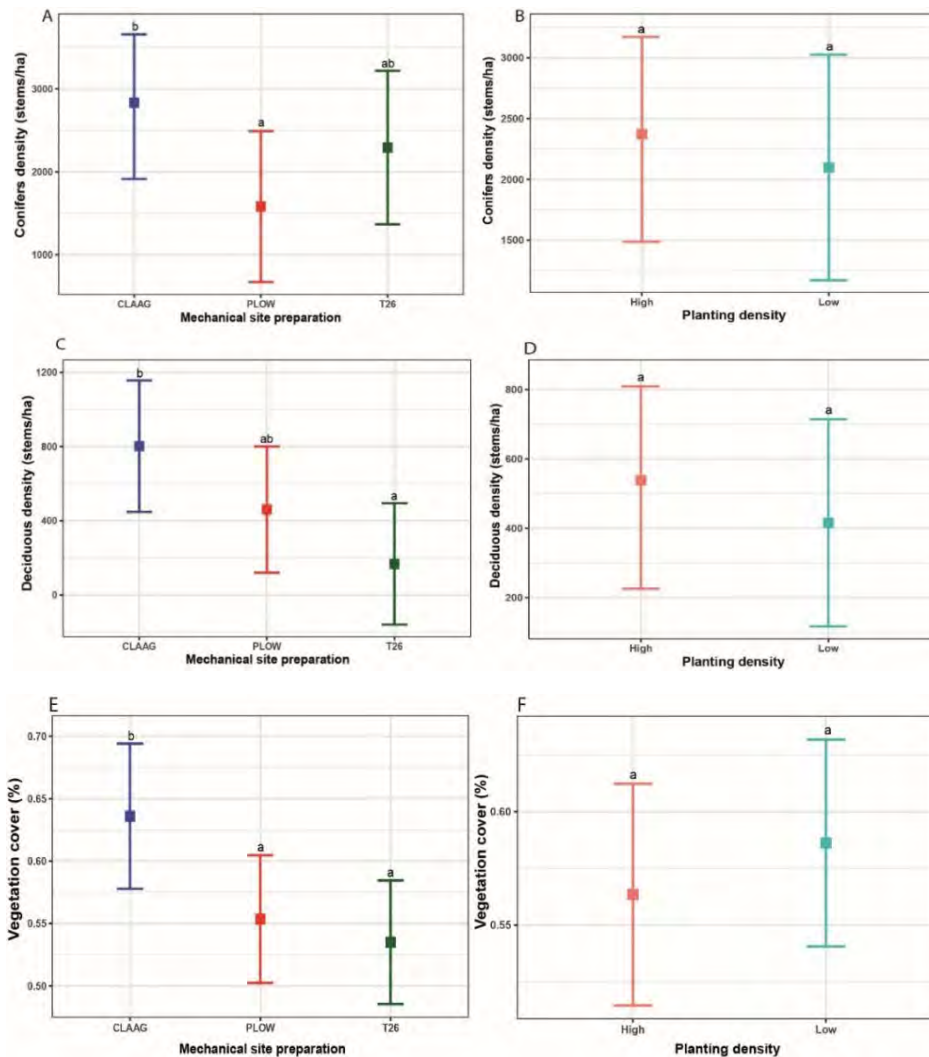
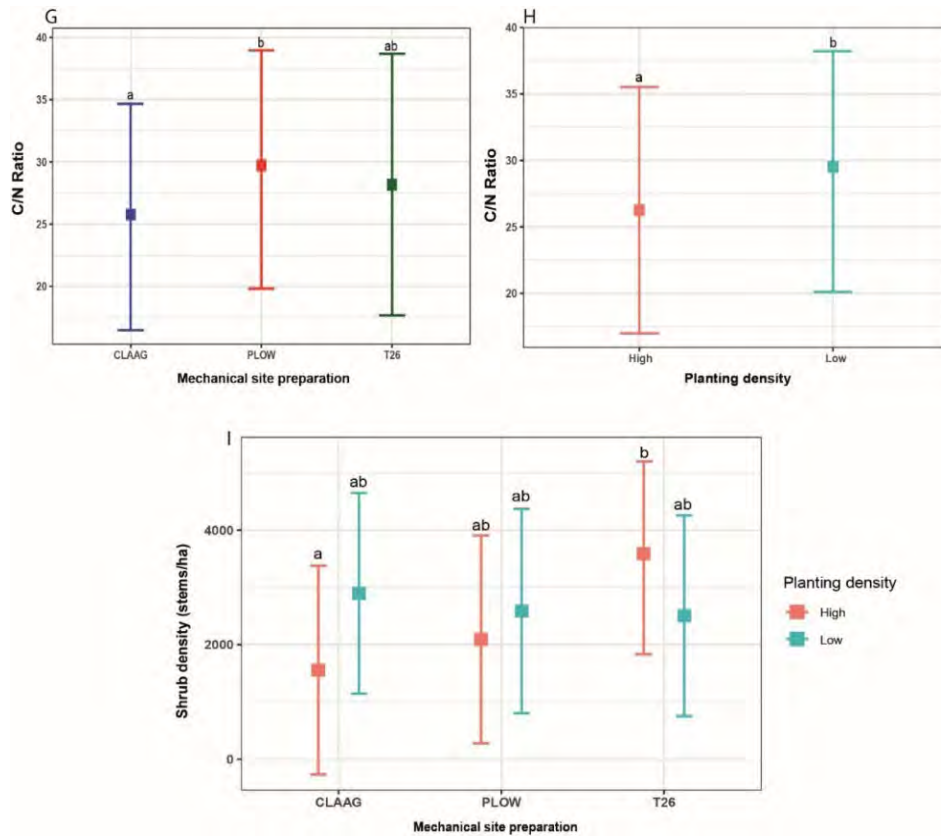


Figure 2.3 Effects of planting density (Low = 1100 seedlings/ha; High = 2500 seedlings/ha;) and mechanical site preparation (CLAAG = careful logging around advanced growth; Plow = plowing; T26 = disk trenching scarification) on naturally regenerated conifer density (A, B), deciduous species density (C, D); vegetation cover (E, F); and soil C/N ratio (G, H). Panel I illustrates the interacting effects of mechanical site preparation and planting density on shrub density. Data are presented as estimated marginal means with 95% confidence intervals. Means followed by the same letter are not significantly different at $\alpha \leq 0.05$ based on linear mixed models with Tukey HSD pairwise comparisons. (Plots CLAAG low, $n=32$; plots CLAAG high, $n=25$; plots Plow low, $n=30$; plots Plow high, $n=29$; plots T26 low, $n=34$; plots T26 high, $n=30$).

