Effets des pratiques de remise en production des sites dans la région des sables bitumineux sur la croissance du peuplier et de l'épinette blanche

Mémoire

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Sous la direction de :

Evelyne Thiffault, directrice de recherche

Brad Pinno, codirecteur de recherche

Résumé

Identifier les principaux facteurs affectant la croissance des arbres sur les sites remis en production après exploitation par l'industrie des sables bitumineux dans le nord de l'Alberta peut nous informer sur ce qui peut être fait pour réduire les délais avant le retour d'un écosystème fonctionnel sur ces sites. Cette étude a examiné le rôle joué par la disponibilité de l'eau, la concentration foliaire des nutriments, de la compétition ainsi que les propriétés chimiques du sol sur la croissance en hauteur de jeunes peupliers faux-tremble et épinettes blanches sur deux types de sol restauré soumis à deux niveaux de fertilisation. Pour fins de comparaison, un site naturel ayant brulé au même moment que la construction du site remis en production a aussi été étudié. Les arbres poussant sur le mélange tourbe-minéral étaient plus grands que ceux du mélange sol forestier-minéral, quoique la différence n'était pas significative dans le cas de l'épinette. La fertilisation n'avait pas d'effet apparent sur la hauteur des arbres sur le mélange sol forestier-minéral et avait un effet négatif sur la hauteur pour les arbres plantés sur le mélange tourbe-minéral. L'utilisation de l'engrais a augmenté le couvert occupé par les plantes concurrentes sur les deux types de sols ce qui, en combinaison avec l'absence d'effet positif sur la hauteur des arbres, suggère que l'effet de la fertilisation est négatif puisqu'elle augmente la compétition pour les ressources sans pour autant favoriser la croissance des deux essences étudiées. Les principaux facteurs affectant la croissance des arbres sur le site d'étude se sont révélés être majoritairement liés à la disponibilité des éléments nutritifs et ne semblent pas être significativement différents entre les deux types de sols. La croissance des drageons de peuplier sur le site naturel n'était pas corrélée avec les variables mesurées ce qui semble indiquer que la hauteur des drageons n'était toujours pas liée aux facteurs environnementaux mesurés après six ans.

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Avant-propos

Ce mémoire contient un article rédigé en anglais précédé d'une introduction générale précisant le contexte du projet de recherche et suivi d'une conclusion générale. L'article sera modifié en fonction des commentaires des évaluateurs du mémoire avant d'être soumis pour publication. J'ai réalisé le protocole de recherche avec l'aide de ma directrice et de mon codirecteur, procédé à la récolte des données, réalisé les analyses statistiques, interprété les résultats ainsi que rédigé le manuscrit. Je serai donc l'auteur principal de l'article. Ma directrice de recherche, Evelyne Thiffault, a participé au développement du protocole de recherche, a fourni d'indispensables avis au fil du projet et a corrigé et commenté les différentes versions du manuscrit au fil de sa rédaction. Elle sera ainsi second auteure de l'article. Mon codirecteur, Brad Pinno, a participé au développement du protocole de recherche, a contribué à l'interprétation des résultats et participé à la rédaction de l'article par ses commentaires. Il sera troisième auteur de l'article inséré.

Introduction générale

La croissance des arbres est déterminée par une variété de facteurs ayant chacun un degré d'importance variant selon l'essence, le site et le stade de développements du peuplement (Brady & Weil, 2007). Un facteur tel que la disponibilité de l'eau peut être le principal facteur limitant la croissance sur certains types de sols alors que la disponibilité des éléments nutritifs pourrait être plus critique sur des sites pauvres. Comprendre ce qui limite la croissance des arbres sur une variété de sites est crucial pour orienter les pratiques de sylviculture et d'aménagement forestier, maintenir les services écologiques présentement offerts par les forêts ainsi que pour les efforts de remise en production des sites affectés par l'activité humaine. Ce dernier aspect est particulièrement d'intérêt en Alberta (Canada) où l'extraction des sables bitumineux entraine la nécessité de développer des pratiques de remise en production des sites applicables sur de larges territoires.

L'Alberta (Canada) possède le troisième plus grand gisement de pétrole au monde (Alberta Energy, 2014) et la majorité de celui-ci est contenue dans les dépôts de sables bitumineux situés dans le nord de la province. Ces dépôts couvrent 142 200 km^2 dont 4800 km^2 sont suffisamment près de la surface pour être exploitables par des mines à ciel ouvert (Alberta Energy, 2014). De cette superficie, 844 km^2 avaient déjà été affectés par les activités reliées à l'extraction des sables bitumineux en date du 31 décembre 2012 (Alberta Energy, 2013). Étant donnée l'obligation règlementaire pour les exploitants de remettre en état le territoire après la fin des activités industrielles (Alberta Government, 2012), des efforts sont faits pour remettre en production les sites après leur exploitation en recréant un sol pouvant supporter une forêt. Des 844 km^2 affectés, 77 km^2 sont considérés comme en cours de restauration, mais seulement 1 km^2 du territoire est certifié comme étant restauré par le gouvernement albertain (Alberta Energy, 2013). Pour être certifié, un site doit être semblable au paysage naturel de la région et doit donc 1) posséder une biodiversité représentative et 2) posséder une productivité équivalente permettant les mêmes usages du territoire qu'auparavant (Audet et al., 2015). Pour une partie significative des sites présentement exploités, cela se traduit par le retour de peuplements boréaux mixtes représentatifs des forêts locales (Alberta Environment, 2010).

Le peuplier faux-tremble (*Populus tremuloides Michx.*) et l'épinette blanche (*Picea glauca Moench.*) sont deux essences qui poussent communément ensemble dans la forêt boréale mixte canadienne (Man & Lieffers, 1999) et occupent les sites forestiers sur sol minéral dans la région des sables bitumineux.

Le peuplier est une essence pionnière à croissance rapide et à courte durée de vie (Perala, 1990) pouvant se régénérer à la fois par graines si un lit de germination et des conditions adéquates sont présents (Romme et al., 2005; Landhäusser et al., 2010; Pinno & Errington, 2015), et de façon clonale par drageonnement (Frey et al., 2003). Cette espèce est intolérante à l'ombre (Ung et al., 2001), exigeante en éléments nutritifs (Maliondo et al., 1990) et réagit fortement aux conditions environnementales (Chen et al., 2002). Le peuplier faux-tremble peut croître sur une variété de milieux, mais il s'agît principalement d'une essence de milieux mésiques bien drainés (Haeussler & Coates, 1986). La disponibilité de l'eau serait l'un des principaux facteurs gouvernant la croissance de cette essence (Fralish & Loucks, 1975); toutefois, le peuplier arrive quand même à croître sur des sites plus secs malgré son taux relativement élevé de transpiration (Peterson & Peterson, 1992). Une étude de Pinno et Bélanger (2011) a identifié la texture et le pH du sol comme ayant le plus grand impact sur la productivité du peuplier dans la forêt boréale de Saskatchewan, bien que les relations observées peuvent varier d'une région à l'autre. Reich et al. (1997) ainsi que Turkington et al. (1998) ont montré que l'azote (N) est un élément nutritif limitant communément la croissance des arbres en forêt boréale. Strong et La Roi (1985) ont observé un lien entre le développement du système racinaire du peuplier et le contenu en phosphate (PO_4) du sol, les menant à conclure que le phosphore est un facteur limitant la croissance du peuplier faux-tremble dans la forêt boréale. De même, une étude sur de jeunes peupliers hybride suggère également que le phosphore (P) peut être limitant chez le genre *Populus* (Pinno & Bélanger, 2009). Lu et Sucoff (2001) ont observé une relation positive entre la concentration en calcium (Ca) dans le sol et la croissance du peuplier faux-tremble, mais la valeur de concentration à laquelle le gain maximal de croissance était atteint était suffisamment faible pour être généralement atteinte par des peuplements naturels.

Contrairement au peuplier, l'épinette blanche est une essence tolérante à l'ombre et à croissance lente (Nienstaedt & Zasada, 1990). Sa croissance est déterminée (Nienstaedt, 1966), c'est-à-dire que la croissance d'une année est déterminée lors de la formation des bourgeons à l'automne de la saison de croissance précédente, ce qui limite sa capacité à réagir à une amélioration de ses conditions de croissance pendant l'année en cours. Elle peut croître sous couvert pendant quelques décennies (Osika et al., 2013) pour ensuite accélérer sa croissance une fois libérée de la compétition (Nienstaedt & Zasada, 1990).

L'épinette blanche atteint sa croissance optimale sur des sols frais et subhydriques (Sutton, 1969); une étude menée en Alberta par Chen et al. (2017) a trouvé une relation positive entre son accroissement en diamètre et la quantité de précipitations reçues dans la dernière année, les menant à conclure que les épisodes de sécheresse sont le principal facteur limitant la croissance de l'épinette blanche dans des milieux en déficit hydrique tel que l'Alberta. Les semis d'épinette blanche semblent particulièrement sensibles à la compétition pendant leurs premières années de croissance. Une étude testant différent niveaux de compétition a trouvé que lors d'une augmentation progressive du nombre de plantes concurrentes l'impact sur la croissance en hauteur suite à l'ajout des premiers compétiteurs était plus fort que celui dû aux compétiteurs ajoutés par la suite (Jobidon, 2000). Sutton (1975) a observé qu'il est possible d'accélérer la croissance en hauteur de l'épinette blanche et d'améliorer la concentration foliaire en éléments nutritifs en contrôlant la compétition végétale. De son côté, Groot (1999) a confirmé qu'il est effectivement possible d'augmenter la croissance en hauteur de l'épinette blanche en contrôlant la végétation concurrente, mais qu'il est tout de même souhaitable de maintenir un minimum de couvert pouvant protéger les jeunes épinettes des conditions climatiques adverses.

Ces deux essences ont déjà été le sujet d'études pour comprendre ce qui affecte leurs taux de croissance en forêt naturelle et en plantation; les connaissances sont par contre beaucoup plus limitées sur les sites remis en production étant données les conditions plus variables de ces sites. Les sites miniers restaurés possèdent souvent plusieurs caractéristiques défavorables au développement de la végétation désirée, tels qu'une forte compétition pour les ressources par des espèces invasives ainsi qu'un sol compacté, pauvre en éléments nutritifs, avec un taux de salinité élevé et un pH soit très faible ou très élevé (Bussler et al., 1984). De plus, étant données les différentes combinaisons possibles de méthodes et matériaux utilisés lors d'un projet de remise en production, les conditions de croissance offertes par chaque site peuvent différer suffisamment pour que des conclusions tirées d'un projet soient difficilement applicables pour un autre. C'est pourquoi il est important de voir dans quelle mesure il est possible de définir des relations plus générales sur les facteurs influençant ou limitant la productivité des espèces dans des conditions de remise en production.

L'objectif général de ce projet est d'améliorer la compréhension des facteurs limitant la croissance du peuplier faux-tremble et de l'épinette blanche sur les sites remis en production après leur exploitation par l'industrie des sables bitumineux. Les objectifs spécifiques sont de 1) caractériser les conditions de croissance résultant de différents traitements de remise en production, en comparaison avec des conditions sur sites naturels, 2) d'évaluer la croissance en hauteur du peuplier faux-tremble et de l'épinette blanche sur sites remis en production et sur sites naturels en fonction des différentes conditions de croissance et 3) d'identifier les principaux facteurs affectant la croissance en hauteur du peuplier faux-tremble et de l'épinette blanche sur les différents sites étudiés.

