UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RECRUTEMENT DES ESSENCES BORÉALES DANS DE JEUNES PLANTATIONS DE PEUPLIERS HYBRIDES DE DIFFÉRENTES DENSITÉS SUR PENTE DE STÉRILES MINIERS

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

EXTENSIONNÉE

DE

L'UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PAR

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JUIN 2018

AVANT-PROPOS

Ce mémoire est le fruit d’un travail de recherche qui s’inscrit dans le cadre d’un projet plus vaste dirigé par Marie Guittonny et cherchant à éprouver l’utilisation de plantations d’arbres à croissance rapide comme méthode de revégétalisation de pentes abruptes de stériles miniers. Il est présenté sous forme d’article, lequel a été soumis et accepté pour publication dans la revue scientifique *Forest Ecology and Management* (2018, vol. 429), avec comme auteurs, moi-même, Hugo Bouchard, ainsi que mes directrice et codirectrice de recherche, Marie Guittonny et Suzanne Brais. Je suis le principal responsable de la collecte des données, de leur analyse et de la rédaction de l'article. Mes directrice et codirectrice m’ont épaulé dans chacune des étapes du travail de recherche et ont révisé de manière critique et constructive le contenu de l’article.

REMERCIEMENTS

La réalisation de ce mémoire a été rendue possible grâce au concours et à l'expertise de plusieurs personnes. Je voudrais d'abord témoigner ma gratitude à ma directrice de recherche, Marie Guittonny, pour la grande qualité de son encadrement, son soutien invariant ainsi que son dévouement à l'égard de la réussite de ce projet. Je souhaiterais également exprimer ma reconnaissance à ma codirectrice de recherche, Suzanne Brais, pour ses conseils généreux et son appui. De même, je souhaiterais remercier les autres membres de mon comité d'encadrement, Brian Harvey, Guy LaRocque, Yves Bergeron et Jean-François Boucher, qui ont fourni des commentaires précieux à différentes étapes du projet. L'enseignement éclairant de Marc Mazerolle est également digne de mention.

De la même manière, la réussite du projet est tributaire des efforts de la technicienne de recherche et des étudiants de 1er cycle qui contribué à la collecte des données sur le terrain, nommément : Avril Jobin, Yoan Goudreau, Charles Frenette-Vallières, Sara Gervais, Paulo-Bernardo Neves-E-Castro, Antoine Beaulieu, Maguelonne Rajot et Liam Boivin.

Enfin, ce projet n'aurait pu être mené à bien sans la participation financière du Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG), du Fonds de recherche du Québec – Nature et technologies (FRQNT) et du Partenariat Canadian Malartic.

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RÉSUMÉ

Les rejets miniers procurent des conditions hostiles au recrutement des essences forestières, notamment les haldes à stériles, dont les pentes érodables sont sujettes à la dessiccation. En région forestière, les plantations d'arbres à croissance rapide pourraient accélérer la conversion de ces sites dégradés en facilitant le recrutement des espèces arborescentes dans leur sous-étage tout en contribuant à stabiliser les pentes. Dans le cadre de cette étude, un dispositif expérimental a été établi dans le parc à résidus de la mine Canadian Malartic en vue d'éprouver cette stratégie de facilitation sur pentes de stériles miniers en contexte boréal. L'effet de la densité de jeunes peupliers hybrides sur la levée et la survie initiale des plantules d'essences forestières ainsi que sur le microenvironnement du sous-étage a été mesuré dans des plantations de différents espacements (1x1, 2x2, 4x4 m et témoin sans arbres). Les résultats ont également été comparés dans des plantations de 2x2 m avec et sans hydroensemencement herbacé, traditionnellement utilisé dans les pentes pour minimiser l'érosion. Lors de la 2^{e} saison de croissance des plantations, un patron quadratique entre les levées de *Salicaceae* issues de la colonisation naturelle et la densité de plantation a été observé, alors que les valeurs les plus élevées ont été mesurées sous un niveau intermédiaire de densité. Cependant, les conditions d'éclairement du sous-étage se sont avérées limitantes pour la survie de ces plantules intolérantes à l'ombre dès l'été suivant. À la suite d'un essai d'ensemencement réalisé pendant la 3^{e} saison de croissance des plantations, les taux de levées de *Picea glauca* et *Abies balsamea* ont augmenté en fonction de la densité de plantations. Pendant leur pic d'émergence printanier, des niveaux d'humidité du sol plus élevés ont été enregistrés sous couverts plus denses. Au terme de la saison de croissance, une augmentation modérée de l'abondance finale des plantules en fonction de la densité du couvert demeurait observable seulement chez *A. balsamea*. Dans les parcelles hydroensemencées, un effet néfaste du couvert herbacé a été mesuré sur les levées des essences pionnières ainsi que sur la survie des plantules d'*A. balsamea*. En somme, ces résultats suggèrent que l'utilisation des peupliers hybrides sans traitement hydroensemencé s'avère une meilleure stratégie en vue de procurer rapidement des opportunités pour le recrutement initial d'espèces typiques de stades plus avancés de la succession forestière dans les pentes de stériles. Malgré cela, une baisse significative des teneurs en humidité enregistrée dans la 2^{e} moitié de la 3^{e} saison de croissance sous espacement 1x1 m comparativement au 2x2 m tend à signaler une influence de plus en plus compétitive des peupliers hybrides susceptible de compromettre leur potentiel facilitant à moyen terme. Un suivi à plus long terme s'avère donc nécessaire afin de vérifier que les mécanismes de compétition ne supplantent pas rapidement ceux de facilitation dans les pentes de stériles, où les contraintes liées à la disponibilité des ressources, notamment en eau, peuvent être sévères.