Figure 2.3 continued



2.4.2 Understory diversity

For vascular plants communities, there was no significant effect of planting density, mechanical preparation, and their interaction on the dominance and the diversity-based Simpson and Shannon indices, respectively (Table 2.1). In bryophyte communities, total cover was significantly influenced by planting density in interaction with mechanical site preparation, with greater bryophyte cover in low

density plantation plots compared to high density plots in the plow treatment (Table 2.1, Figure. 2.4).

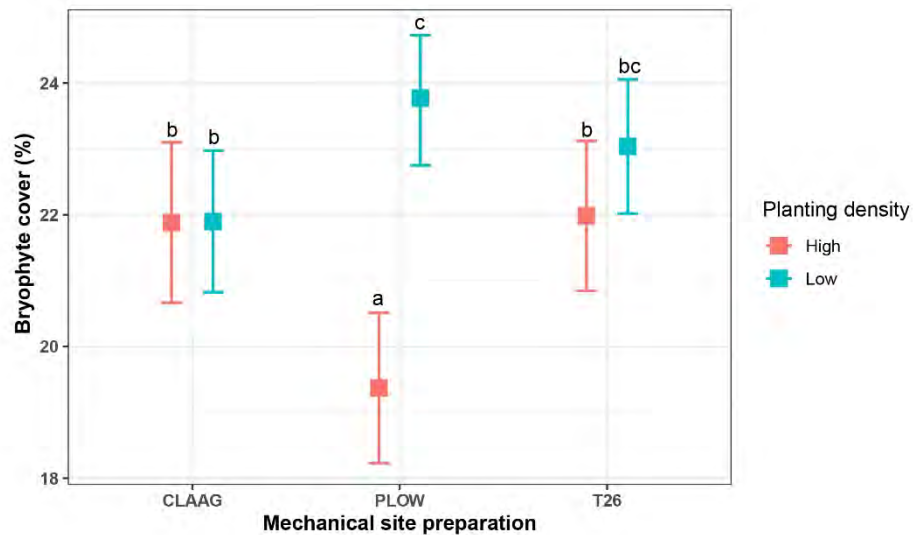


Figure 2.4 The interacting effects of planting density (Low = 1100 seedlings/ha; High = 2500 seedlings/ha;) and mechanical site preparation (CLAAG = careful logging around advance growth; Plow = plowing; T26 = disk trenching scarification) on total bryophyte cover. Data are presented as estimated marginal means with 95% confidence intervals. Means followed by the same letter are not significantly different at $\alpha \leq 0.05$ based on linear mixed models with Tukey HSD pairwise comparisons. (Plots CLAAG low, n=18; plots CLAAG high, n=14; plots Plow low, n=20; plots Plow high, n=16; plots T26 low, n=20; plots T26 high, n=16).

2.4.3 Understory composition

Understory vascular plant composition was affected by mechanical site preparation and the interaction with planting density (Table 2.2). The results of the pairwise Permanova showed that vascular plant communities were significantly different in

high planting density plots in the three treatments, but not in low planting density plots (Table 2.3). The principal coordinates analysis (PCoA) also supported the results of the Permanova (Figure 2.5). Overall, the plots on the upper side of PCoA were dominated by Plow in both high and low density plots. The lower side was dominated by T26 and CLAAG. However, in low density plots, the three treatments overlapped considerably, while in high density plots, the shape and position of the ellipses differed among treatments (Figure 2.5). Soil C/N ratio and deciduous species density had the strongest relationship with the community pattern for vascular plants on PCoA 1, while conifer density was strongly associated with PCoA 2 (Figure 2.5). There were 3 species (*Chamaedaphne calyculata* (L.) Moench, *Scirpus cyperinus* (Linnaeus) Kunth and *Equisetum arvense* (Linnaeus)) associated positively with C/N ratio on the left of PCoA 1, and species associated with deciduous density on the right (e.g., *Ribes triste* Pallas and *Rubus pubescens* Rafinesque) (Figure 2.5).

When analyzing bryophyte community composition, the results of the Permanova showed significant differences in bryophyte composition associated with the interaction between planting density and mechanical site preparation (Table 2.2). The results of pairwise Permanova showed that bryophyte communities differed only in high density with CLAAG and T26 (Table 2.3). The principal coordinates analysis (PCoA) also supported the results of Permanova. For high planting density conditions, plots on the right side at the top and the bottom of the PCoA were dominated by Plow and T26, while in the middle-left side the CLAAG plots were dominant. In the low planting density conditions, the convex hulls of the plots of the three treatments largely overlap each other (Figure 2.6). Shrub and deciduous density had the strongest relationship with community patterns for bryophytes on PCoA 1, whereas vegetation cover, soil C/N ratio and conifer density appeared related with community patterns for bryophytes on PCoA 2, (Figure 2.6). In terms of species *Ptilidium ciliare*

(L.) Hampe and *Dicranum scoparium* Hedw were positively associated to PCoA 1, while *Polytrichum commune* Hedw and a group of *Sphagnum* spp. were associated positively with shrub density to PCoA 1 (Figure 2.6).

Table 2.2 Influence of planting density and mechanical site preparation (MSP) and their interaction on vascular plant and bryophytes dissimilarity using permutational multivariate analysis of variance (Permanova) based on the Bray–Curtis dissimilarity index. Df = degrees of freedom.