Effects of land reclamation practices on the productivity of young trembling aspen and white spruce on a reclaimed oil sands mining site in northern Alberta

Résumé

Identifier les principaux facteurs affectant la croissance des arbres sur les sites remis en production après exploitation par l'industrie des sables bitumineux dans le nord de l'Alberta peut nous informer sur ce qui peut être fait pour réduire les délais avant le retour d'un écosystème fonctionnel sur ces sites. Cette étude a examiné le rôle joué par la disponibilité de l'eau, la concentration foliaire des nutriments, de la compétition ainsi que les propriétés chimiques du sol sur la croissance en hauteur de jeunes peupliers faux-tremble et épinettes blanches sur deux types de sol restauré soumis à deux niveaux de fertilisation. Pour fins de comparaison, un site naturel ayant brulé au même moment que la construction du site remis en production a aussi été étudié. Les arbres poussant sur le mélange tourbe-minéral étaient plus grands que ceux du mélange sol forestier-minéral, quoique la différence n'était pas significative dans le cas de l'épinette. La fertilisation n'avait pas d'effet apparent sur la hauteur des arbres sur le mélange sol forestier-minéral et avait un effet négatif sur la hauteur pour les arbres plantés sur le mélange tourbe-minéral. L'utilisation de l'engrais a augmenté le couvert occupé par les plantes concurrentes sur les deux types de sols ce qui, en combinaison avec l'absence d'effet positif sur la hauteur des arbres, suggère que l'effet de la fertilisation est négatif puisqu'elle augmente la compétition pour les ressources sans pour autant favoriser la croissance des deux essences étudiées. Les principaux facteurs affectant la croissance des arbres sur le site d'étude se sont révélés être majoritairement liés à la disponibilité des éléments nutritifs et ne semblent pas être significativement différents entre les deux types de sols. La croissance des drageons de peuplier sur le site naturel n'était pas corrélée avec les variables mesurées ce qui semble indiquer que la hauteur des drageons n'était toujours pas liée aux facteurs environnementaux mesurés après six ans.

Abstract

Identifying the main drivers of tree height growth on reclaimed oil sands sites of northern Alberta can provide useful information on what can be done to shorten the recovery time of these disturbed sites. The effect of water availability, foliar nutrient concentrations, competition, and soil chemical properties on young trembling aspen and white spruce height across two soil types (peat-mineral mix and forest floor-mineral mix) and two fertilizer levels (200 kg NPK ha^{-1} and no fertilizer) was examined. For comparison, we also studied a natural site that burned the same year the reclaimed site was established. The peat-mineral soil had the greatest tree height for both species, though not by a significant margin in the case of white spruce. The fertilizer treatment had no apparent effect on tree height on the forest floor-mineral soil and a negative effect on the peat-mineral soil. Fertilization increased vegetation cover on both soil types, which, when combined with the negative or lack of durable effect of fertilization on tree height, suggest that the increase in competition for resources could have had a stronger effect on tree height than the increase in immediately available nutrients following fertilization. The majority of tree height growth drivers found were related to nutrient availability and, as far as we can tell, did not significantly differ between reclamation soil types. Aspen sucker height on the burned site was not strongly correlated to the measured variables, suggesting that suckers do not yet fully rely on their environment for height growth.

Introduction

Tree productivity is determined by a variety of factors that each has a varying degree of importance depending on location, species and tree and stand development stage (Brady & Weil, 2007). Water availability may be the overarching factor limiting growth on some types of soils or when seedlings are establishing, while nutrient supply rate could be a driver of greater importance on other sites where nutrient availability is limited or when stands approach canopy closure. Understanding drivers and constraints of tree productivity on a variety of sites is crucial to informing forest and land management practices: it has the potential to improve the efficiency of treatments aimed at optimising wood production of stands, restoring degraded forests or reclaiming non-forest sites such as mining areas.

Trembling aspen (*Populus tremuloides Michx.*) and white spruce (*Picea glauca Moench.*) are two ecologically and economically important species that commonly grow together in mixedwood stands on upland sites of the Canadian boreal forest (Man & Lieffers, 1999). Understanding drivers of productivity of aspen and white spruce has become more important recently in northern Alberta (Canada) where the exploitation of oil sands deposits has driven the need for effective land reclamation methods of post-mining areas. According to provincial regulations, requirements for successful reclamation projects include the return of the land to “equivalent land capability” (Alberta Government, 1999). In most instances of mined upland sites, the natural land equivalent is a productive boreal forest. Promoting fast establishment and growth of native tree species is an important step towards effective reclamation by accelerating site capture and crown closure. Providing the right conditions for fast initial growth of aspen and white spruce on reclaimed soils and being able to predict tree productivity can therefore help accelerate this process.

Aspen is a short-lived fast-growing pioneer specie (Perala, 1990) that can regenerate both clonally, by suckering from its root system, and from seeds when the right seedbed and conditions are present (Romme et al., 2005; Landhäusser et al., 2010; Pinno & Errington 2015). It is shade intolerant (Ung et al., 2001), nutrient demanding (Maliondo et al., 1990) and reacts strongly to changes in environmental conditions (Chen et al., 2002). Aspen is able to grow in diverse conditions but it mostly occupies well-drained upland sites (Haeussler & Coates, 1986). Water availability is often identified as one of the main drivers governing aspen growth (Fralish & Loucks, 1975); the species can nevertheless tolerate moderately dry sites despite its greater transpiration rate relative to other tree species typically associated with these types of sites (Peterson & Peterson, 1992). Soil pH also has an impact on aspen growth (Pinno & Bélanger, 2011) in part due to its effect on soil nutrients availability (Mengel & Kirby, 1982). Nitrogen (N) is commonly limiting tree growth in the boreal forest (Reich et al., 1997, Turkington et al., 1998) while phosphorus (P) is also limiting for the *Populus* genus (Pinno & Bélanger, 2009) and soil calcium (Ca) also influences aspen growth but is usually found at sufficient concentration in natural aspen stands (Lu & Sucoff, 2001).

White spruce is a slow growing shade tolerant species (Nienstaedt & Zasada, 1990) that has determinate growth (Nienstaedt, 1966), limiting its ability to react to current-year environmental conditions. It grows on a diversity of sites but prefers moist fertile soils (Sutton, 1969). Current and previous year precipitations are positively linked to white spruce diameter growth (Chen et al., 2017) indicating that water availability should be one of the main drivers of spruce growth, especially in water-deficit environments (Chen et al., 2017). Planted white spruce seedlings seem to be particularly sensitive to competition during the early years of establishment. An increase in competition incrementally reduces height growth of white spruce seedlings, with the greatest decrease happening at low levels of competition (Jobidon, 2000). Height growth of white spruce seedlings can be increased using early vegetation control methods when the seedlings are sheltered from adverse environmental conditions, but this increase is weaker in more open conditions where competition removal exposes the seedlings to unfavourable microclimatic conditions (Groot, 1999). Planted white spruce height growth and foliar nutrient concentration can also be improved by using a vegetation control treatment (Sutton, 1975).

The two most commonly used reclamation cover soils in the oil sands are peat-mineral mix (PMM) and forest floor-mineral mix (FFMM). FFMM comprises organic matter from the surface layer of upland forest floors mixed with the underlying mineral soil. It contains upland forest plant propagules adapted to mixedwood stands. Compared with PPM, FFMM has characteristics that are somewhat closer to natural forest soils due to its origin. PMM is made from peat from lowland wetlands mixed with the underlying mineral soil. It has a high moisture holding capacity and high organic matter content but lacks upland vegetation propagules. Both mixtures are often imperfectly mixed, resulting in an uneven distribution of organic matter over the reclaimed site. Reclaimed oil sands sites typically differ from surrounding natural forests in terms of organic matter composition and nutrient availability (Turcotte et al., 2009; Rowland et al., 2009). PMM and FFMM soils also tend to have higher pH due to the mixing of mineral soil with the organic matter, resulting in increased nitrification activity in reclaimed soils when compared to the surrounding boreal forest (Jamro et al., 2014). Nevertheless, FFMM is considered to be a better growth medium in terms of nutrient availability when compared to PMM due to its greater potential for N mineralization and concentration of P and K (MacKenzie & Naeth, 2010), three commonly limiting elements in upland boreal forests (Turkington et al., 1998). Plant communities growing on sites reclaimed with either FFMM or PMM have also been found to be different from the surrounding boreal forests, with some native species still absent a few years after reclamation, and non-native plants often representing a significant part of the vegetation cover (Errington & Pinno, 2015).

Fertilization is commonly used in oil sands reclamation with the goal of accelerating early tree growth by improving the bioavailability of some soil nutrients perceived to be limiting. Broadcast application of a fertilizer is often used to deliver mixes of immediately available nutrients. However, it has been shown to have a low nutrient recovery rate (Sloan et al. 2016), and to mostly benefit competing vegetation (Sloan & Jacobs, 2013), which can in turn have a negative effect on tree seedling establishment (Pinno & Errington, 2015).

Drivers of aspen and white spruce productivity have already been studied in a variety of environments (Ung et al., 2001; Hogg et al., 2005; Sutton, 1995; Jobidon, 2000). However, the distinct nature of reclaimed soils can create contrasting growing conditions from those observed in natural forest ecosystems, making tree productivity hard to predict with existing data, especially in the early years following reclamation. Environmental factors typically influencing growth on natural soils (i.e. soil moisture, soil pH, soil carbon, nutrient availability, competition, and light availability) could have a different impact on young trees growing on reclaimed soils resulting in different factors driving tree growth on reclaimed sites. Duan et al. (2015) have suggested that drivers of tree growth differ between various reclamation treatments; however, results from this study are difficult to extrapolate since tree species effect was confounded with the effect of the reclamation treatment. As the choice of tree species to be planted on a site is based on the characteristics of the reconstructed soil, opportunities to compare growth drivers of one species between reclamation soil types or different species on the same soil type are limited. A study by Sloan et al. (2016) on different fertilization methods used on reclaimed sites found that white spruce and trembling aspen have different resource allocation strategies: aspen allocates resources more evenly between roots, stems and leaves while white spruce allocates most of its resources to needles and stems. These different strategies could mean that these two species also have different growth drivers. Moreover, most studies conducted on reclaimed sites have been done using older reclaimed sites where trees are already well established (Duan et al., 2015; Huang et al., 2014) which makes their results difficult to extrapolate to younger trees. Tree growth requirements usually change between early establishment stages, during which the tree tries to establish its rooting system and is usually very sensitive to light and microclimate, and later stages when the stand nears canopy closure and nutrient needs are at its highest; whether this generalisation holds true for reclaimed sites remain to be tested. Better knowledge of what is influencing tree growth on reclaimed sites at an early stage could accelerate recovery by allowing stakeholders to intervene early if a problem is detected.

The aim of this study was to identify, analyze and contrast the drivers of tree height growth for young aspen and white spruce as influenced by reclamation soils (PMM vs. FFMM). The specific objectives were (*i*) to characterize reclamation soils (PMM vs. FFMM) and practices (fertilization or no fertilization), (*ii*) to compare tree height between the four reclamation treatments (i.e. combinations of reclamation soils and fertilization practices), and (*iii*) to identify the main drivers of tree height growth on each reclamation soil. Results were also compared with natural i.e. non-reclaimed forest conditions, in order to gain better insight of differences between natural and anthropogenic environments and disturbances.