Mots clés : revégétalisation minière, boisement, plantation-abri, hydroensemencement herbacé, microenvironnement du sous-étage, succession forestière

CHAPITRE 1

INTRODUCTION

1.1 Problématique

Les activités minières transforment de vastes superficies dans plusieurs régions du monde, où les écosystèmes d'origine sont remplacés par des accumulations de rejets miniers (Singh *et al.* 2004). L'intensification des activités d'extraction en réponse à la demande mondiale sans cesse croissante en ressources minérales souligne l'importance de l'écologie de la restauration et du développement de pratiques aptes à mitiger les impacts environnementaux de l'industrie. Les aires d'accumulation de rejets miniers solides suppriment non seulement la végétation, mais détruisent le sol, le réservoir de graines et de propagules ainsi que les microorganismes (Burger & Zipper 2002). Ces rejets miniers offrent, quant à eux, un substrat carencé en nutriments et en matière organique, au potentiel phytotoxique parfois élevé, qui s'avère peu propice à l'implantation végétale (Singh *et al.* 2002; Borden & Black 2005; Juwarkar *et al.* 2009). Dans ces conditions, le rétablissement de la végétation d'origine par succession naturelle peut s'avérer un processus lent et incertain (Parrotta *et al.* 1997a; Alday *et al.* 2011).

Au Québec, dans le contexte du Plan Nord et de la multiplication anticipée des grands projets miniers, la restauration des sites miniers s'impose comme un enjeu environnemental crucial. La *Loi sur les mines* (RLRQ, chapitre M-13.1) oblige la mise en végétation des sites miniers après leur fermeture de manière à contrôler l'érosion et à limiter la propagation des substances pouvant contaminer le milieu récepteur. En vertu de cette loi, le *Guide de préparation du plan de réaménagement et de restauration des sites miniers au Québec* (MERN 2017) stipule que les attributs des zones revégétalisées devraient redonner au site un aspect naturel en harmonie avec le milieu environnant et être compatibles avec l'usage futur des sites restaurés. Puisque les forêts dominent le paysage boréal et sont au cœur du développement économique de plusieurs régions du Québec, le rétablissement de l'écosystème forestier devrait donc être l'objectif fixé d'un grand nombre de travaux de restauration de sites miniers.

Les stériles miniers comptent parmi les deux principaux types de rejets solides rencontrés sur les sites miniers avec les résidus de concentrateur. Ce sont les matériaux rocheux recouvrant le gisement exploité, extraits par explosion et empilés (Brooks 1990). La méthode conventionnelle de revégétalisation des pentes de stériles miniers consiste à implanter une couche herbacée. L'ensemencement herbacé permet de stabiliser rapidement la surface et de limiter l'érosion (Helm 1995). Cependant, le recours aux herbacées satisfait davantage un objectif de remise en état à court terme et ne favorise pas forcément le retour à l'écosystème d'origine (Holl 2002). L'incidence négative de la compétition herbacée pour l'eau, les nutriments et la lumière sur l'implantation des arbres a été démontrée en contexte minier (Rizza *et al.* 2007; Franklin *et al.* 2012). De plus, un couvert herbacé dense peut diminuer la disponibilité des lits de germination propices à l'établissement des espèces arborescentes (Coates *et al.* 1994). Conséquemment, la survie et la croissance des plantules arborescentes s'avèrent souvent faibles sur les sites revégétalisés à l'aide de cette technique (Andersen *et al.* 1989).