Assemblage	Treatment	Df	SS	F	R ²	p-value
Vascular plant						
	Planting density	1	0.33	1.24	0.011	0.316
	Mechanical site preparation	2	2.13	4.02	0.07	0.162
	Planting ×MSP	2	0.84	1.58	0.02	0.048
	Residual	98	25.9		0.89	
Bryophytes						
	Planting density	1	0.63	2.83	0.026	0.036
	Mechanical site preparation	2	0.81	1.81	0.034	0.008
	Planting ×MSP	2	1.14	2.56	0.048	0.016
	Residual ¹	94	21.10		0.89	

¹ four plots without bryophytes

Table 2.3 Results from post-hoc pairwise tests for vascular plant and bryophytes between mechanical site preparation treatments (CLAAG = careful logging around advanced growth; Plow = plowing; T26 = disk trenching scarification). Df = degrees of freedom; SS = sum of squares. Bold indicates significance at $\alpha = 0.05$.

Vascular plant									
	Pairs		Df	SS	F	R ²	P-value	adjusted p	
CLAAG	vs PLOW	High	1	1.01	3.97	0.12	0.001	0.005	
CLAAG	vs T26	High	1	0.49	2.15	0.07	0.019	0.038	
PLOW	vs T26	High	1	0.51	2.05	0.06	0.030	0.005	
CLAAG	vs PLOW	Low	1	0.64	2.16	0.05	0.012	0.035	
CLAAG	vs T26	Low	1	0.47	1.74	0.04	0.083	0.13	
PLOW	vs T26	Low	1	1.27	4.74	0.11	0.001	0.0056	

Table 2.3 continued

Bryophytes				Df	SS	F	R ²	<i>p</i> -value	adjusted <i>p</i>
Pairs									
CLAAG	vs	PLOW	High	1	0.76	3.12	0.10	0.028	0.1
CLAAG	vs	T26	High	1	1.29	6.33	0.18	0.002	0.02
PLOW	vs	T26	High	1	0.20	0.71	0.02	0.605	0.68
CLAAG	vs	PLOW	Low	1	0.18	0.75	0.02	0.564	0.64
CLAAG	vs	T26	Low	1	0.08	0.47	0.01	0.658	0.7
PLOW	vs	T26	Low	1	0.42	2.08	0.05	0.090	0.26

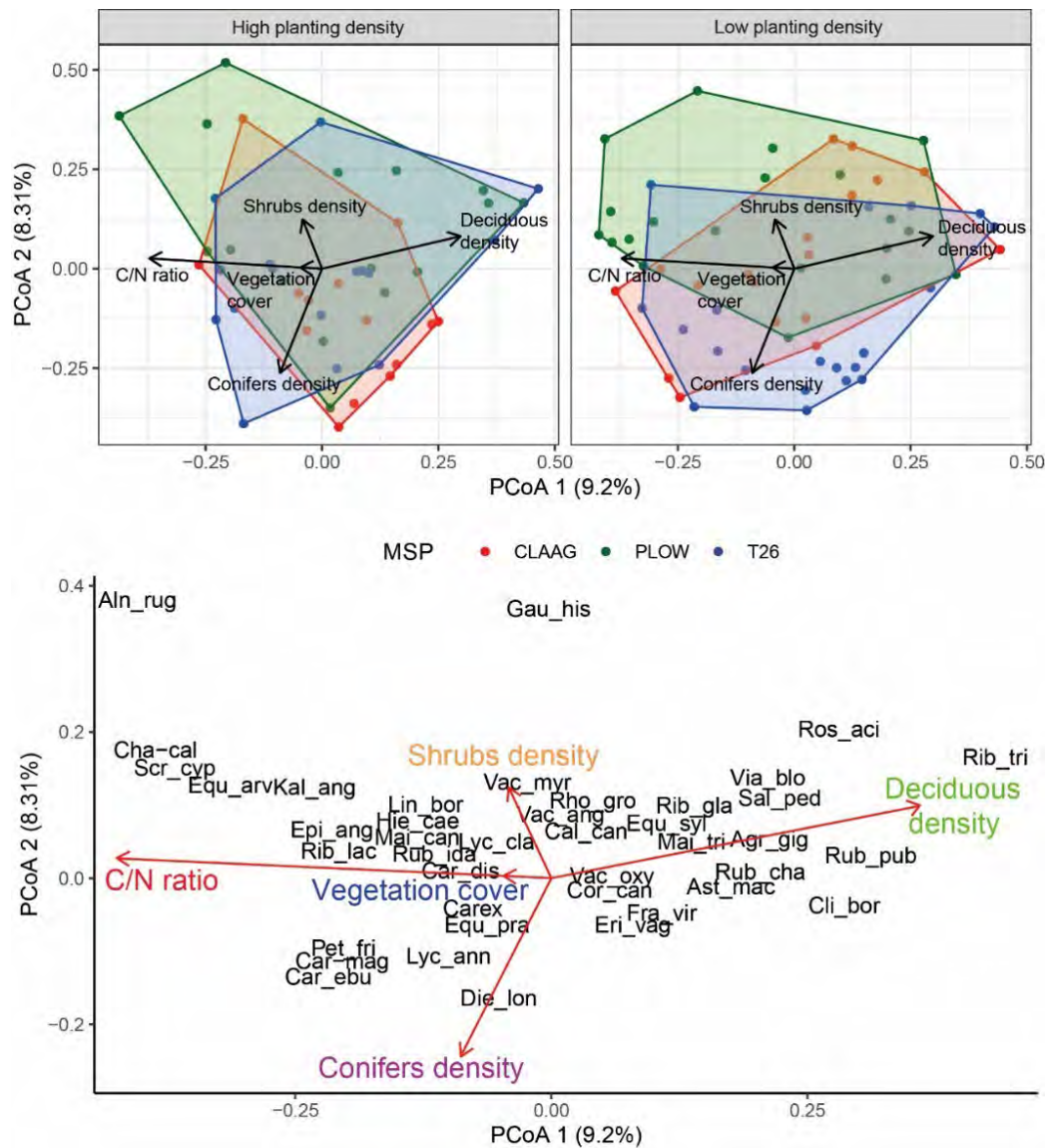


Figure 2.5 Principal coordinates analysis (PCoA) for the vascular plant composition using the Bray-Curtis dissimilarity index and a Cailliez correction. Species names and environmental conditions were added by correlation to the axes. Colors in convex hull indicate different mechanical site preparation (MSP) treatments. See Appendix A for full species names.