Methods

Study site characterization

The study was conducted on a 88.6 hectares (ha) reclaimed overburden dump at an oil sands mine, located north of Fort McMurray, Alberta, Canada (57º 20' N, 111º 49' W, figure 1). The climate is continental boreal with long and cold winters and short and cool summers. The average temperature in July is 17.1ºC with mean annual precipitations of 418.6 mm (Fort McMurray 1981-2010, Environment Canada climate normal).

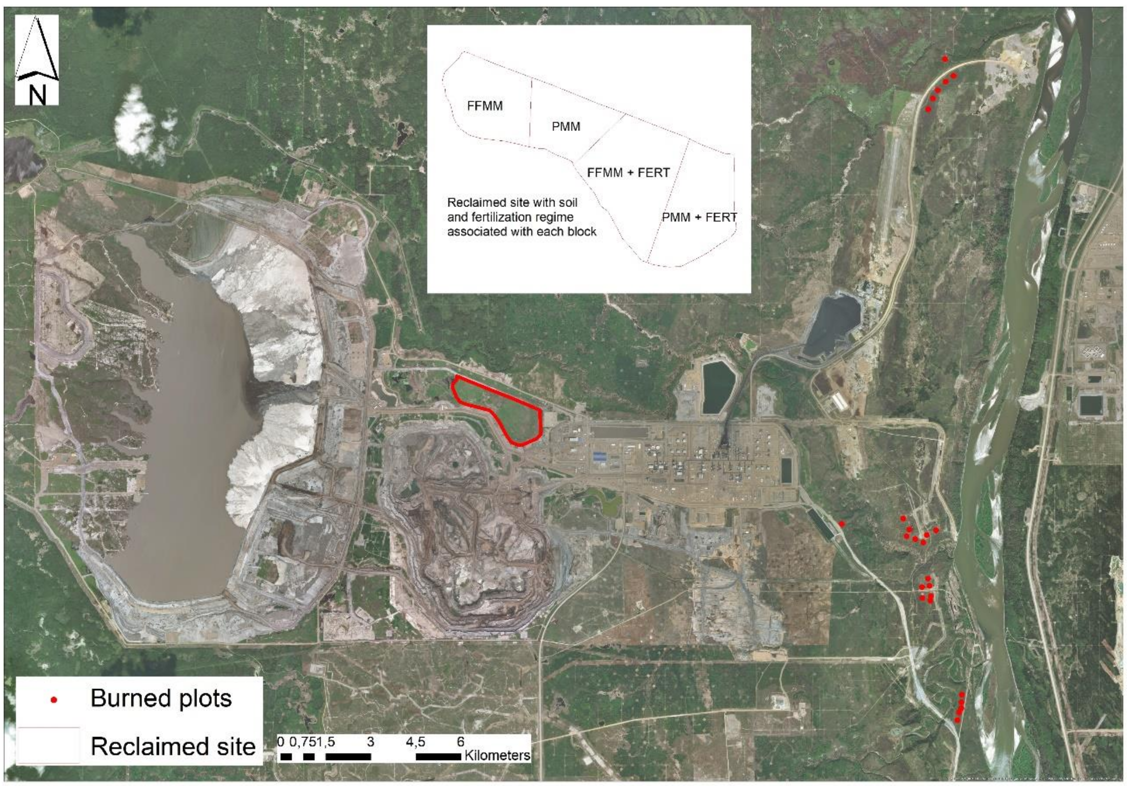

Fig. 1. Study area and plots location

The site was reconstructed in 2011 from saline-sodic overburden covered with 1.5 m of non-saline overburden. This was then capped with an organic-mineral cover soil mixture; either a forest floor-mineral mix (FFMM) or a peat-mineral mix (PMM) was used. The reclaimed site was split into four blocks of about 20 ha each, with two of them receiving the FFMM soil type while the other two received the PMM soil type. One block of each soil type was then fertilized with a 29-9-9-9 mix of nitrogen (N) – phosphorus (P)- potassium (K)- sulfur (S) at a rate of 100 kg N ha^{-1} each year for the first two years, resulting in a factorial experimental design of two soil types (FFMM or PMM) x two fertilizer regimes (fertilized or not fertilized). The whole site was seeded with barley (*Hordeum vulgare*) to limit risks of erosion during its first growing season. Locally sourced white spruce seedlings were planted the same year at a density of 2000 stems ha^{-1} while trembling aspen regenerated naturally from windblown seeds coming from nearby mature aspen stands (Pinno & Errington, 2015).

To compare height and environmental drivers of tree height growth between natural and reclaimed forests, regenerating stands, located close to the reclamation site, and that burned during the 2011 Richardson Fire, i.e. at the same time as the construction of the reclamation site, were selected as natural analogues. The following criteria were used for the selection of burned stands: they had to be aspen dominated, and had to be located at least 50 m from the nearest road or opening and at least 100 m from each other.

Field sampling

Data collection was done during the summer of 2016, corresponding to the sixth growing season since reclamation or disturbance. On the reclaimed site, data was collected from 96 sampling plots following a systematic grid pattern, and from 25 additional plots established on burned sites. Due to the shape and size of the different reclamation treatments, the number of plots for each treatment combination varied between 17 and 29. On the reclaimed site, each plot was circular with a 3.99 m radius (50 m^2). On the burned sites, plots had a 1.78 m radius due to the much greater tree density. The sampling plots on the reclaimed and burned sites were all considered to be independent replicates as they were located at least 100 meters apart from each other.

Height (5-cm incremental classes) of each tree (either aspen or spruce) was measured in each plot (96 reclaimed + 25 burned) in September. Leaves and current year needles were collected inside each tree plot from the top third of the five tallest trees of both species. Measurements of soil moisture and competing vegetation cover and sampling of soil and leaves were performed in four subplots located immediately outside of the circumference of the tree plots at each cardinal point (to avoid disturbances within plots). Soil moisture was measured at a depth of 12 cm in June, July, and August using a TDR soil moisture probe (Field Scout TDR 300, Spectrum Technologies Inc., Aurora, IL). The plot value used for statistical analyses was the combined average of the three measurements. Competing vegetation cover was visually estimated to the nearest percent at the functional group level (lichens, bryophytes, graminoids, shrubs, native forbs, non-native forbs, tree) inside a 1 X 1 m frame. On the reclaimed site, soil samples were collected in each subplot at a depth of 0-15 cm from the surface. On the fire sites, the first 15 cm of the A horizon (under the forest floor) was collected. Samples were then bulked volumetrically to obtain one composite sample per plot.

Lab analysis

Soil samples were air dried for a month and passed through a 2 mm sieve. Soil pH was measured with a VWR H30PCD handheld pH meter in deionized water using a 1:3 (w/v) water:soil ratio. Soil subsamples were finely ground with a ball mill prior to determination of total C and N by combustion using a Costech Model EA 4010 Elemental Analyzer (Costech International Strumatzione, Florence, ITA) and PO_4-P by colorimetry using a SmartChem Discrete Wet Chemistry Analyzer, Model 200 (Westco Scientific, Limited, Brookfield, CT, USA). Foliar samples were air dried, foliar unit mass was determined and the samples were then ground and analyzed for total N by combustion using a Costech Model EA 4010 Elemental Analyzer (Costech International Strumatzione, Florence, ITA) and P, K, S, Ca and Mg concentration analysis by ICP-OES after acidic digestion using a Thermo iCAP6300 Duo (Thermo Fisher Corp., Cambridge, UKS).

Statistical analysis

Average tree height from the tallest five individual aspen or white spruce trees within each plot (equivalent to 1000 stems/ha, hereafter referred to as "crop tree average height") was used as the main response variable and as an indicator of potential tree growth. Environmental factors (i.e. soil moisture, soil pH, soil carbon, nutrient availability, and competing cover) were used as explanatory variables. It was assumed that these five tallest crop trees would eventually grow to become dominant or co-dominant and are therefore good indicators of potential productivity of each plot, similar to site index calculation (Carmean & Li, 1998). Moreover, continual ingress of aspen seedlings on the reclaimed site prevented us from getting an accurate portrait of potential tree growth using simple average height.

Of the 96 reclaimed plots, 81 contained aspen seedlings, but only 64 had five or more individuals and could be used for height analyses, whereas all of the burned plots had aspen root suckers growing on them but one plot had less than the required five. 94 of the reclaimed plots had white spruce growing on them, with 80 of them having five or more seedlings; since only one of the burned plots contained spruce seedlings, the burned sites were not considered for this species.

Differences between treatments in environmental factors that are thought to influence tree growth (i.e. soil moisture, soil pH, soil carbon, nutrient availability, and competing cover) were assessed using Kruskal-Wallis tests followed by a Dunn's post-hoc test since the data did not respect the assumptions of parametric tests based on Shapiro and Bartlett tests and a visual inspection of the residuals.

Two-way analysis of variance (ANOVA) with soil cover treatment (FFMM vs. PMM) and fertilizer treatment (fertilized or not) as the main effects were used to determine, for each species, whether there was a significant difference between treatments in crop tree average height. For height data to conform to the ANOVA's assumptions, they were transformed using a square-root transformation.

The influence of environmental variables (soil moisture, soil pH, soil carbon, nutrient availability, and competing cover) on tree height, i.e. average crop tree height, was evaluated by building and comparing a set of generalized linear models (GLM). Five separate analyses were performed, one for each of the two studied tree species and the three soil/site types (PMM vs. FFMM vs. burned). Fertilized and unfertilized plots of a same soil x species combination were pooled for the analysis to isolate the effect of soil types on the drivers of tree height. For the purpose of these analyses, foliar nutrient concentrations were used as a proxy for soil nutrient availability. Tested variables consisted of soil moisture (VWC), soil pH (pH), soil carbon concentration (TC), soil available P (PHOS), graminoid cover (GRAM), native forb cover (NAT), non-native forb cover (INV), shrub cover (SHRU), total competing vegetation cover (TVEG), foliar N concentration (fol.N), foliar P concentration (fol.P), foliar K concentration (fol.K), foliar S concentration (fol.S), foliar Ca concentration (fol.Ca), and foliar Mg concentration (fol.Mg). Soil N concentration was strongly correlated to soil carbon concentration and was therefore not included in the analysis to avoid collinearity.

Model comparison was done using the second-order Akaike information criterion (AICc), which corrects for small sample size (Burnham & Anderson, 2002). A set of 60 models including up to six variables each was created by combining variables so that each variable is placed in the presence of every other variables for a roughly equal amount of times. Multimodel inference was then used to assess the importance of each variable across all the models it was included in by averaging and weighing the models. This method avoids uncertainty caused by choosing a "best" model by using information from all the models rather than from only one of them (Burnham et al., 2011). Variables that had an average estimate in which 90 % unconditional confidence intervals (UCI) excluded 0 were considered good predictors of tree height.

Data analysis was done using the R statistical programming environment (Version 3.4.1; R Core Team, 2017). Dunn's tests were done using the *dunn.test* package (Version 1.3.4; Dinno, 2017). The *AICcModAvg* package (Version 2.1-1; Mazerolle, 2017) was used for model selection and multimodel inference based on AICc. Pseudo R^2 for the generalized linear models was calculated using the *rms* package (Version 5.1-1; Harrell, 2017).

Results

After six growing seasons, aspen crop tree height on the PMM cover soil was greater than on FFMM (Fig.2A); however, this was counteracted by the addition of the fertilizer on the PMM soils (significant soil x fertilizer interaction $p<0.001$) and resulted in smaller natural aspen seedlings on fertilized PMM. Root suckers of aspen on burned sites were taller than the seedling origin aspen on reclaimed sites.