Le sol minier superficiel, excavé avant empilement des rejets ou avant creusage de la fosse, peut être conservé afin de recouvrir les rejets miniers et créer un substrat plus propice à l'implantation végétale. Dans ces circonstances, il est envisageable de planter des essences forestières dans les pentes de stériles, mais l'érosion peut compromettre la pérennité de la couverture de sol (Espigares *et al.* 2011). Une autre stratégie de restauration du milieu forestier pourrait miser sur la capacité de techniques de revégétalisation à freiner l'érosion tout en stimulant la recolonisation naturelle des espèces arborescentes. Le modèle théorique de la facilitation (Connell & Slatyer 1977) suggère que les espèces pionnières, aptes à coloniser les sites suite à une perturbation, préparent le milieu pour l'établissement des espèces apparaissant plus tardivement dans la succession végétale. L'équilibre entre la facilitation et la compétition dépendrait des conditions abiotiques observées (Callaway & Walker 1997) : il est prédit que l'importance relative des interactions positives augmente en fonction de l'intensité du stress abiotique (Bertness & Callaway 1994). L'effet facilitant des plantations sur la colonisation des espèces arborescentes indigènes a été étudié en climat tropical (Guariguata *et al.* 1995; Parrotta 1995; Otsamo 2000; Carnevale & Montagnini 2002) et tempéré (Seiwa *et al.* 2012; Boothroyd-Roberts *et al.* 2013), mais reste à démontrer en conditions minières boréales. Sur les pentes de stériles miniers, les plantations d'espèces arborescentes à croissance rapide pourraient faciliter le recrutement des essences forestières plus tolérantes à l'ombre. Ces plantations contribueraient, d'une part, à pérenniser la couche de sol mise en place face à l'érosion. D'autre part, elles pourraient accélérer le retour d'un microenvironnement favorable dans leur sous-étage, lequel influence de manière marquée le succès de recrutement des plantules en conditions forestières (DeLong *et al.* 1997; Greene & Johnson 1998; Simard *et al.* 1998; Wang & Kemball 2005).

Le peuplier hybride, doté d'une croissance plus élevée que d'autres feuillus (Casselman *et al.* 2006) et dont certains clones allouent une forte proportion de leur biomasse vers les racines (Larchevêque *et al.* 2011a) pourrait jouer un rôle facilitant par l'intermédiaire du développement accéléré d'un système racinaire extensif et d'un couvert arborescent. La densité utilisée est un facteur important du design de plantation, dont l'effet structurant sur le microenvironnement du sous-étage pourrait conditionner l'effet facilitant des peupliers hybrides dans le milieu restauré (Geldenhuys 1997; Paquette *et al.* 2008; Trindade & Coelho 2012).

L’objectif général de ce projet consiste à tester l’hypothèse de facilitation en pentes de stériles miniers en étudiant l’influence de différents agencements de plantation de peupliers hybrides semi-exotiques sur le recrutement des espèces arborescentes boréales. L’effet de la densité de plantation sur la levée et la survie initiale des plantules d’essences forestières ainsi que sur le microenvironnement du sous-étage est d’abord examiné. La réponse des plantules est ensuite comparée à celle enregistrée dans des parcelles avec hydroensemencement herbacé, soit le traitement de restauration utilisé traditionnellement dans les pentes pour contrer l’érosion.

1.2 État des connaissances

1.2.1 Recrutement des espèces arborescentes boréales

1.2.1.1 Perturbations et dynamiques successionnelles

La régénération des espèces arborescentes suite à une perturbation est fonction des conditions d’établissement observées. Le recrutement des essences forestières comporte de nombreuses exigences, notamment une source de graines ou de propagules, des lits de germination favorables, des conditions microclimatiques propices ainsi qu’un degré de compétition relativement faible (Macdonald *et al.* 2012). Les sites miniers répondent difficilement à certaines ou à l’ensemble de ces exigences, alors que les conditions rencontrées correspondent davantage aux étapes initiales de la succession végétale primaire qu’à celles de la succession secondaire (Bradshaw 1983; Macdonald *et al.* 2012). Les mécanismes de la succession naturelle y opèrent en effet très lentement en raison de la suppression de la couche de surface, laquelle entraîne notamment la perte des composantes biotiques du sol (Parrotta *et al.* 1997a). Un des principaux objectifs des stratégies de restauration des sites miniers devrait être d’accélérer ces mécanismes en recréant les conditions microenvironnementales propices au redéveloppement de la végétation (Lugo 1997). À cet égard, les connaissances tirées des dynamiques de succession de la forêt boréale peuvent s’avérer utiles pour comprendre l’importance relative des facteurs biotiques et abiotiques limitant le recrutement des espèces arborescentes sur les sites dégradés (Walker & del Moral 2009; Alday *et al.* 2011).