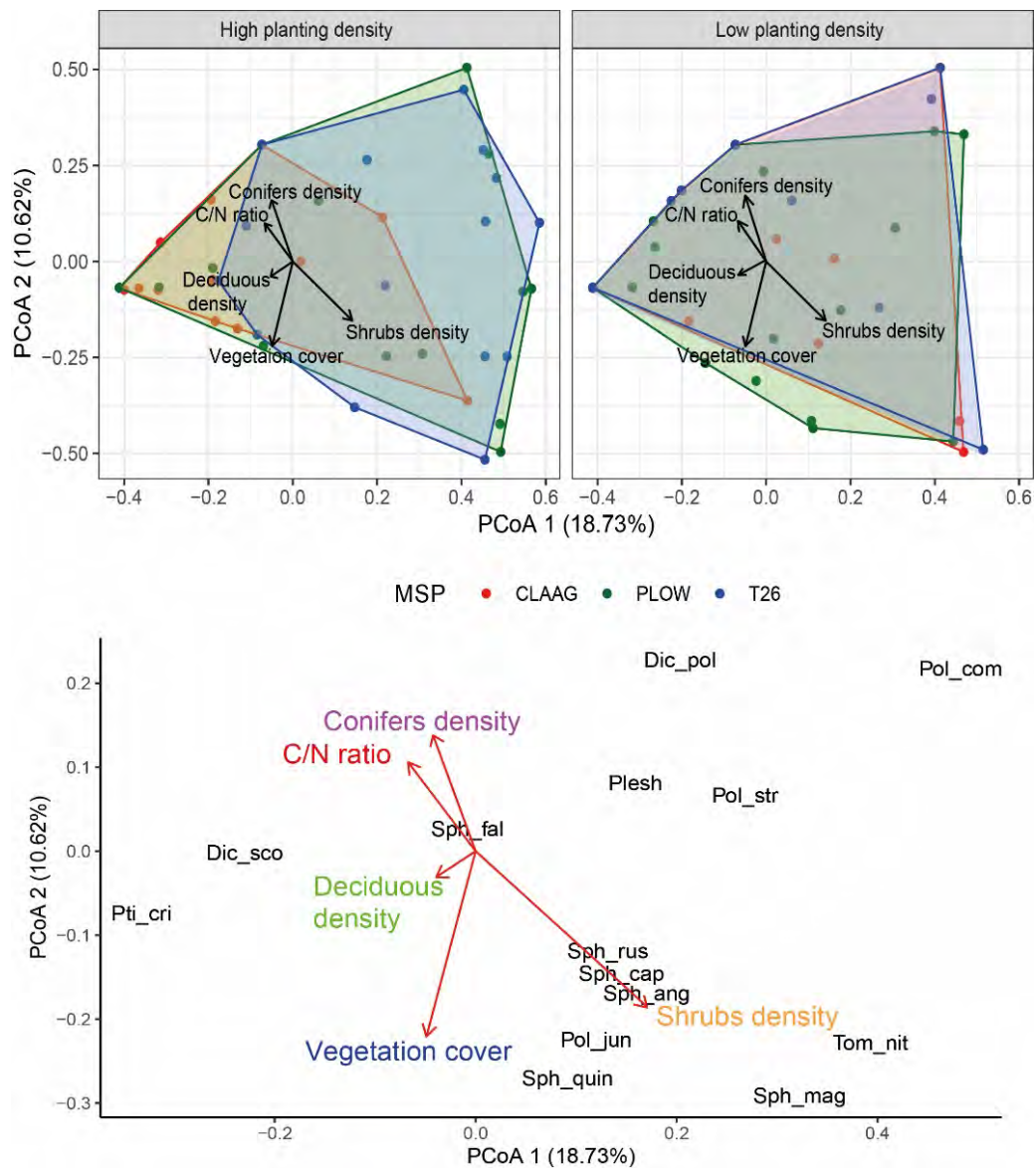


Figure 2.6 Principal coordinates analysis (PCoA) for the bryophyte composition using the Bray-Curtis dissimilarity index and a Cailliez correction. Species names and environmental conditions were added by correlation to the axes. Colors in convex hull indicate different mechanical site preparation (MSP) treatments. See Appendix A for full species names.

2.4.4 Functional traits of the understory

One of the bryophytes and two of the vascular plant functional traits varied with planting density and mechanical site preparation (Table 2.4). For bryophyte traits, water content at field capacity was significantly affected by mechanical site preparation (Table 2.4), as it was higher in the plowing treatment compared to the other treatments (Figure 2.7A). For vascular plant communities, the abundance of small shrubs was influenced by the interaction between planting density and MSP, while herbaceous plants were only affected by planting density (Table 2.4). Small shrub abundance was higher in Plow – low density plots than in other treatment combinations, while herbaceous abundance was higher in high density plots than in low planting density plots (Figure 2.7B, C).

Table 2.4 Results from linear mixed model for the main and interacting effects of planting density and mechanical site preparation on functional trait of vascular plant and bryophytes. Bold indicates significance at $\alpha \leq 0.05$.

Response variable	Treatment effect					
	Planting density		Mechanical site preparation (MSP)		Planting density *MSP	
	Df	<i>p</i> - value	Df	<i>p</i> - value	Df	<i>p</i> - value
Functional trait of bryophytes						
Water content at field capacity (%)	1	0.77	2	0.02	2	0.5
Colony density (mg.cm ⁻³)	1	0.93	2	0.51	2	0.09
Absorption capacity (ml.cm ⁻³)	1	0.13	2	0.86	2	0.16
Percolation (%.cm ⁻³)	1	0.74	2	0.95	2	0.58
Functional trait of vascular plants						
Maximum height (cm)	1	0.86	2	0.91	2	0.09
Specific leaf area (cm ² /g)	1	0.93	2	0.43	2	0.14
Small shrubs abundance	1	0.55	2	0.05	2	0.055
Herbaceous abundance	1	0.01	2	0.7	2	0.84