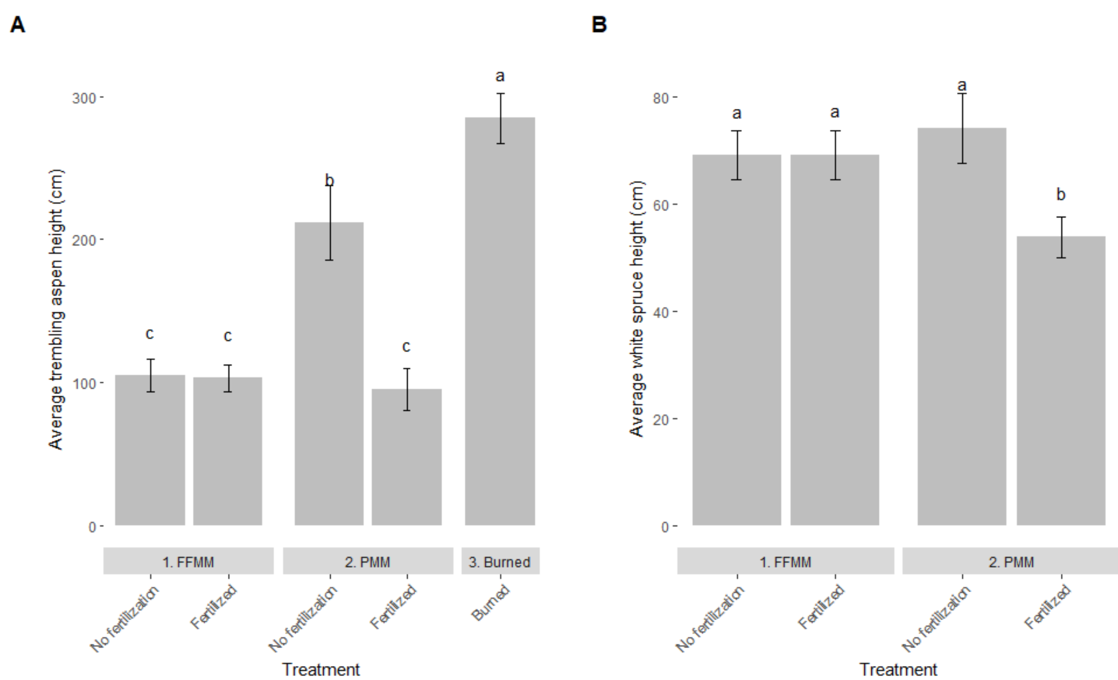

Fig. 2. Tree height on each treatment for (a) trembling aspen and (b) white spruce. Values are crop tree average height and standard error. Bars accompanied by a different letter are statistically different ($p<0.05$)

Similarly to what was observed with aspen, a significant soil x fertilizer interaction ($p<0.001$) affected white spruce height due to fertilization decreasing spruce height on PMM while having no effect on FFMM (Fig. 2B).

Average soil moisture was not significantly different among reclamation treatments but was significantly higher than in the burned plots (Table 1, $p<0.001$). Soil pH varied across reclamation plots from 3.19 to 8.31 but on average, pH was highest ($p<0.001$) in the unfertilized FFMM and lowest in the unfertilized PMM, which was similar to the burned sites soil pH ($p=0.310$). Soil PO_4-P concentration was lower ($p<0.001$) on the reclaimed plots than on the burned sites; among reclamation treatments, the fertilized FFMM had a higher concentration than the other reclamation treatments ($p=0.023$). Differences were also found in soil carbon concentration ($p<0.001$) with PMM soils having higher concentration than FFMM and the burned sites.

Table 1. Basic site and soil characteristics of reclamation treatments and burned sites

Soil	Total carbon (%)	Total nitrogen (%)	Available phosphorus (PO_4-P mg kg^{-1})	pH	Average soil moisture (%)
FFMM	3.52 c (0.52)	0.15 c (0.01)	8.81 c (1.35)	7.35 a (0.12)	25.93 a (1.15)
FFMM + fertilizer	5.26 b (0.94)	0.25 b (0.03)	11.25 b (1.08)	6.85 b (0.10)	26.56 a (1.07)
PMM	10.44 a (1.77)	0.40 a (0.04)	6.73 c (0.97)	5.77 c (0.31)	25.61 a (1.31)
PMM + fertilizer	8.51 a (1.24)	0.36 ab (0.04)	8.25 c (1.44)	6.57 b (0.18)	26.31 a (0.92)
Burned sites	1.29 d (0.18)	0.08 d (0.01)	41.99 a (7.27)	6.05 c (0.08)	13.78 b (0.64)

Values are mean and (standard error). Different letters indicate significant differences between soil types ($p<0.05$).

Total competing vegetation cover was greater on FFMM than on PMM ($p=0.020$) and increased with fertilization on both types of soil ($p<0.001$) (Fig. 3). Non-native forb cover did not significantly differ between PMM and FFMM ($p=0.279$). The most common non-native forbs observed on the reclaimed site were *Melilotus alba*, *Sonchus arvensis* and *Taraxacum officinal*; this group increased in cover with the application of the fertilizer on both reclamation soils (FFMM $p=0.037$; PMM $p=0.017$). Native forb cover was greater on FFMM than on PMM ($p<0.001$); fertilization did not significantly affect this functional group on FFMM ($p=0.150$) or PMM ($p=0.230$). Graminoid cover was greater on FFMM than on PMM ($p<0.001$); the fertilizer treatment increased the cover of this functional group on FFMM ($p=0.021$) but not on PMM ($p=0.245$). Shrubs, the most commonly observed species being *Salix sp.* and *Rosa acicularis*, occupied less space on PMM than on FFMM ($p=0.025$); all the reclamation treatments had lower shrub cover than the natural burned plots ($p<0.001$). Fertilizer had a positive effect on shrub cover on FFMM ($p=0.042$).

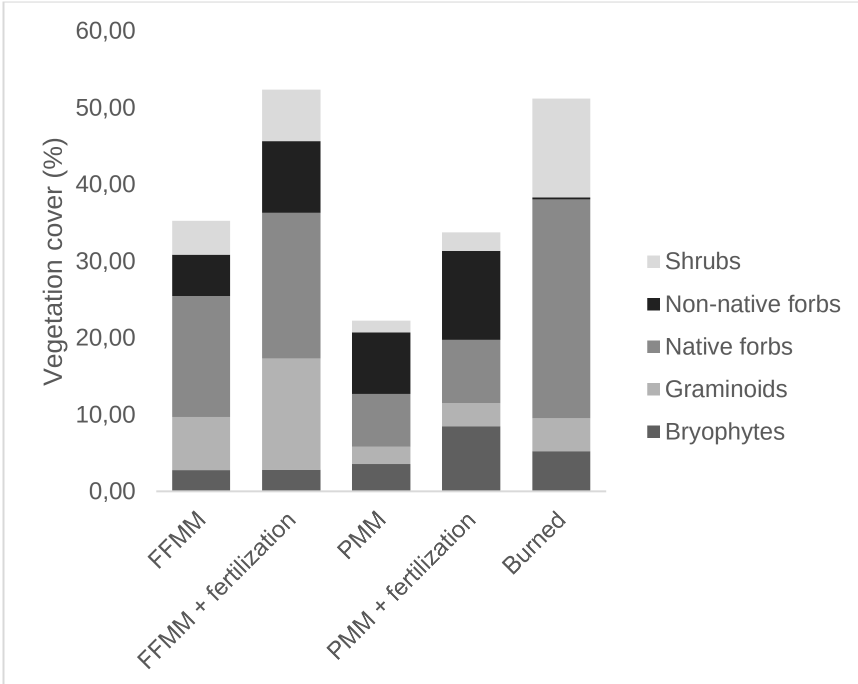

Fig. 3. Vegetation cover of functional groups of competing vegetation on the different soil types

Foliar N concentration of trembling aspen was greatest on unfertilized PMM ($p<0.001$) and lowest on burned sites (table 2). Aspen foliar P concentration was greater on the burned sites than the unfertilized reclamation treatments ($p<0.001$); there was no significant difference among the reclamation treatments. Foliar K concentration was significantly higher in aspen on the burned sites than on reclaimed plots ($p<0.001$). Aspen foliar S was the lowest in the burned sites ($p=0.006$) and was greater on PMM than on FFMM ($p<0.001$). Foliar Ca was lowest in aspen on the burned sites compared to trees on the reclaimed plots ($p=0.010$) except for unfertilized FFMM. Foliar Mg was also significantly lower in the burned sites ($p<0.001$).

Table 2. Foliar nutrient concentrations by tree species

Trembling aspen	N		P		K		S		Ca		Mg	
Soil	(%)		(%)		(%)		(%)		(%)		(%)	
FFMM	1.71 b	(0.04)	0.14 b	(0.01)	0.59 bc	(0.02)	0.26 b	(0.02)	1.66 bc	(0.05)	0.43 b	(0.02)
FFMM + fertilizer	1.57 bc	(0.03)	0.15 ab	(0.01)	0.56 c	(0.02)	0.24 b	(0.02)	1.79 ab	(0.06)	0.46 bc	(0.02)
PMM	1.89 a	(0.06)	0.14 b	(0.01)	0.60 bc	(0.03)	0.55 a	(0.04)	1.86 ab	(0.10)	0.52 c	(0.03)
PMM + fertilizer	1.67 b	(0.05)	0.15 ab	(0.01)	0.63 b	(0.03)	0.53 a	(0.03)	1.99 a	(0.08)	0.50 c	(0.02)
Burned sites	1.45 c	(0.03)	0.17 a	(<0.01)	0.84 a	(0.04)	0.17 c	(<0.01)	1.60 c	(0.05)	0.17 a	(0.01)
White spruce	N		P		K		S		Ca		Mg	
Soil	(%)		(%)		(%)		(%)		(%)		(%)	
FFMM	1.06 a	(0.03)	0.14 a	(<0.01)	0.42 b	(0.02)	0.09 b	(<0.01)	0.60 b	(0.03)	0.14 ab	(<0.01)
FFMM + fertilizer	1.07 a	(0.03)	0.15 a	(<0.01)	0.44 b	(0.02)	0.09 b	(<0.01)	0.58 b	(0.03)	0.13 b	(<0.01)
PMM	1.17 a	(0.04)	0.14 a	(0.01)	0.54 a	(0.02)	0.16 a	(0.01)	0.82 a	(0.05)	0.13 b	(<0.01)
PMM + fertilizer	1.07 a	(0.03)	0.14 a	(<0.01)	0.58 a	(0.02)	0.17 a	(0.01)	0.88 a	(0.03)	0.15 a	(<0.01)
Burned sites	N/A		N/A		N/A		N/A		N/A		N/A	

Foliar nutrient concentrations (%) for trembling aspen and white spruce. Values are mean and (standard error). Different letters indicate significant differences between soil types ($p<0.05$).

White spruce foliar N and P concentrations were not different among reclamation treatments (p=0.140 and 0.738, respectively). Foliar K, Ca and S concentrations were highest on the PMM plots, irrespective of fertilization, whereas foliar Mg concentration presented only minor differences between reclamation treatments.