En forêt boréale mixte, l’espace disponible suite à une perturbation importante (feu, épidémie, coupe) profite notamment aux espèces intolérantes à l’ombre (Chen & Popadiouk 2002) comme les peupliers, dotés de capacités de dispersion des graines sur de grandes distances et caractérisés par une croissance rapide (Landhäusser *et al.* 2010). Ces essences dites pionnières dominent souvent le couvert arborescent des jeunes peuplements, mais s’avèrent plus ou moins incapables de s’établir sous leur propre ombrage. Lors des stades de développement ultérieurs des peuplements, la place occupée par les espèces à croissance plus lente, plus tolérantes à l’ombre, comme l’épinette blanche et le sapin baumier, devient typiquement plus importante (Galipeau *et al.* 1997; Pastor *et al.* 1999). Ces changements dans la composition et l’abondance des espèces se montrent intimement liés aux modifications des conditions de recrutement sous le couvert arborescent (De Grandpré *et al.* 1993). Par ailleurs, les plantules des espèces arborescentes ne sont pas distribuées aléatoirement sur le parterre forestier, mais leur succès de recrutement est associé à des microsites particuliers (DeLong *et al.* 1997; Simard *et al.* 1998; Wang & Kemball 2005).

1.2.1.2 Lits de germination

La faible qualité des lits de germination a été identifiée comme un facteur limitant le recrutement des essences forestières. Les sols minéraux et les litières de feuilles mortes sont reconnus respectivement comme des substrats favorables et défavorables à la survie initiale des jeunes plantules (DeLong *et al.* 1997; Greene & Johnson 1998; Wang & Kemball 2005). Des conditions d’humidité plus stables sont en effet associées aux sols minéraux, alimentés en eau par remontée capillaire via les micropores (Greene & Johnson 1998). Inversement, la structure plus poreuse de l’horizon organique diminue la capacité de rétention en eau, ce qui entraîne des taux de germination et de survie initiale plus faibles (Greene & Johnson 1998; Calogeropoulos *et al.* 2004). De cette manière, le développement rapide de la litière sous le couvert arborescent réduit la proportion des lits de germination favorables au recrutement (Greene *et al.* 1999). Néanmoins, l'étude de Hesketh *et al.* (2009) souligne qu'une mince couche de litière peut servir de paillis qui retient l'eau et s'avérer avantageuse pour la survie des germinants.

La dépendance des essences forestières vis-à-vis des microsites favorables est d'autant plus marquée que leurs graines sont petites (Johnstone & Chapin III 2006; Greene *et al.* 2007). Les espèces dotées de graines plus volumineuses se caractérisent par un hypocotyle et une radicule plus développés, ce qui présente un atout pour traverser la couche de litière et exploiter les ressources en eau du sol minéral (Greene & Johnson 1998; Hesketh *et al.* 2009). À l'opposé, les semis de peupliers, issus de graines minuscules, tardent à développer leur radicule suite à la germination, ce qui les rend vulnérables à la dessiccation (Perala 1990). De cette manière, l'épinette blanche, qui possède des graines deux à trois fois plus grosses que le bouleau blanc, devrait comparativement s'établir plus facilement sur les sites moins favorables, même lorsque les conditions d'éclairement ne sont pas contraignantes (Robert *et al.* 2012). Davantage encore, le sapin baumier, doté de graines volumineuses, se montre plus ubiquiste que l'épinette blanche sous couvert feuillu dans la mesure où les germinants de cette espèce s'avèrent en comparaison plus performants sur une couverture morte (Simard *et al.* 1998).

Bien que l'augmentation de la taille des graines influence positivement la survie initiale des plantules (Greene & Johnson 1998), elle est généralement associée à une baisse de la production annuelle des semences et de la capacité de dispersion (Greene *et al.* 1999). Conséquemment, si la faible disponibilité de lits de germination adéquats contraint souvent le recrutement de l'épinette blanche sous couvert, la faible disponibilité des graines peut constituer un facteur davantage limitant pour le recrutement du sapin baumier (Wang & Kemball 2005).