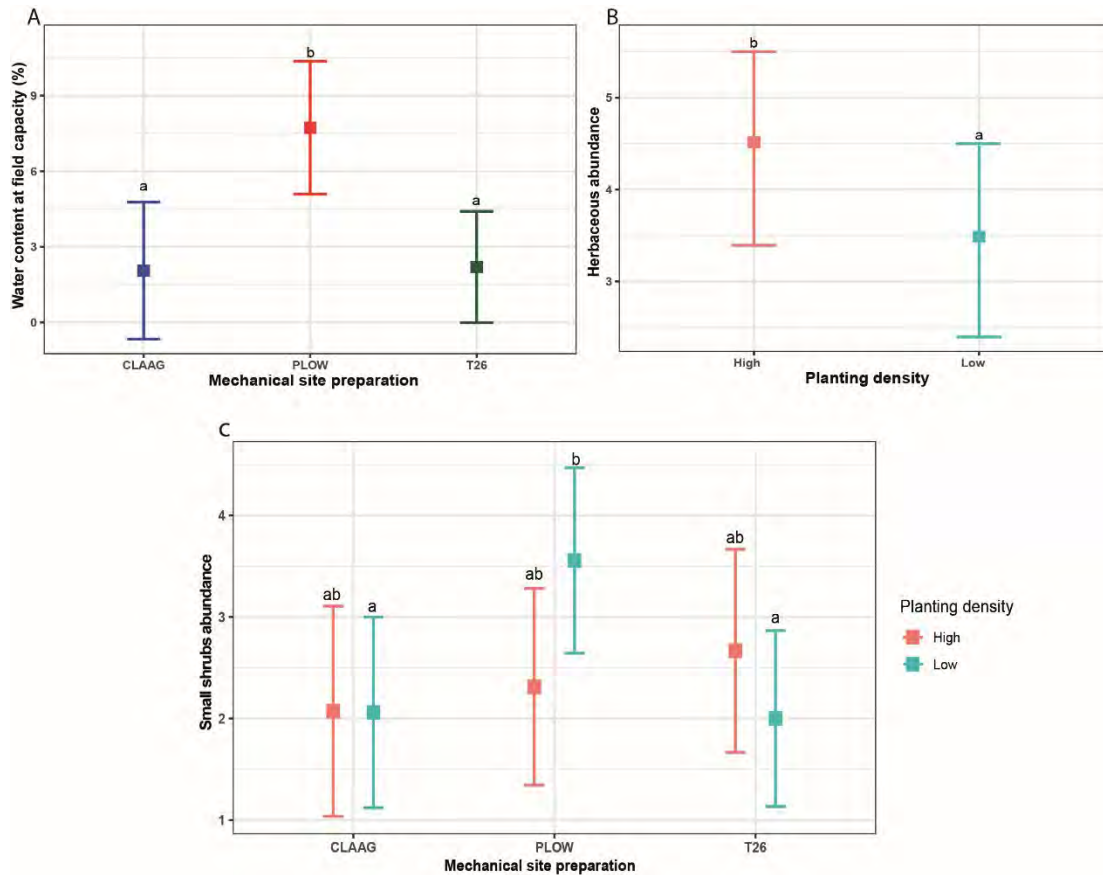


Figure 2.7 Effects of planting density (Low = 1100 seedlings/ha; High = 2500 seedlings/ha;) and mechanical site preparation (CLAAG = careful logging around advance growth; Plow = plowing; T26 = disk trenching scarification) on water content at field capacity and the herbaceous abundance (A, B). Panel C illustrates the interacting effects of mechanical site preparation and planting density on the small shrubs abundance. Data are presented as estimated marginal means with 95% confidence intervals. Means followed by the same letter are not significantly different at $\alpha \leq 0.05$ based on linear mixed models with Tukey HSD pairwise comparisons. (Plots CLAAG low, n=18; plots CLAAG high, n=14; plots Plow low, n=20; plots Plow high, n=16; plots T26 low, n=20; plots T26 high, n=16).

2.4.5 Planted black spruce

Neither mechanical site preparation, planting density or their interaction had a significant effect on planted black spruce height and ground-level diameter in 2020 (Table 2.5). Foliar N concentration was affected by mechanical site preparation; it was higher in plots submitted to the plowing treatment than in the CLAAG plots, but not different than in the T26 plots (Table 2.5; Figure 2.8A, B). Foliar C concentration and sapling growth between 2016 and 2020 were affected by the interacting effects of planting density and mechanical site preparation (Table 2.5). Foliar C concentration was higher in low planting density conditions in CLAAG and plow treatment plots, and lower in T26 – low density plots (Fig. 2.8 C). Sapling growth was higher in the high density plow treatment plots, and lower in CLAAG and T26 – high planting density plots (Fig. 2.8 D).

Table 2.5 Results from linear mixed model for the main and interacting effects of planting density and mechanical site preparation on height, growth, diameter at ground level, N and C foliar concentration of planted trees. Bold indicates significance at $\alpha \leq 0.05$.

Response variable	Treatment effect					
	Planting density		Mechanical site preparation (MSP)		Planting density \times MSP	
	Df	<i>p</i> - value	Df	<i>p</i> - value	Df	<i>p</i> - value
Height trees measured in 2020 (cm)	1	0.32	2	0.75	2	0.47
Diameter at ground-level (mm)	1	0.6	2	0.35	2	0.42
Sapling growth measured between 2016-2020 (cm)	1	0.89	2	0.88	1	0.03
N foliar %	1	0.88	2	0.02	2	0.29
C foliar %	1	0.2	2	0.001	2	<0.001