Of the 60 models predicting average crop tree height of aspen seedling growing on PMM, the top-scoring model had an AICc score of 403.98 and a pseudo R^2 of 0.582 (Table 3) (Figures of actual versus predicted height of the best scoring models can be found in appendix C). Most of the 10 best scoring models included pH and fol.N parameters (The complete equations of those models can be found in appendix A). When looking at the unconditional confidence intervals (UCI) obtained from multimodel inference (Table 4), pH, PHOS, fol.N, and fol.Ca had intervals excluding zero, suggesting that those four variables have the most influence on tree height among the tested variables. Foliar N concentration and soil available P were positively correlated with aspen height while soil pH and foliar Ca concentration were negatively correlated.

For aspen seedlings growing on FFMM, the best scoring model had an AICc score of 276.89 and a pseudo R^2 of 0.523 (Table 3). Fol.N was present in all of the 10 best scoring models while VWC and pH were present in most of them. When looking at the resulting UCI, soil moisture, soil pH, foliar N concentration, and foliar Ca concentration all excluded zero from their confidence intervals (Table 4), indicative of a strong influence on aspen height on this reclamation soil. Foliar N and foliar Ca were positively correlated with aspen height while soil moisture and soil pH were negatively correlated with aspen height.

On burned plots, the set of models gave much weaker results. The best scoring model had an AICc score of 287.13 and a pseudo R^2 of 0.108 (Table 3). Other models did have a greater R^2 but were penalized by their greater number of variables. Fol.N was included in 8 of the 10 best scoring models. UCIs resulting from multimodel inference showed that only foliar P and K concentrations excluded zero from their intervals (Table 4). Foliar K was positively correlated with aspen sucker height while foliar P showed a negative correlation with aspen height.

Table 3. Results of model selection for trembling aspen height prediction using AICc

PMM Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight	Pseudo R^2
pH + PHOS + INV + fol.N + fol.P + fol.S	8	403.98	0	0.20	0.20	0.582
pH + fol.N	4	404.53	0.55	0.15	0.35	0.413
VWC + pH + PHOS + TVEG + fol.N + fol.P	8	405.64	1.66	0.09	0.44	0.545
pH + INV + fol.N + fol.K + fol.S	7	405.67	1.69	0.09	0.52	0.576
VWC + pH + fol.N	5	406.14	2.16	0.07	0.59	0.419
pH + GRAM + NAT + fol.N + fol.P + fol.K	8	406.48	2.50	0.06	0.65	0.668
TC + PHOS + GRAM + INV + fol.Ca	7	406.6	2.61	0.05	0.70	0.521
pH + GRAM + NAT + fol.N + fol.Mg	7	406.88	2.89	0.05	0.75	0.599
VWC + SHRU + fol.N + fol.K + fol.S + fol.Ca	8	407.43	3.45	0.04	0.78	0.535
VWC + GRAM + fol.N + fol.K + fol.S + fol.Ca	8	408.12	4.14	0.03	0.81	0.559
FFMM Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight	Pseudo R^2
VWC + pH + fol.N	5	276.89	0	0.79	0.79	0.523
pH + fol.N	4	280.88	3.99	0.11	0.90	0.350
VWC + pH + TVEG + fol.N + fol.P	7	282.68	5.79	0.04	0.94	0.533
VWC + pH + TC + PHOS + INV + fol.N	8	286.14	9.24	0.01	0.95	0.534
VWC + GRAM + fol.N + fol.K + fol.S + fol.Ca	8	286.14	9.25	0.01	0.95	0.552
VWC + pH + PHOS + TVEG + fol.N + fol.Mg	8	286.32	9.43	0.01	0.96	0.545
VWC + TVEG + fol.N	5	286.39	9.50	0.01	0.97	0.365
VWC + pH + PHOS + TVEG + fol.N + fol.P	8	286.44	9.55	0.01	0.97	0.538
VWC + pH + TC + TVEG + fol.N + fol.P	8	286.54	9.65	0.01	0.98	0.535
TVEG + fol.N	4	287.14	10.25	0	0.99	0.226
Burned Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight	Pseudo R^2
TVEG + fol.N	4	287.13	0	0.28	0.28	0.108
pH + fol.N	4	287.52	0.39	0.23	0.51	0.096
TVEG + fol.N + fol.P + fol.K + fol.S	7	288.28	1.15	0.16	0.67	0.377
VWC + TVEG + fol.N	5	290	2.87	0.07	0.74	0.123
VWC + pH + fol.N	5	290.65	3.52	0.05	0.79	0.102
NAT + fol.N + fol.P + fol.K + fol.Ca	7	291.42	4.29	0.03	0.82	0.356
PHOS + TVEG + fol.P + fol.K + fol.S + fol.Ca	8	291.66	4.53	0.03	0.85	0.416
VWC + pH + TC	5	292.49	5.36	0.02	0.87	0.400
fol.N + fol.P + fol.K + fol.S + fol.Ca + fol.Mg	8	292.55	5.42	0.02	0.89	0.421
VWC + NAT + fol.N + fol.P + fol.K	7	293.15	6.02	0.01	0.90	0.323

Results from model selection using AICc. Tested variables are soil moisture (VWC), soil pH (pH), soil carbon concentration (TC), soil available P (PHOS), graminoid cover (GRAM), native forb cover (NAT), non-native forb cover (INV), shrub cover (SHRU), total competing vegetation cover (TVEG), foliar N concentration (fol.N), foliar P concentration (fol.P), foliar K concentration (fol.K), foliar S concentration (fol.S), foliar Ca concentration (fol.Ca), and foliar Mg concentration (fol.Mg). The K value indicates the number of parameters included in each model. Only the 10 best scoring models are shown for concision.

Table 4. Model averaged parameter estimates for trembling aspen

Aspen PMM Parameter	Estimate	Lower UCI	Upper UCI	**Aspen FFMM** Parameter	Estimate	Lower UCI	Upper UCI	**Aspen Fire** Parameter	Estimate	Lower UCI	Upper UCI
VWC	3.10	-1.75	7.96	VWC	-2.40	-3.92	-0.87	VWC	1.90	-8.26	12.05
pH	-39.25	-64.91	-13.60	pH	-26.95	-40.83	-13.08	pH	20.08	-56.20	96.37
TC	4.57	-2.99	12.12	TC	-0.17	-3.65	3.32	TC	21.54	-38.31	81.38
PHOS	7.35	0.58	14.11	PHOS	0.28	-2.26	2.81	PHOS	-1.14	-3.24	0.96
GRAM	9.09	-0.47	18.64	GRAM	1.19	-0.04	2.43	GRAM	5.82	-6.17	17.80
NAT	-0.20	-5.45	5.06	NAT	-0.61	-1.95	0.73	NAT	0.80	-2.12	3.72
INV	-4.97	-10.60	0.65	INV	0.69	-0.86	2.23	INV	5.62	-41.79	53.04
SHRU	4.20	-3.25	11.66	SHRU	-0.16	-2.23	1.92	SHRU	-1.00	-5.35	3.35
TVEG	0.24	-2.02	2.50	TVEG	0.35	-0.41	1.11	TVEG	1.22	-1.52	3.96
fol.N	149.95	50.67	249.24	fol.N	73.88	28.59	119.16	fol.N	-172.46	-398.15	53.22
fol.P	-997.64	-2033.40	38.12	fol.P	-151.85	-528.82	225.13	fol.P	-1734.25	-3226.21	-242.29
fol.K	-277.55	-590.65	35.55	fol.K	65.40	-50.30	181.09	fol.K	191.00	40.28	341.72
fol.S	126.90	-66.22	320.02	fol.S	7.63	-122.64	137.89	fol.S	1372.35	-251.06	2995.77
fol.Ca	-118.06	-206.35	-29.78	fol.Ca	48.29	9.13	87.46	fol.Ca	23.91	-122.93	170.75
fol.Mg	32.79	-360.82	426.40	fol.Mg	62.89	-84.90	210.68	fol.Mg	322.67	-380.06	1025.41

Model averaged parameter estimates with 90% UCI. Parameters excluding zero are shaded. Tested variables are soil moisture (VWC), soil pH (pH), soil carbon concentration (TC), soil available P (PHOS), graminoid cover (GRAM), native forb cover (NAT), non-native forb cover (INV), shrub cover (SHRU), total competing vegetation cover (TVEG), foliar N concentration (fol.N), foliar P concentration (fol.P), foliar K concentration (fol.K), foliar S concentration (fol.S), foliar Ca concentration (fol.Ca), and foliar Mg concentration (fol.Mg).

The 60 models were fitted with the data from the white spruce seedlings growing on PMM. The best scoring model had an AICc score of 309.01 and a pseudo R^2 of 0.391 (Table 5) (Figures of actual versus predicted height of the best scoring models can be found in appendix D). Fol.Mg and fol.Ca were the two most common parameters in the 10 best scoring models and were included 10 and 9 times respectively (The complete equations of those models can be found in appendix B). They were also the only two parameters which UCIs excluded zero. Both Ca and Mg foliar concentration were negatively correlated with spruce height (Table 6); however, upon further examination of the needle unit mass and relative concentration it was determined that these negative correlations were both due to a dilution effect.

When fitted with the data from the seedlings growing on FFMM, the best model predicting white spruce height had an AICc score of 416.70 and a pseudo R^2 of 0.271 (Table 5). Soil pH was included in all of the best scoring models. The UCIs of pH, TC, and SHRU all excluded zero (table 6), indicating that they are the strongest predictors of white spruce height on this reclamation soil. Shrub cover had a positive correlation with spruce height while both soil pH and soil carbon concentration were both negatively correlated with white spruce height.

Table 5. Results of model selection for white spruce height prediction using AICc

PMM Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight	Pseudo R^2
VWC + INV + SHRU + fol.Ca + fol.Mg	7	309.01	0	0.32	0.32	0.391
PHOS + TVEG + fol.N + fol.Ca + fol.Mg	7	309.05	0.04	0.31	0.63	0.352
TC + INV + fol.S + fol.Ca + fol.Mg	7	311.59	2.58	0.09	0.72	0.425
fol.N + fol.P + fol.K + fol.S + fol.Ca + fol.Mg	8	312.21	3.20	0.06	0.78	0.520
INV + SHRU + fol.N + fol.P + fol.Ca + fol.Mg	8	312.78	3.77	0.05	0.83	0.474
SHRU + fol.N + fol.K + fol.S + fol.Ca + fol.Mg	8	312.84	3.83	0.05	0.88	0.554
TC + NAT + SHRU + fol.N + fol.Ca + fol.Mg	8	313.29	4.28	0.04	0.91	0.334
pH + GRAM + SHRU + fol.K + fol.Ca + fol.Mg	8	314.21	5.20	0.02	0.94	0.533
TC + TVEG + fol.K + fol.S + fol.Ca + fol.Mg	8	315.06	6.05	0.02	0.95	0.588
VWC + pH + INV + fol.P + fol.Mg	7	315.68	6.67	0.01	0.96	0.355
FFMM Model	K	AICc	ΔAICc	AICc weight	Cumulative AICc weight	Pseudo R^2
VWC + pH + TC	5	416.70	0	0.28	0.28	0.271
pH + fol.N	4	417.02	0.32	0.24	0.52	0.221
VWC + pH + fol.N	5	419.52	2.82	0.07	0.59	0.226
pH + TC + SHRU + TVEG + fol.P + fol.Mg	8	420.42	3.73	0.04	0.64	0.337
VWC + pH + TC + TVEG + fol.N + fol.P	8	421.39	4.69	0.03	0.66	0.309
pH + TC + PHOS + NAT + fol.S	7	421.53	4.83	0.03	0.69	0.296
VWC + pH + TC + PHOS + TVEG	7	421.80	5.10	0.02	0.71	0.280
VWC + pH + PHOS + GRAM + fol.P + fol.K	8	422.11	5.42	0.02	0.73	0.272
pH + GRAM + NAT + fol.N + fol.P + fol.K	8	422.14	5.44	0.02	0.75	0.268
pH + TC + GRAM + INV + fol.P + fol.Mg	8	422.21	5.51	0.02	0.77	0.306

Results from model selection using AICc. Tested variables are soil moisture (VWC), soil pH (pH), soil carbon concentration (TC), soil available P (PHOS), graminoid cover (GRAM), native forb cover (NAT), non-native forb cover (INV), shrub cover (SHRU), total competing vegetation cover (TVEG), foliar N concentration (fol.N), foliar P concentration (fol.P), foliar K concentration (fol.K), foliar S concentration (fol.S), foliar Ca concentration (fol.Ca), and foliar Mg concentration (fol.Mg). The K value indicates the number of parameters included in each model. Only the 10 best scoring models are shown for concision.