1.2.1.3 Paramètres abiotiques : éclairement disponible, humidité et température

Conditions d'éclairement disponible. Les conditions d'éclairement influencent la succession végétale, au cours de laquelle les variations interspécifiques de tolérance à l'ombre modifient le succès d'établissement et la croissance des espèces. L'apport de la lumière n'est pas essentiel pour initier la germination des graines même chez les espèces intolérantes à l'ombre (Perala 1990), mais s'avère déterminant pour la croissance qui s'ensuit, à plus forte raison chez les espèces pionnières comme les peupliers et les saules. En effet, les graines de ces espèces étant dépourvues d'endosperme, la croissance de leurs germinants est immédiatement tributaire de l'activité photosynthétique (Karrenberg *et al.* 2002). Pour le bouleau blanc, il est rapporté que des sites ombragés sont généralement plus favorables à la germination (Safford *et al.* 1990). Les semis du bouleau peuvent prospérer sous des conditions d'ensoleillement réduit à 45 % du plein rayonnement lumineux (Logan 1965), mais leur tolérance à l'ombre diminue rapidement avec l'âge (Perala & Alm 1990). Quant à l'épinette blanche, bien qu'elle soit davantage caractéristique des peuplements de mi et fin de succession, elle s'établit souvent en concurrence avec les espèces intolérantes à l'ombre lors de la phase initiale de recolonisation suite à une perturbation (Galipeau *et al.* 1997). Dans les grandes ouvertures, le recrutement du sapin baumier est pour sa part plus faible, alors que les conditions d'humidité (McLaren & Janke 1996; Duchesneau & Morin 1999) et la compétition accrue par les espèces intolérantes (Galipeau *et al.* 1997) s'avèrent défavorables à sa germination et à sa survie initiale. En d'autres mots, le taux de germination et la survie des germinants de sapin baumier diminuent avec l'augmentation de l'éclairement disponible (Calogeropoulos *et al.* 2004). Par ailleurs, les études de Wang & Kemball (2005) et de Simard *et al.* (2003) tendent à indiquer que les conditions d'éclairement ne contraignent pas le recrutement de l'épinette blanche et du sapin baumier sous un couvert de peupliers faux-trembles lors des deux premières années de croissance des semis. L'épinette blanche s'observe sur des parterres forestiers où la lumière transmise atteint à peine 8 % et parvient à une croissance en hauteur optimale avec aussi peu que 40 % du rayonnement lumineux (Lieffers & Stadt 1994). Le sapin baumier tolérerait quant à lui des niveaux d'ensoleillement encore plus défavorables (Landhäusser & Lieffers 2001). Néanmoins, sous conditions ombragées, une croissance racinaire moins prononcée s'observe chez les plantules des deux espèces (Landhäusser & Lieffers 2001), ce qui pourrait contribuer à augmenter leur vulnérabilité au stress hydrique.

Conditions d'humidité. Les banques de semis de la plupart des espèces arborescentes connaissent des pertes considérables pendant les première et deuxième années de croissance des plantules. Par la suite, les taux de mortalité diminuent fortement (Greene & Johnson 1998). Or, la majorité des pertes initiales s'expliquerait par la dessiccation (Greene *et al.* 1999). Comme souligné précédemment, les différences en termes de succès de recrutement entre les types de lits de germination sont d'abord attribuables aux conditions d'humidité (Wang & Kemball 2005). Les semences de grande taille comme celles du sapin baumier requièrent un fort taux d'humidité pour germer (Harper *et al.* 1970). Une humidité relative faible à la surface du sol augmente les pertes d'eau par évaporation chez les graines et diminue ainsi le taux de germination (Oleskog *et al.* 2000). Puis, tout au long de la saison de croissance, les semis demeurent vulnérables vis-à-vis des fluctuations du taux d'humidité dans le sol, alors qu'un stress hydrique même modéré peut perturber les activités photosynthétiques et la croissance (Gärtner *et al.* 2011).

Conditions de température. Les semences germent dès que la température à la surface du sol est suffisante si les exigences d'humidité sont satisfaites (Nienstaedt & Zasada 1990). Ces paramètres abiotiques apparaissent en effet comme les principaux facteurs limitant le processus de germination (Gärtner *et al.* 2011). Les températures de germination optimales se situent entre 15 et 20 degrés pour le peuplier faux-tremble, alors qu'elles se trouvent entre 10 et 24 °C pour l'épinette blanche (Nienstaedt & Zasada 1990) et entre 18 et 28 °C pour le sapin baumier (Fraser 1970). La grande pénétration de la lumière avant le débourrement en peuplements feuillus favorise le réchauffement printanier du parterre forestier, ce qui stimule le processus de germination des graines disséminées à l'automne (conifères, bouleaux) (Simard *et al.* 2003). Les plantules qui émergent en début de saison de croissance ont de meilleures chances de survie lors du premier hiver que celles plus tardives (Nienstaedt & Zasada 1990; Farmer 1996). En milieu ouvert, les plantules d'épinette blanche et de sapin baumier sont néanmoins vulnérables aux extrêmes de température printaniers : les gels tardifs endommagent fréquemment les bourgeons à peine débourrés et les nouvelles pousses (Sims *et al.* 1990). Des perturbations de l'activité photosynthétique et des hausses de mortalité sont également associées aux gels nocturnes durant la saison de croissance (Man & Lieffers 1999).