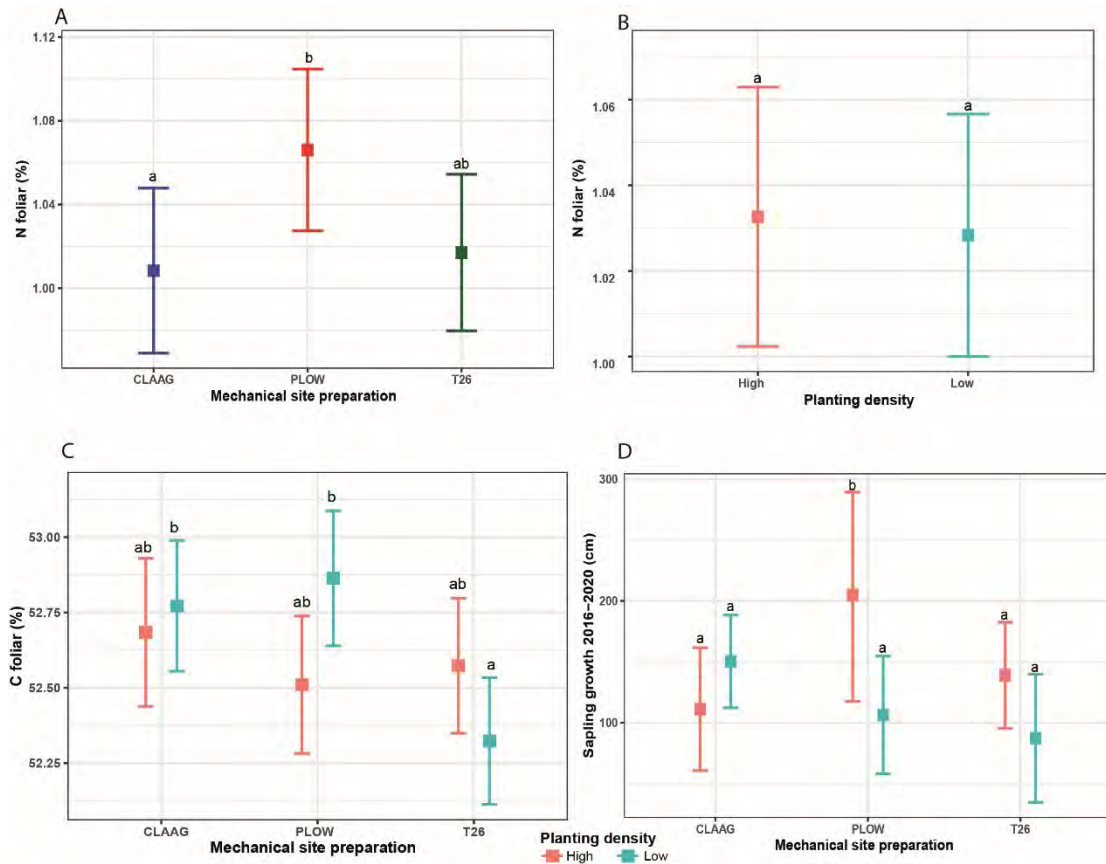


Figure 2.8 Effects of planting density (Low = 1100 seedlings/ha; High = 2500 seedlings/ha;) and mechanical site preparation (CLAAG = careful logging around advanced growth; Plow = plowing; T26 = disk trenching scarification) on foliar N concentration (A, B). Panel C and D illustrates the interacting effects of mechanical site preparation and planting density on foliar C concentration and on sapling growth. Data are presented as estimated marginal means with 95% confidence intervals. Means followed by the same letter are not significantly different at $\alpha \leq 0.05$ based on linear mixed models with Tukey HSD pairwise comparisons. (Plots CLAAG low, $n=32$; plots CLAAG high, $n=25$; plots Plow low, $n=30$; plots Plow high, $n=29$; plots T26 low, $n=34$; plots T26 high, $n=30$).

2.5 Discussion

As observed elsewhere (Henneb *et al.*, 2019 ; Akers *et al.*, 2013), planting density and mechanical site preparation both affected environmental conditions and plant growth, though their effects seem limited in our study. We found that mechanical site preparation had a greater effect than planting density on environmental conditions (Objective 1). Bryophyte cover was the only understory variable affected by planting density and mechanical site preparation (Objective 2), most probably because of the higher sensitivity of bryophytes to environmental changes than other understory groups (Frego, 2007). For example, Bu *et al.*, (2011) found that responses to environmental changes depend on the species surrounding the bryophytes; by changing interspecific interactions, environmental changes modify the effects on bryophytes and further change species composition in communities. Mechanical site preparation also led to some dissimilarities in understory composition (Objective 2), as has been reported before (Löf *et al.*, 2012). Furthermore, plant functional traits of vascular plants and bryophytes (abundance of small shrubs, herbaceous abundance, and water content at field capacity) were affected by planting density and mechanical site preparation (Objective 3). Sapling growth depended on the interaction between planting density and mechanical site preparation (Objective 4); high planting density in plots submitted to plowing resulted in greater growth than in the other treatments.

2.5.1 Effect of planting density and MSP on environmental conditions

We found a higher density of naturally established conifers after CLAAG than after the other treatments, which differs from the results of previous studies that reported greater conifer density after CLAAG + mechanical site preparation. These studies were conducted decades after treatments, while our study was carried out after just nine years, which encompasses the normal black spruce establishment time after disturbance (Greene *et al.*, 1999). Time after treatment and the time to canopy closure could explain this difference in our results, as a closed canopy normally occurs after more than 30 years in this portion of the boreal forest (Kane *et al.*, 2010 ; Taylor *et al.*, 1988).

We found no effect of planting density on regenerated conifer density, which was a surprising result. We posit that stands with low planting density provided more space and opportunities for spontaneous colonization by natural trees than high density planted stands, as there would be a greater availability of resources such as light, water and nutrients (Shaoxiong *et al.*, 2012). In contrast, higher plantation density can lead to greater intraspecific competition (Boyden *et al.*, 2008), which could induce a decrease in survival compared to lower planting density conditions (Akers *et al.*, 2013). Therefore, based on our results only 9 years after planting, it is not clear which planting density is best for forest management (with an objective of producing wood fibre), as some advantages of both high and low planting densities were detectable.

2.5.2 Effect on the understory composition and the functional traits

Understory composition was affected by the interaction between planting density and mechanical site preparation, while these differences detected by Permanova were not visually obvious on the PCoA. The composition of vascular plant communities differed among mechanical site preparation at both lower and higher planting densities. Only plots submitted to CLAAG and T26 did not present a difference in vascular plant composition at the low planting density. The composition of the bryophyte community differed among treatments at the higher planting density, with a clear difference between CLAAG vs the plow and T26 treatments. This difference might have been caused by the environmental conditions found under high planting density regime (lower light availability, higher nutrients availability and higher moisture), which would be affected by the higher deciduous sapling density in this treatment (Tinya *et al.*, 2009 ; Rodríguez-Calcerrada *et al.*, 2008 ; Cole and Newton, 1986). Few studies are available to explore potential reasons for these findings; further studies are needed to clarify the mechanisms behind this response.