Table 6. Model averaged parameter estimates for white spruce

Spruce PMM Parameter	Estimate	Lower UCI	Upper UCI	**Spruce FFMM** Parameter	Estimate	Lower UCI	Upper UCI
VWC	0.84	-0.06	1.74	VWC	0.07	-0.98	1.11
pH	1.37	-4.23	6.97	pH	-17.96	-28.11	-7.82
TC	0.11	-1.22	1.44	TC	-2.41	-4.80	-0.02
PHOS	-0.68	-1.78	0.43	PHOS	0.27	-1.52	2.06
GRAM	-0.57	-2.42	1.28	GRAM	-0.12	-0.70	0.46
NAT	-0.24	-1.17	0.69	NAT	0.04	-0.65	0.73
INV	-0.10	-0.67	0.47	INV	0.45	-0.47	1.37
SHRU	-0.15	-1.42	1.13	SHRU	1.07	0.03	2.12
TVEG	-0.02	-0.34	0.30	TVEG	0.12	-0.35	0.59
fol.N	16.58	-6.03	39.19	fol.N	-10.56	-53.15	32.03
fol.P	91.28	-171.25	353.81	fol.P	335.40	-113.01	783.82
fol.K	-17.12	-78.52	44.29	fol.K	-68.27	-148.08	11.54
fol.S	-31.31	-151.61	89.00	fol.S	-125.17	-506.94	256.61
fol.Ca	-38.31	-62.69	-13.93	fol.Ca	8.09	-42.68	58.85
fol.Mg	-679.02	-944.92	-443.13	fol.Mg	22.37	-339.05	383.79

Model averaged parameter estimates with 90% UCI. Parameters excluding zero are shaded. Tested variables are soil moisture (VWC), soil pH (pH), soil carbon concentration (TC), soil available P (PHOS), graminoid cover (GRAM), native forb cover (NAT), non-native forb cover (INV), shrub cover (SHRU), total competing vegetation cover (TVEG), foliar N concentration (fol.N), foliar P concentration (fol.P), foliar K concentration (fol.K), foliar S concentration (fol.S), foliar Ca concentration (fol.Ca), and foliar Mg concentration (fol.Mg).

Discussion

In the reclaimed plots, natural aspen seedlings height was greater on PMM than on FFMM, but the addition of the fertilizer resulted in smaller aspen seedlings, seemingly negating the advantage of PMM over FFMM. The results point toward a negative effect of broadcast fertilization on aspen seedlings growing on PMM, confirming results from Pinno & Errington (2015) that found lower aspen seedling regeneration density on both PMM and FFMM when a fertilizer was used. Fertilization increased competing plant cover on PMM (from 22% to 34% of the surveyed plot area), probably increasing competition for resources at the same time, which resulted in lower aspen and spruce height. A similar increase in vegetation cover also happened on FFMM (from 35% to 52%) when fertilized; however, there was no significant effect of fertilization on tree average height for this reclamation treatment, possibly because a threshold above which additional competitors have a smaller effect had already been crossed on this reclamation soil. It is thus possible that the increase in competition due to fertilization had a greater effect on PMM due to its lower initial vegetation cover compared with FFMM. Graminoids and forbs were the two functional groups who benefited the most from fertilization in terms of increased cover and have been shown to have a greater negative effect on tree growth in the first few years before canopy closure comparatively to woody competition (Bell et al., 2000; Wagner, 2000). Schott et al. (2016) have reported that immediately available fertilization can increase aspen height growth on reclaimed sites, but this effect was gone one year after fertilization was discontinued. It is possible that the fertilizer treatment did increase early aspen height growth on this reclaimed site but the combination of the short-lived positive effect and the increase in competing vegetation cover resulted in no height gain on fertilized FFMM and slower height growth on fertilized PMM after six years.

The negative effect of the fertilizer treatment when applied to PMM can also be observed in white spruce height. The only significant difference found between the four tested reclamation treatments was with fertilized PMM, on which white spruce average height was lower than for other treatments. This is again likely due to an increase in competition for resources from the increased cover of competing vegetation. Duan et al. (2015) have shown that fertilization can have a positive effect on white spruce growth on reclaimed sites but this was not the case in our study. The different results could be due to the different developmental stage of the studied trees as their experiment was conducted on 18 to 23 years old white spruce trees, which are possibly less vulnerable to competition from lower vegetation than the seedlings used in our study. If fertilization did improve the seedlings nutritional status, it likely did not last very long: four years after fertilization, the white spruce foliar nutrient concentrations that we observed were very similar between the fertilized and unfertilized plots. The short-lived effect of fertilization on this species has already been observed on reclaimed sites (Sloan & Jacobs, 2013; Duan et al., 2015) and on natural sites (Phu & Gagnon, 1975). Planted white spruce seedlings may have suffered from N deficiency as the measured average foliar N concentration on each treatment was around 1.1% while optimal foliar N concentration has been reported to be between 1.5 and 2.5% for white spruce growth (Nienstaedt & Zasada, 1990). The low foliar N concentration across all treatments and the absence of an improvement after fertilization could explain why fertilization did not increase spruce height on this reclaimed site.

Similarly to foliar N, foliar P, and foliar K concentrations did not show a significant improvement of tree nutrition due to fertilization 4 years after the treatment ended. In fact, the only noticeable difference between fertilized and unfertilized plots could be observed in aspen foliar N, which was actually lower in fertilized plots. It appears that fertilization of this reclaimed site did not increase tree height, did not improve foliar nutrient concentrations, and only resulted in an increase in vegetation cover.

Drivers of aspen seedlings height on both reclaimed soil types were mostly related to nutrient availability; soil pH, foliar N concentration, and foliar Ca concentration came out as important factors affecting aspen height on both FFMM and PMM while soil moisture and soil available P also played a role on FFMM and PMM respectively. These results mirror observations made by Duan et al. (2015) that concluded that soil nutrient are more limiting for tree height than soil moisture on reclaimed sites with a fine textured subsoil such as overburden.

The three main drivers of white spruce height on FFMM were soil pH, soil carbon concentration, and shrub cover. No strong predictor of white spruce height on PMM was found. White spruce is a determinate growth species that grows slowly and it is possible that not enough time has passed for site conditions to affect height growth enough to allow clear patterns to develop. Other determinate growth species such as Engelmann spruce (*Picea engelmannii Parry ex Engelm.*) have been shown to take years before showing a growth response to improved site conditions such as lowered competition (Biring et al., 2003). Another explanation may be the repeatedly observed slow and erratic height growth of young planted white spruce (Thompson & McMinn, 1989; Sutton, 1995; Carmean et al.,

2006) sometimes attributed to planting check (Sutton, 1995) due to the smaller root system of planted trees limiting water and nutrient uptake (Burdett et al., 1984). White spruce growing on the fertilized PMM soil type did show some signs of planting check (small greenish-yellow needles, low retention of needles from previous years) and this may have slowed height growth enough to explain why white spruce did not seem to react to environmental conditions on this reclamation soil.

Soil pH has a compounding effect on vegetation growth due to its influence on the ability of plants to access soil nutrients, which resulted in this variable being the only one shared by both tree species. It influences such factors as nutrient availability and uptake (Mengel & Kirkby, 1982), N mineralization and nitrification rate (Cookson et al., 2007; DeBoer et al., 1996) and root growth (Jamro et al., 2015). In terms of nutrient availability, the strong influence of pH may be tied to soil P: it is the macronutrient whose availability is most affected by pH (Mengel & Kirby, 1982), is less available on reclaimed sites than in the surrounding boreal forest (Rowland et al., 2009), and has been shown to be positively related to tree growth in reclaimed soils (Pinno et al., 2012).

Foliar N concentration was positively correlated with aspen average height on both cover soil types and was at its highest on the PMM soil that did not receive the fertilizer treatment. This treatment also showed the greatest average height for aspen, indicating that N availability may be one of the main drivers of aspen productivity on this site. FFMM is usually considered to have greater N availability than PMM as shown by Jamro et al. (2014) but this may have been counteracted here by the stronger competition for resources due to the greater vegetation cover on FFMM. The effect on increased competition can also be observed in the lower foliar N concentration of aspens growing on the two fertilized treatments. Rowland et al. (2009) showed that N availability on reclaimed sites using PMM is similar or greater than the surrounding natural sites but this does not necessarily mean N is not still limiting aspen height growth on this reclaimed site. Boreal forest productivity is often limited by N availability (Cheng et al., 2011) and a comparison of foliar N concentrations found in this study with the national averages reported by Paré et al. (2013) suggest that the reclaimed site N supply might be low enough to limit aspen growth.

Soil moisture did not have a strong influence on tree height most of the time and only seems to influence aspen seedlings height slightly negatively on FFMM. Duan et al. (2015) found that soil moisture is not as limiting to tree growth as nutrient availability when a fine-textured subsoil like overburden is used for reclamation as was the case in our study. The negative correlation between aspen height and soil moisture on FFMM may be caused by some other factor negatively impacting vegetation growth on this reclamation soil and consequently lowering water uptake, and thus increasing soil moisture, rather than a negative effect of soil moisture on aspen height *per se*. No significant difference in soil moisture was found between the two reclamation soil types, which goes against the results of other studies, which found higher soil moisture in PMM due to its superior moisture holding capacity (Errington & Pinno, 2015; Schott et al., 2016). Local annual precipitations in 2016 were greater than average (517 mm versus 418.6 mm; Environment Canada) which may explain the lack of a difference in soil moisture between reclamation soils as there was simply more water than normally available to the vegetation.

The negative correlation between white spruce height and soil carbon concentration on FFMM could be explained by an increase in the C:N ratio in plots where there is a greater amount of organic matter. An elevated C:N ratio can reduce the potential for nitrogen mineralization (MacKenzie & Naeth, 2010) and the lower C:N ratio of FFMM comparatively to PMM (MacKenzie & Naeth, 2010; Jamro et al., 2014) partly explains why FFMM is considered the superior soil type in term of nitrogen availability.

The positive correlation between shrub cover and white spruce height could be related to the importance of shrubs for facilitating the development of a forest floor (Rowland et al., 2009; Sorenson et al., 2011) and thus helping to establish a functioning soil-plant nutrient cycle. Results from Sorenson et al. (2011) also suggest that the role of shrubs is more important in reclaimed conifer sites due to their lower litterfall rate comparatively to aspen sites. No direct negative effect of competing vegetation on tree height was found but it is possible that any negative effect has been captured by other variables such as foliar nutrient concentrations. As the vegetation cover increases over time, it is possible that competition starts affecting tree height but for now we cannot definitely say if competing vegetation is a driver of tree height on reclaimed sites.