1.2.1.4 Compétition herbacée

Les interactions biotiques constituent un autre facteur important qui contribue à définir le succès d'établissement des espèces arborescentes. Suite à une perturbation, les herbacées peuvent atteindre rapidement des densités élevées et accaparer les ressources (Hart & Chen 2006), créant de la sorte des conditions adverses pour la régénération des conifères (Hogg & Lieffers 1991). L'incidence négative de la compétition herbacée sur les plantules se traduit le plus souvent par une diminution de la croissance (Hogg & Lieffers 1991; Cater & Chapin III 2000). L'étude de Wang & Kemball (2005) souligne néanmoins l'influence positive des conditions ombragées produites par la végétation du sous-étage sur le recrutement de l'épinette blanche, potentiellement en raison d'une diminution de l'évapotranspiration chez les plantules.

Dans ces circonstances, leur étude tend à souligner que la compétition pour la lumière est moins limitante qu'un déficit hydrique à l'égard de la survie initiale des semis.

De même, la litière du sous-étage peut exercer un rôle limitant. D'une part, la litière d'un couvert herbacé dense forme une barrière physique contraignant l'établissement des plantules arborescentes (Coates *et al.* 1994). D'autre part, la litière du sous-étage, au même titre que celle du couvert arboré, menace d'ensevelir les jeunes recrûs. Le risque de mortalité est amplifié lors de l'hiver subséquent alors que l'accumulation de neige contribue à compacter la litière et à écraser les plantules (Wang & Kemball 2005; Gärtner *et al.* 2011).

1.2.2 Restauration écologique en contexte minier

1.2.2.1 Restauration et succession

La restauration des sites miniers en conditions forestières boréales pose un défi de taille en raison des conditions d'établissement adverses qui limitent la régénération des espèces arborescentes. Del Moral & Walker (2007) mentionnent que l'identification des facteurs limitant l'implantation de la végétation ainsi que des processus naturels qui permettent de les surmonter représente une étape clé d'une entreprise de restauration écologique. En ce sens, il est suggéré que la mise en œuvre de pratiques cherchant à tirer parti des mécanismes derrière la succession naturelle peut améliorer significativement le succès de revégétalisation des sites dégradés (Walker & del Moral 2009).

1.2.2.2 Pratiques de restauration écologique : couverture de sol superficiel et plantation-abri

Suite à une perturbation, les mécanismes de la succession naturelle opèrent plus rapidement sur un substrat bénéficiant d'un legs biologique (Turner *et al.* 1998), notamment une banque de graines ou de propagules pouvant contribuer au recrutement (Marcus 1997). Or, les exploitations minières à ciel ouvert génèrent des monticules de rejets dénudés et sans précurseurs biologiques (Marcus 1997; Parrotta *et al.* 1997a). Par ailleurs, les rejets miniers offrent un substrat peu fertile qui réduit d'autant plus les probabilités d'établissement des espèces en place avant la perturbation, non adaptées à ces nouvelles conditions (Alday *et al.* 2011). Dans ces circonstances, l'utilisation d'une couverture de sol superficiel peut contribuer à accélérer la succession végétale (Marcus 1997), d'une part, en réintroduisant potentiellement des graines dans le milieu (Singh *et al.* 2002), et d'autre part, en améliorant les conditions de croissance (Wong 2003). En effet, le sol superficiel décapé et récupéré contient généralement des graines des espèces de l'écosystème environnant (Singh *et al.* 2002), de sorte que son utilisation permet d'ensemencer les sites restaurés avec des espèces indigènes locales (Holl 2002). Puis, la couverture de sol facilite l'établissement des espèces arborescentes en fournissant une zone d'enracinement propice à la croissance (Burger *et al.* 2005; Larchevêque *et al.* 2014) de même qu'en améliorant les conditions d'humidité et la disponibilité des nutriments (Macdonald *et al.* 2012). La matière organique contenue dans la couverture de sol renforce notamment la cohésion entre les particules minérales, améliorant de la sorte la rétention de l'eau et la structure du sol tout en réduisant la vulnérabilité à l'érosion (Van Wesemael & Brahy 2013), ce qui apparaît essentiel sur pentes de stériles.