Moreover, understory composition was affected by the soil C/N ratio, coniferous species, and deciduous species density. Deciduous species density was the main driver of many vascular plant community composition patterns. This is consistent with previous findings that show how deciduous stands tend to have an understory with higher species richness than coniferous stands, as they are characterized by higher understory light and soil nutrient availability (Tinya *et al.*, 2009 ; Roberts, 2004 ; Légaré *et al.*, 2002). Furthermore, the topsoil of coniferous stands usually have higher C/N ratios, lower pH values and lower nutrient availability compared to that found in deciduous stands (Augusto *et al.*, 2003 ; Légaré *et al.*, 2001), which

might be a limiting factor for vascular species establishment and growth (Barbier *et al.*, 2008). In contrast to the vascular plants, the environmental conditions had little effect on the first axis of bryophyte composition. However, as observed for vascular plants, conifer density, C/N ratio, and shrub density drove the pattern on the second axis of bryophyte composition. The first axis may have been affected by other variables influencing the bryophyte community that we did not measure, such as thickness of the organic layer or the position of the water table (Fenton and Bergeron, 2006).

To our knowledge, our study is the first to evaluate the potential interacting effects of planting density and mechanical site preparation on functional traits of vascular plants and bryophytes. Small shrub abundance, herbaceous abundance and bryophyte water content at field capacity were the only functional traits affected by planting density or mechanical site preparation. Our findings for some vascular plant traits were similar to those reported by Wei *et al.*, (2019), who found that mechanical site preparation affected vascular plants traits after soil disturbance and as a function of light availability. Hence, mechanical site preparation played an important role in understory functional composition and diversity (Wei *et al.*, 2019). The positive effect of higher planting density in interaction with mechanical site preparation on small shrub and herbaceous species abundance suggests that their abundance could be responsive to environmental changes (Haeussler *et al.*, 2002). The effects that we observed for small shrub and herbaceous species support that trait–growth rate relationships are much stronger for small plants than for large trees. Interspecific variation in functional traits (demographic attributes) is indeed much larger for small plants than for large trees, which makes it statistically easier to detect environmental changes–functional trait relationships (Poorter *et al.*, 2008).

Functional trait values have important consequences for ecosystem processes, properties, and services (Conti and Díaz, 2013 ; Fortunel *et al.*, 2009 ; Garnier *et al.*, 2004). The relationship between vascular plants traits and sapling growth was not significant (results not shown), contrary to the results of Wei *et al.*, (2021), who found a significant relationship between vascular plant traits and sapling growth in CLAAG sites after 25 years. This indicates that time since treatment, age, and tree size play an important role on this trait–growth relationship. Further studies about functional traits and sapling growth are needed to further understand these results.

Among the traits we measured, only the water content of bryophytes was affected by mechanical site preparation. Previous studies also support the role of water content as an indicator of environmental changes (Rice and Schneider, 2004 ; Zotz *et al.*, 2000 ; Proctor, 1982); water content in bryophytes is controlled by forest canopy structural properties as it mediates the amount of light reaching the understory (Michel *et al.*, 2013). Consequently, our results suggest that mechanical site preparation could affect bryophyte water content through its effects on stand structure. Mechanical site preparation could ultimately affect ecological services provided by bryophytes, as leaf water content is an important limiting factor for bryophyte photosynthesis (Newmaster *et al.*, 2007). The water dynamics of nonvascular plants are not as well understood or quantified as those of vascular plants and are rarely modelled (Bond-Lamberty *et al.*, 2011, 2007 ; Sonnentag *et al.*, 2008). Therefore, further studies are needed to better understand this relationship.

2.5.3 Black spruce growth

Planting density only affected sapling growth in the plow treatment; higher growth was observed in high planting density compared to low density conditions. We posit that after the plowing treatment, higher planting density probably led to higher tree litter production and lower ericaceous shrub litter, which resulted in higher nutrient availability for sapling growth (see Joannis *et al.*, 2007) than in the lower planting density (Guo and Sims, 1999). Previous studies conducted on the same site demonstrated that plowing favoured early seedling growth, compared to the other treatments (Henneb *et al.*, 2019, 2015). The higher growth of black spruce in plowed plots (highest severity disturbance) can be explained by the resultant higher soil temperatures and lower interception of water by competing vegetation, which is known to increase soil water availability and favours root growth (Thiffault and Roy, 2011 ; Hébert *et al.*, 2006 ; Boucher *et al.*, 1998). In support of this interpretation, we found that foliar nutrient concentrations, especially N, were higher in plots submitted to plowing compared to plots treated by CLAAG only or T26. Other studies have found positive effects of plowing, even in the long-term (Mäkitalo *et al.*, 2010 ; Örlander *et al.*, 1998).

2.6 Conclusion

The interacting effects of planting density and mechanical site preparation on plantation characteristics was demonstrated with consequences for sapling growth, some understory functional traits, and in subtle shifts in understory community composition. Generally, planting density had a greater effect in the plow treatments than in the other treatments. Plowing favoured nutrient cycling through an increased abundance of herbaceous species and small shrubs, thus, plowing paired with higher planting density would be a better choice for black spruce tree growth than other treatments. In addition, bryophyte cover seems to be a good indicator to evaluate treatment effects on understory communities as they responded more strongly than vascular plants. However, no significant effect of planting density on tree diameter was found after nine years. Silvicultural experiments need to be followed in the long term to assess treatment effects on productivity, especially in the context of global change (Achim *et al.*, 2022).

CHAPITRE III

CONCLUSION GÉNÉRALE

Le projet visait à étudier les effets principaux et les interactions entre la densité de plantation et la préparation mécanique du sol sur la croissance des jeunes plants d'épinettes noires, la composition du sous-bois et les traits fonctionnels du sous-bois. Nous avons observé une densité plus élevée de conifères naturellement établis après une CPRS (coupe avec protection de la régénération et des sols) sans préparation mécanique du sol qu'après les autres traitements, ce qui diffère des résultats des études précédentes. Nous n'avons trouvé aucun effet de la densité de plantation sur la densité des conifères régénérés. Nous posons l'hypothèse que les peuplements à faible densité de plantation offrent plus d'espace et d'opportunités pour la colonisation spontanée par les arbres que les peuplements à forte densité, étant donné que la disponibilité des ressources telles que la lumière, l'eau et les nutriments est plus grande (Shaoxiong *et al.*, 2012). Pour la composition du sous-bois, les résultats indiquaient que les différences de communauté entre les traitements ont été affectées par la densité de plantation.