Aspen in the burned natural plots was taller than in the reclaimed plots. This is possibly because its sucker origin gave it a head start (relative to the seed origin aspen in reclaimed plots). Compared with aspen seedlings, aspen suckers grow from the clonal root network of the stand established prior to disturbance and therefore already have an established root system when they emerge. They rely on carbohydrates stored in this root system for their initial growth until they have the leaf area to sustain themselves and the root system (Landhäusser & Lieffers, 2002). Aspen sucker height in the burned sites is still not well correlated to the measured environmental variables. The measured variables were found to have low predictive power with only foliar K (positive effect) and foliar P (negative effect) concentration contributing to aspen suckers height variability according to statistical results. Foliar P was negatively correlated with aspen height, which was judged to be due to a dilution effect, leaving foliar K as the only measured variable contributing to predict aspen sucker height on burned sites. These results seem to suggest that environmental variables such as the one used for this project are poor predictors of early height growth of aspen suckers, possibly because they are at an intermediate phase of their development where they are partly influenced by their sucker origin and partly by environmental variables. Soil temperature (Landhäusser & Lieffers, 1998), fire severity (Fraser et al., 2004), and time of disturbance (Landhäusser et al., 2006) have all been shown to impact aspen sucker initiation and early growth.

Our results show that early broadcast fertilization has no observable benefits on tree height six years after reclamation. It did increase vegetation cover, however much of that increase went to non-native forb cover and graminoids. If the goal of fertilization is to promote tree growth we suggest using other methods of fertilization that can more efficiently target crop trees such as directed application of controlled-release fertilizer. However, if the goal is to increase total overall vegetation cover, steps should be taken to avoid promoting non-native species as they can be aggressive competitors preventing the establishment of native species. Some graminoids species can also be problematic due to their ability to dominate disturbed sites (Landhäusser & Lieffers, 1998). Our findings also indicate that special care should be given to soil pH of reclaimed sites as this driver was one of the main predictor of tree height for all species/soil combination where conclusive results could be obtained. Practitioners should aim for a soil pH around 6 as this was the value around which both species attained their greatest height in this experiment. Care should be taken when extrapolating the results of this study as this was conducted on an operational field trial without true replication of the treatments. However, our results suggest that nutrient availability is driving tree height on reclaimed sites.

Conclusion générale

L’objectif principal de cette étude était d’identifier les principaux facteurs qui affectent la croissance du peuplier faux-tremble et de l’épinettes blanche dans les premières années suivant la remise en production de sites exploités pour les sables bitumineux. Il est bien connu que la lumière, les éléments nutritifs, l’eau ainsi que leur interaction avec la compétition et le climat affectent la croissance des plantes et peuvent être limitants en forêt naturelle ou aménagée, mais les connaissances sont plus limitées en ce qui a trait à la croissance de la végétation dans des écosystèmes anthropisés comme les sites miniers. Avec l’impact grandissant des activités humaines sur l’environnement, le développement de méthodes de remise en production des sites et de restauration des écosystèmes se fait de plus en plus urgent et nécessaire au maintien des services écologiques. Étant donné les différences environnementales entre les sites naturels et les sites remis en production, il est possible que les relations entre les plantes et leur environnement soient aussi différentes dans ces milieux. Plusieurs études sur la croissance des arbres sur sites remis en production ont été réalisées en serre ou sur des arbres issus de plantation approchant le stade de maturité, ce qui limite les conclusions pouvant être faite sur la croissance de jeunes plants. La connaissance des principaux facteurs affectant la croissance des arbres à cette étape de leur vie est particulièrement importante si on souhaite pouvoir apporter des correctifs dès les premières années d’un projet et ainsi minimiser les délais avant le retour d’un écosystème fonctionnel. Étant donné la grande variabilité et complexité des deux principaux mélanges de sols utilisés par cette industrie pour reconstruire un sol pouvant supporter la végétation, il était aussi nécessaire de bien caractériser les conditions de croissance offertes par ces sites plutôt que de se limiter à une description basée sur l’origine du matériel. Les résultats de cette caractérisation indiquent qu’en plus des différences entre les traitements de remise en production, il y a aussi une grande variabilité d’une placette à l’autre à l’intérieur d’un même traitement, possiblement due à une répartition inégale du mélange matière organique-minérale.

Une comparaison de la hauteur des cinq plus grands arbres par placette confirme des résultats obtenus précédemment sur le même site indiquant que le mélange tourbe-minéral permet une croissance en hauteur plus rapide chez les deux essences étudiées, quoique la différence n’était pas significative chez l’épinette blanche. Il semblerait donc, au moins à court terme, que le mélange tourbe-minéral soit le meilleur choix pour favoriser une croissance rapide du peuplier et de l’épinette blanche sur site remis en production. Il serait pertinent de continuer le suivi de la croissance des arbres sur ce site pour observer si la différence entre les deux sols se maintient. Étant donné la plus grande résistance à la décomposition du mélange tourbe-minéral et son plus faible taux de minéralisation (Hemstock et al., 2010) il est possible qu'avec l'augmentation du couvert végétal au fil du temps ce sol devienne comparativement plus pauvre que le mélange sol forestier-minéral. Un maintien du suivi serait d'autant plus pertinent du fait qu'il a été observé que la composition végétale sur site remis en production était toujours en évolution après 20 ans (Pinno & Hawkes, 2015).

Puisque le succès d'un projet de remise en production dans la région des sables bitumineux ne se limite pas seulement à la croissance des arbres et même s'il est observé que le mélange tourbe-minéral continu à être le sol supérieur pour la croissance des arbres, il serait intéressant de continuer à tester différentes façons de combiner les aspects positifs des deux mélanges. Une possibilité serait de placer la tourbe, qui est disponible en plus grande quantité, sur la majorité des superficies à remettre en production et de créer des îlots régulièrement espacés de sol forestier contenant les propagules nécessaires au développement d'une communauté végétale représentative des forêts locales.

Un traitement de fertilisation appliqué pendant les deux premières années s'est révélé sans effet sur la croissance en hauteur des arbres lorsqu'appliqué au mélange sol forestier-minéral, et nuisible lorsqu'appliqué au mélange tourbe-minéral. Ces effets seraient dus à une augmentation du couvert végétal suite à l'apport en éléments nutritifs résultant ensuite en une plus forte compétition pour les ressources. Le plus faible couvert végétal sur le mélange tourbe-minéral non fertilisé pourrait être une cause partielle de la croissance supérieure des arbres et expliquerait pourquoi la hauteur moyenne des arbres diminue sur le même sol après fertilisation. Ces résultats suggèrent que l'utilisation d'un engrais ne donne pas les résultats escomptés et peut même être dommageable en ce qui a trait à la croissance en hauteur des arbres sur sites remis en production. Le besoin de fertiliser les semis au début de leur croissance devrait être réévalué; si cela s'avère vraiment nécessaire d'autres méthodes de fertilisation que celle à la volée utilisée sur ce site pourraient potentiellement donner de meilleurs résultats en ciblant les semis pour ainsi éviter de favoriser les plantes concurrentes. Une autre alternative serait de laisser le temps aux arbres de développer leur réseau racinaire et d'attendre que le couvert végétal se ferme avant de fertiliser et ainsi éviter d'augmenter la compétition pour les ressources.

L’analyse des facteurs gouvernant la croissance en hauteur de jeune arbres sur sites remis en production a révélé que la disponibilité des éléments nutritifs ainsi que les facteurs qui l’influencent ont, pour le moment, plus d’influence que d’autres facteurs tel que la disponibilité de l’eau. Il serait intéressant de vérifier si l’importance de la disponibilité des éléments nutritifs se maintient au fil du temps à mesure que le site, le couvert végétal ainsi que les arbres évoluent. De plus, de futurs efforts de recherche devraient se concentrer sur l’impact qu’à la végétation concurrentes sur la croissance des arbres sur ces sites et si les graminées et les plantes non-natives, deux groupes ayant le plus bénéficié de l’application de l’engrais dans cette étude, se maintiennent ou déclinent à mesure que le couvert se ferme.

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Appendix A: Complete equations of the ten best scoring models for trembling aspen on each soil types

Full models of trembling aspen height

PMM Model	AICc	Pseudo R^2
169.203 - 33.963(pH) + 7.872(PHOS) - 3.954(INV) + 153.136(fol.N) - 1174.506(fol.P) + 91.287(fol.S)	403.98	0.582
180.524 - 41.114(pH) + 117.681(fol.N)	404.53	0.413
140.076 + 3.214(VWC) - 47.978(pH) + 9.954(PHOS) + 0.347(TVEG) + 161.854(fol.N) - 1100.072(fol.P)	405.64	0.545
64.437 - 25.819(pH) - 3.731(INV) + 175.549(fol.N) - 187.836(fol.K) + 121.058(fol.S)	405.67	0.576
84.597 + 2.947(VWC) - 41.262(pH) + 129.742(fol.N)	406.14	0.419
337.281 - 48.372(pH) + 11.479(GRAM) - 0.226(NAT) + 158.704(fol.N) - 692.451(fol.P) - 178.084(fol.K)	406.48	0.668
306.329 + 6.004(TC) + 3.291(PHOS) + 5.052(GRAM) - 7.825(INV) - 108.32(fol.Ca)	406.6	0.521
67.714 - 44.431(pH) + 11.109(GRAM) - 0.576(NAT) + 129.826(fol.N) + 173.354(fol.Mg)	406.88	0.599
95.101 + 4.266(VWC) + 5.819(SHRU) + 195.678(fol.N) - 455.892(fol.K) + 197.445(fol.S) - 133.483(fol.Ca)	407.43	0.535
65.53 + 4.116(VWC) + 5.654(GRAM) + 183.983(fol.N) - 408.134(fol.K) + 228.506(fol.S) - 129.179(fol.Ca)	408.12	0.559

FFMM Model	AICc	Pseudo R^2
238.935 - 2.391(VWC) - 27.357(pH) + 71.279(fol.N)	276.89	0.523
135.597 - 24.282(pH) + 83.523(fol.N)	280.88	0.350
239.117 - 2.511(VWC) - 27.534(pH) + 0.319(TVEG) + 79.21(fol.N) - 154.298(fol.P)	282.68	0.533
223.951 - 2.31(VWC) - 29.168(pH) - 0.45(TC) + 0.204(PHOS) + 0.765(INV) + 83.655(fol.N)	286.14	0.534
- 146.994 - 2.471(VWC) + 1.42(GRAM) + 89.968(fol.N) + 92.01(fol.K) + 39.709(fol.S) + 51.407(fol.Ca)	286.14	0.552
142.497 - 2.4(VWC) - 22.148(pH) + 0.121(PHOS) + 0.334(TVEG) + 81.985(fol.N) + 59.396(fol.Mg)	286.32	0.545
- 2.912 - 1.978(VWC) + 0.507(TVEG) + 81.33(fol.N)	286.39	0.365
227.81 - 2.516(VWC) - 26.696(pH) + 0.412(PHOS) + 0.339(TVEG) + 81.438(fol.N) - 177.059(fol.P)	286.44	0.538
237.792 - 2.505(VWC) - 27.381(pH) + 0.107(TC) + 0.321(TVEG) + 79.278(fol.N) - 158.538(fol.P)	286.54	0.535
- 68.762 + 0.48(TVEG) + 91.112(fol.N)	287.14	0.226

Burned Model	AICc	Pseudo R^2
548.591 + 1.166(TVEG) - 225.665(fol.N)	287.13	0.108
430.316 + 16.346(pH) - 171.425(fol.N)	287.52	0.096
308.913 + 1.118(TVEG) - 120.289(fol.N) - 1907.27(fol.P) + 177.969(fol.K) + 1470.692(fol.S)	288.28	0.377
494.056 + 3.197(VWC) + 1.437(TVEG) - 228.335(fol.N)	290	0.123
410.809(VWC) + 14.969(pH) - 168.23(fol.N)	290.65	0.102
291.986 + 0.615(NAT) - 34.342(fol.N) - 1581.986(fol.P) + 195.537(fol.K) + 73.523(fol.Ca)	291.42	0.356
139.552 - 1.454(PHOS) + 1.35(TVEG) - 1736.162(fol.P) + 247.111(fol.K) + 1298.805(fol.S) - 9.666(fol.Ca)	291.66	0.416
41.133 + 2.602(VWC) + 29.394(pH) + 19.98(TC)	292.49	0.400
224.896 - 91.275(fol.N) - 1650.468(fol.P) + 195.77(fol.K) + 1714.795(fol.S) - 35.759(fol.Ca) + 330.85(fol.Mg)	292.55	0.421
444.627 - 0.221(VWC) + 0.314(NAT) - 58.061(fol.N) - 1425.633(fol.P) + 177.569(fol.K)	293.15	0.323

Appendix A. Full equations of the ten best scoring models according to their AICc score predicting trembling aspen height.