Un certain nombre d'études tendent à démontrer que les plantations d'arbres peuvent contribuer au rétablissement de conditions favorables au processus de régénération des espèces arborescentes sur les sites dégradés (Guariguata *et al.* 1995; Parrotta 1995; Otsamo 2000; Carnevale & Montagnini 2002). Le rôle facilitant des plantations a surtout été étudié en milieu tropical – où la déforestation massive a stimulé la recherche en restauration forestière – et quelque peu en zone tempérée (Seiwa *et al.* 2012; Boothroyd-Roberts *et al.* 2013), mais reste à démontrer en conditions minières boréales. L'*effet catalyseur* (Parrotta *et al.* 1997b) des plantations sur la succession végétale s'expliquerait d'abord par le développement rapide d'un couvert arborescent. Celle-ci peut faciliter la régénération d'espèces arborescentes indigènes qui s'avéreraient plus ou moins incapables de s'installer en milieu ouvert (Carnevale & Montagnini 2002). Un certain nombre de mécanismes contribuent à expliquer le succès de recrutement plus élevé sous le couvert de plantations-abris, notamment la modification des conditions microclimatiques (Lugo 1997; Otsamo 2000), la réduction de la compétition par les espèces herbacées pionnières (Powers *et al.* 1997; Otsamo 2000) et l'augmentation de la fertilité du sol via l'apport de la litière (Filcheva *et al.* 2000). D'autre part, les plantations d'arbres peuvent jouer un rôle important de protection du sol par l'intermédiaire d'un système racinaire robuste et extensif (Abrutat *et al.* 1994). Les racines des arbres augmentent notamment la stabilité des pentes (Abe & Ziemer 1991), où les pertes de sol par érosion peuvent contraindre la régénération naturelle des plantules en réduisant la disponibilité en eau, en nutriments et en graines (Espigares *et al.* 2011).

1.2.2.3 Matériel de plantation

Bien que la majorité des arbres puissent exercer un rôle facilitant, les feuillus sont généralement reconnus comme de meilleurs catalyseurs, en particulier les espèces pionnières à croissance rapide (Parrotta *et al.* 1997b). À plus forte raison, la topographie des sites miniers, marquée par de nombreuses pentes sujettes à l'érosion (Espigares *et al.* 2011), accentue l'importance du développement accéléré du système racinaire (Macdonald *et al.* 2012). Le peuplier hybride, dont certains clones montrent un ratio racine/tige élevé (Larchevêque *et al.* 2011a), compte parmi les espèces capables de s'établir sur sites dégradés les plus vigoureuses (Guy & Bateman 1989). De surcroît, le potentiel facilitant du peuplier a été récemment étudié dans des champs abandonnés, où les plantations ont accéléré la transition vers les peuplements forestiers naturels en favorisant la colonisation par les espèces arborescentes et la restauration du sous-étage forestier (Boothroyd-Roberts *et al.* 2013).

1.2.2.4 Influence sur les facteurs limitants

Lits de germination. Les stériles miniers forment généralement un substrat de texture hétérogène dont les particules fines sont rapidement perdues par érosion dans les pentes, ce qui diminue la capacité de rétention en eau (Brooks 1990) et entraîne des conditions d'humidité peu propices à la germination. L'ajout d'une couverture de sol superficiel augmente la capacité du sol à emmagasiner l'eau (Macdonald & Fenniak 2007) et fournit un lit de germination plus favorable (Pinno *et al.* 2012). Il a en effet été observé précédemment qu'un sol minéral et des conditions d'humidité stables sont propices à la germination des graines et à la survie initiale des plantules d'espèces arborescentes (Wang & Kemball 2005).

L'établissement rapide du couvert de la plantation encourage la formation d'une litière, laquelle contribue au redéveloppement du sol forestier sur les sites dégradés (Filcheva *et al.* 2000; Macdonald *et al.* 2012). Néanmoins, la réceptivité des lits de germination diminue en fonction de l'épaisseur de la couche morte (DeLong *et al.* 1997; Greene *et al.* 1999), notamment pour les espèces arborescentes dotées de petites graines comme les espèces pionnières et, dans une moindre mesure, l'épinette blanche (Nienstaedt & Zasada 1990). La densité de plantation influencera l'apport quantitatif en matière organique à la surface du sol (Macdonald *et al.* 2012), et conséquemment, la disponibilité des lits de germination les plus favorables.

À cet égard, un rapprochement peut être établi entre la densité de plantation et la proportion du couvert maintenue suite à des coupes à rétention variable. Calogeropoulos *et al.* (2004) ont étudié la capacité de régénération de l'épinette blanche et du sapin baumier sur sol minéral (débarrassé manuellement de l'humus et de la litière) sous différentes intensités de récolte, incluant l'absence de coupe, la coupe partielle d'un tiers ou des deux tiers de la surface terrière du peuplement et la coupe totale. Leur étude, réalisée en peuplement dominé par le peuplier faux-tremble, démontre sans surprise que l'accumulation de la litière est inversement proportionnelle à l'intensité de la récolte. Parallèlement, les tests d'ensemencement indiquent, dès la deuxième année postrécolte, une diminution croissante des taux de germination avec la fermeture du couvert pour l'épinette comme pour le sapin, c'est-à-dire que la réceptivité des lits de germination diminue d'autant plus vite que le couvert contribue à l'accumulation de la litière.