En général, la densité de plantation a eu un effet plus important dans les sites traités par le hersage que dans les parcelles soumises aux autres traitements. Le hersage a favorisé le cyclage des nutriments en augmentant l'abondance des herbacées et les

petits arbustes. De ce fait, une densité de plantation plus élevée avec le traitement hersage serait un meilleur choix pour la croissance des épinettes noires que les autres interactions. Cependant, aucun effet significatif de la densité de plantation sur le diamètre des arbres n'a été trouvé. Il importe de procéder à des suivis à plus long terme afin de vérifier ces tendances.

Bien que cette étude ne rapporte les résultats des effets de la préparation du sol sur la croissance des semis que pendant les premières années suivant les traitements, il est probable que cet effet se maintienne au fil du temps. Des études futures, après la fermeture de la canopée, aideront les sylviculteurs à prendre des décisions sur la densité de plantation de l'épinette noire. La rentabilité des approches de régénération des peuplements de la forêt boréale est un argument important si l'on considère le potentiel qu'elles représentent en regard, notamment, des possibilités de fixation du carbone. La sélection d'un niveau optimal de densité de plantation est, en fin de compte, une décision économique et doit prendre en compte les effets de la densité sur les coûts de plantation et de transport, les implications sur les régimes d'éclaircies, les coûts des futures récoltes, ainsi que sur la qualité et la valeur du bois. Nos résultats constituent une base pour de futures études sur la régénération des forêts paludifiées.

APPENDIX A

Code Name	Full Species name (Vascular plants)
AGGIG	<i>Agrostis gigantea</i> Roth
ALNRUG	<i>Alnus incana</i> subsp. <i>Rugosa</i> (Du Roi) R.T. Clausen
ASTMAC	<i>Aster macrophyllus</i> Linnaeus
CALCAN	<i>Calamagrostis canadensis</i> (Michaux) Palisot de Beauvois
CARDIS	<i>Carex disperma</i> Dewey
CAREBU	<i>Carex eburnea</i> Boott
CAREX	<i>Carex</i> sp.
CARMAG	<i>Carex magellanica</i> Lamarck
CHACAL	<i>Chamaedaphne calyculata</i> (L.) Moench
CLIBOR	<i>Clintonia borealis</i> (Aiton) Rafinesque
CORCAN	<i>Cornus canadensis</i> L.
DIELON	<i>Diervilla lonicera</i> Miller
EPIANG	<i>Epilobium angustifolium</i> Linnaeus
EQUARV	<i>Equisetum arvense</i> Linnaeus
EQUpra	<i>Equisetum pratense</i> Ehrhart
EQUsyl	<i>Equisetum sylvaticum</i> Linnaeus
ERIVAG	<i>Eriophorum vaginatum</i> Linnaeus
FRAVIR	<i>Fragaria virginiana</i> Miller
GAUHIS	<i>Gaultheria hispidula</i> (L.) Muhl.
HIECAE	<i>Pilosella caespitosa</i> (Dumortier) P.D. Sell & C. West
KALANG	<i>Kalmia angustifolia</i> Linnaeus
LINBOR	<i>Linnaea borealis</i> Linnaeus
LYCCLA	<i>Lycopodium clavatum</i> Linnaeus
LYCANN	<i>Spinulum annotinum</i> (Linnaeus) A. Haines subsp. <i>Annotinum</i>
MAICAN	<i>Maianthemum canadense</i> Desfontaines
MAITRI	<i>Maianthemum trifolium</i> (Linnaeus) Sloboda
PETFRI	<i>Petasites frigidus</i> (Linnaeus) Fries
RHOGRO	<i>Rhododendron groenlandicum</i> (Oeder) Kron & Judd

RIBGLA	<i>Ribes glandulosum</i> Grauer
RIBLAC	<i>Ribes lacustre</i> (Persoon) Poiret
RIBTRI	<i>Ribes triste</i> Pallas
ROSACI	<i>Rosa acicularis</i> Lindley
RUBPUB	<i>Rubus pubescens</i> Rafinesque
RUBIDA	<i>Rubus idaeus</i> Linnaeus
RUBCHA	<i>Rubus chamaemorus</i> Linnaeus
SALPED	<i>Salix pedicellaris</i> Pursh
SCRCYP	<i>Scirpus cyperinus</i> (Linnaeus) Kunth
VACANG	<i>Vaccinium angustifolium</i> Aiton
VACMYR	<i>Vaccinium myrtilloides</i> Michx
VACOXY	<i>Vaccinium oxycoccos</i> L.
VIOLLA	<i>Viola blanda</i> Willdenow
Code name	Full Species name (Bryophytes)
DICSCO	<i>Dicranum scoparium</i> Hedw
DICPOL	<i>Dicranum polysetum</i> Sw.
SPHANG	<i>Sphagnum angustifolium</i> (Warnst.) C.E.O. Jensen
SPHCAP	<i>Sphagnum capillifolium</i> (Ehrh.) Hedw.
SPHFAL	<i>Sphagnum fallax</i> H. Klinggr.
SPHMAG	<i>Sphagnum magellanicum</i> Brid
SPHQIN	<i>Sphagnum quinquefarium</i> (Lindb.) Warnst.
SPHRUS	<i>Sphagnum russowii</i> Warnst
TOMNIT	<i>Tomentypnum nitens</i> (Hedw.) Loeske
PLESCH	<i>Pleurozium schreberi</i> (Willd. ex Brid.) Mitt.
POLCOM	<i>Polytrichum commune</i> Hedw.
POLJUNI	<i>Polytrichum juniperinum</i> Hedw.
POLSTR	<i>Polytrichum strictum</i> Menzies ex Brid
PTICRI	<i>Ptilium crista-castrensis</i> (Hedw.) De Not

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