Appendix B: Complete equations of the ten best scoring models for white spruce on each soil types

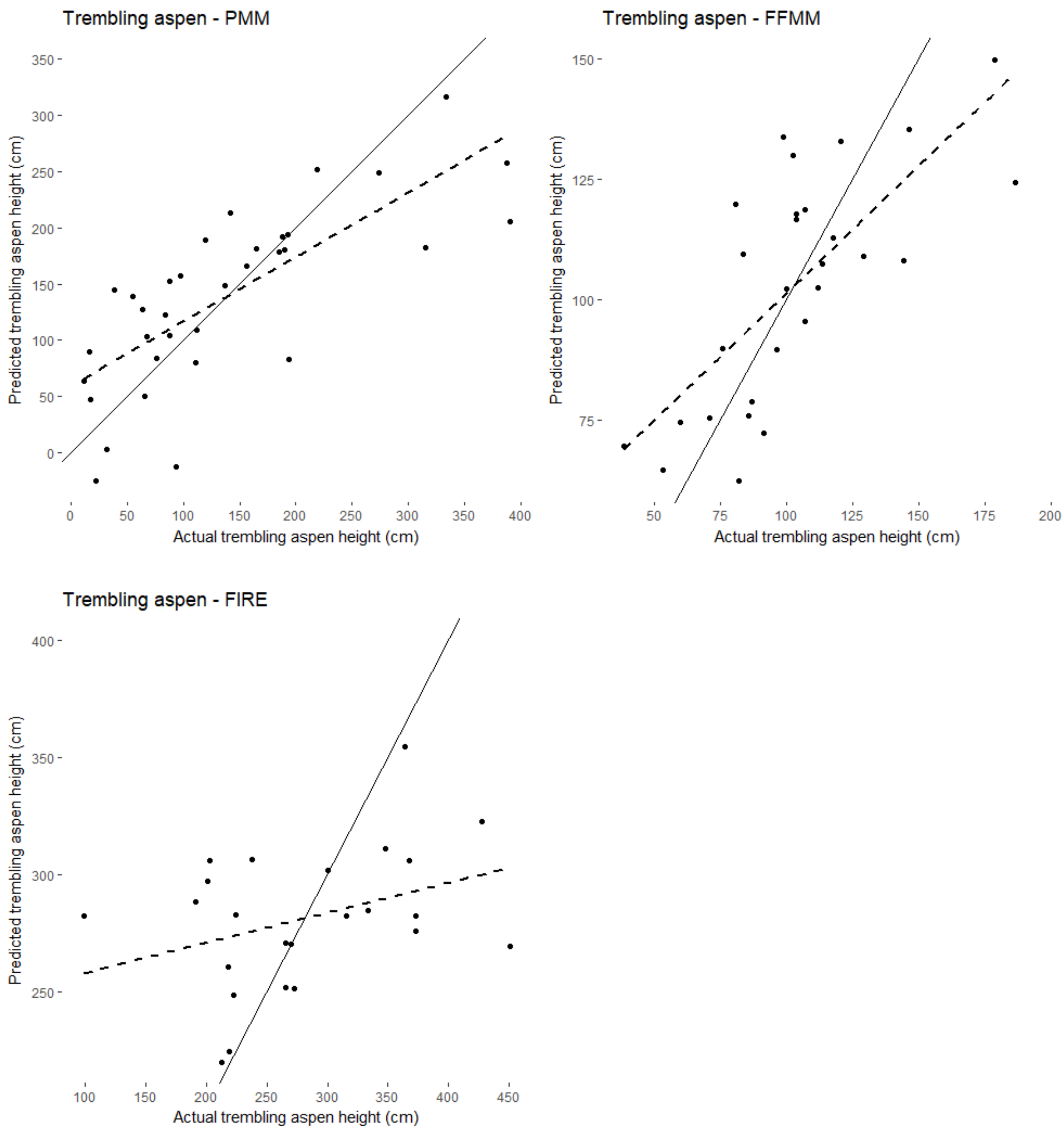
Full models of white spruce height

PMM Model	AICc	Pseudo R^2
174.779 + 0.848(VWC) - 0.058(INV) - 0.104(SHRU) - 36.044(fol.Ca) - 746.234(fol.Mg)	309.01	0.391
169.181 - 0.69(PHOS) - 0.019(TVEG) + 15.598(fol.N) - 42(fol.Ca) - 605.274(fol.Mg)	309.05	0.352
190.855 + 0.07(TC) - 0.146(INV) - 35.496(fol.S) - 34.355(fol.Ca) - 676.082(fol.Mg)	311.59	0.425
168.729 + 17.757(fol.N) + 122.157(fol.P) - 30.475(fol.K) - 21.726(fol.S) - 37.983(fol.Ca) - 661.488(fol.Mg)	312.21	0.520
161.858 - 0.23(INV) - 0.389(SHRU) + 17.367(fol.N) + 43.025(fol.P) - 36.688(fol.Ca) - 662.436(fol.Mg)	312.78	0.474
171.727 - 0.178(SHRU) + 20.428(fol.N) - 16.06(fol.K) - 30.003(fol.S) - 37.737(fol.Ca) - 625.791(fol.Mg)	312.84	0.554
168.203 + 0.019(TC) - 0.26(NAT) - 0.209(SHRU) + 17.29(fol.N) - 38.429(fol.Ca) - 658.387(fol.Mg)	313.29	0.334
189.405 + 1.94(pH) - 0.955(GRAM) - 0.052(SHRU) + 5.441(fol.K) - 42.057(fol.Ca) - 755.461(fol.Mg)	314.21	0.533
189.943 + 0.176(TC) - 0.052(TVEG) - 2.256(fol.K) - 39.753(fol.S) - 34.297(fol.Ca) - 662.825(fol.Mg)	315.06	0.588
141.749 + 0.743(VWC) + 0.954(pH) - 0.197(INV) + 99.44(fol.P) - 844.748(fol.Mg)	315.68	0.355

FFMM Model	AICc	Pseudo R^2
217.758 - 0.03(VWC) - 19.673(pH) - 2.298(TC)	416.70	0.271
199.676 - 17.349(pH) - 8.662(fol.N)	417.02	0.221
195.024 + 0.094(VWC) - 17.136(pH) - 7.991(fol.N)	419.52	0.226
161.83 - 15.805(pH) - 2.695(TC) + 0.899(SHRU) - 0(TVEG) + 182.257(fol.P) - 16.004(fol.Mg)	420.42	0.337
182.912 - 0.001(VWC) - 17.985(pH) - 2.798(TC) + 0.132(TVEG) - 32.342(fol.N) + 365.549(fol.P)	421.39	0.309
224.658 - 19.058(pH) - 2.843(TC) + 0.384(PHOS) - 0.108(NAT) - 127.881(fol.S)	421.53	0.296
196.037 + 0.022(VWC) - 17.866(pH) - 2.585(TC) + 0.469(PHOS) + 0.09(TVEG)	421.80	0.280
140.911 + 0.377(VWC) - 14.761(pH) - 0.195(PHOS) - 0.128(GRAM) + 419.39(fol.P) - 82.136(fol.K)	422.11	0.272
165.814 - 15.645(pH) - 0.068(GRAM) - 0.006(NAT) - 17.626(fol.N) + 458.531(fol.P) - 78.528(fol.K)	422.14	0.268
170.834 - 18.119(pH) - 2.379(TC) - 0.206(GRAM) + 0.346(INV) + 242.389(fol.P) + 3.142(fol.Mg)	422.21	0.306

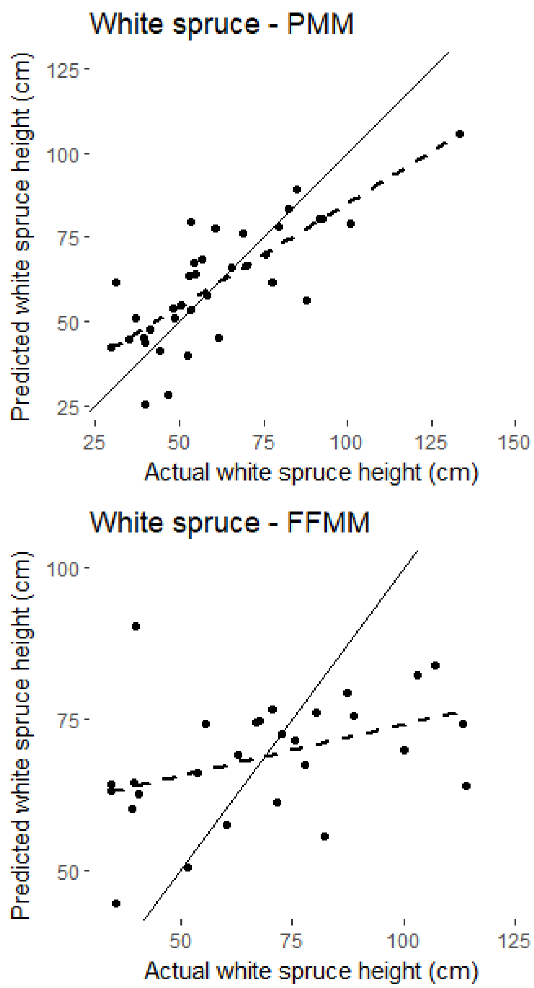
Appendix B. Full equations of the ten best scoring models according to their AICc score predicting white spruce height.

Appendix C: Actual versus predicted trembling aspen height of the best performing model on each soil type



Appendix C. Actual versus predicted trembling aspen height on each soil type. The solid line is the ideal 1:1 line and the dashed line is the linear relation between actual and predicted values.

Appendix D: Actual versus predicted white spruce height of the best performing model on each soil type



Appendix D. Actual versus predicted white spruce height on each soil type. The solid line is the ideal 1:1 line and the dashed line is the linear relation between actual and predicted values.