Conditions abiotiques. Les sites ouverts présentent des conditions abiotiques instables, alors que les fluctuations microclimatiques sont plus importantes que sous couvert (Gärtner *et al.* 2011). De manière générale, l'humidité relative est une fonction inverse de l'ouverture du couvert et de l'intensité du rayonnement lumineux (Man & Lieffers 1999). Le couvert arborescent réduit le gradient de pression de vapeur d'eau du sol vers l'air ainsi que les déplacements d'air (Geiger 1965), ce qui diminue l'évaporation à la surface du sol. Néanmoins, lorsque les arbres procurant le couvert se caractérisent par un développement racinaire superficiel et par des taux d'évapotranspiration qui excèdent les taux d'évaporation sur sol dénudé, le couvert peut réduire la disponibilité en eau à la surface du sol (Burton & Bazzaz 1991).

Il a été suggéré que les plantations peuvent jouer un rôle protecteur vis-à-vis des conditions abiotiques adverses comparable aux peuplements résiduels laissés en place après une coupe (Paquette *et al.* 2008). L'étude de Calogeropoulos *et al.* (2004) indique que le taux de germination des graines de sapin baumier est significativement plus élevé dans les aires de coupe partielle que dans les aires de coupe totale – lorsque par ailleurs la qualité des lits de germination est équivalente –, possiblement en raison de carences en humidité associées au fort ensoleillement en milieu exposé. De manière similaire, l'étude de McLaren & Janke (1996) signale une baisse du taux de germination des graines de sapin sous un couvert <40 %. Le taux de germination des graines d'épinette blanche semble quant à lui moins fortement influencé par l'intensité de la récolte (Calogeropoulos *et al.* 2004). Subséquemment, la survie des plantules peut aussi être affectée par la densité du couvert. Ainsi, les résultats de

Calogeropoulos *et al.* (2004) témoignent d'une survie cumulative moins élevée dans les aires non perturbées (absence de coupe), où la transmission de la lumière est faible, que dans les aires de coupe partielle, chez les semis de sapin et d'épinette à la fin de la troisième saison de croissance. Dans le même sens, McLaren & Janke (1996) ont noté des taux de mortalité plus élevés sous couvert >80 % chez des semis de sapin au cours de la deuxième saison de croissance. En somme, l'effet protecteur bénéfique d'un couvert caractérisé par un degré de fermeture entre 40 et 80 % pourrait être attribuable aux taux de germination des graines généralement plus faibles en l'absence de couvert (carence en humidité) ainsi qu'aux taux de mortalité des plantules plus élevés sous couvert fermé (carence en éclairement) (Calogeropoulos *et al.* 2004).

Il a également été observé que le couvert exerce un rôle régulateur vis-à-vis des extrêmes de température (Man & Lieffers 1999). D'une part, la plus grande exposition à l'ensoleillement et aux températures élevées en milieu ouvert augmente les risques de stress hydrique par l'augmentation de l'évapotranspiration chez les jeunes plantules (Gärtner *et al.* 2011). D'autre part, les risques de gel nocturne au sol liés aux pertes de chaleur par radiation infrarouge sont plus élevés en milieu exposé (Man & Lieffers 1999). Man & Lieffers (1997), comparant la croissance de plantules d'épinette blanche d'un an sous couvert et en l'absence de couvert, ont noté des baisses d'activité photosynthétique significativement plus grandes en milieu ouvert, au printemps et à l'automne, alors que la fréquence des gels nocturnes était élevée. De même, ils ont signalé un taux de mortalité des bourgeons apicaux à peine débourrés significativement plus élevé en milieu exposé.

Compétition herbacée. Le couvert herbacé, qu'il soit ensemencé ou issu de la recolonisation naturelle par les espèces pionnières, exerce une pression compétitive sur la régénération des espèces arborescentes en monopolisant rapidement les ressources suite à une perturbation (Halofsky & McCormick 2005; Rizza *et al.* 2007).

Il a été suggéré que la plus faible abondance des herbacées compétitrices sous couvert arboré facilite le recrutement des espèces arborescentes (Boothroyd-Roberts *et al.* 2013). Plus précisément, le développement d'un couvert arborescent précarise la survie des espèces intolérantes à l'ombre, telles les graminées, et crée ainsi des opportunités d'établissement pour les espèces plus tolérantes à l'ombre, notamment pour les espèces arborescentes (Macdonald *et al.* 2012; Boothroyd-Roberts *et al.* 2013). Dans cet esprit, le potentiel d'utilisation d'un couvert partiel a été étudié en vue de limiter la croissance du calamagrostide du Canada et de l'épilobe à feuilles étroites, afin de favoriser la régénération de l'épinette blanche en forêt boréale (Lieffers *et al.* 1993; Lieffers & Stadt 1994; Maundrell & Hawkins 2004). L'étude de Lieffers & Stadt (1994) indique qu'une transmission de 40 % du plein rayonnement lumineux diminue considérablement le recouvrement de ces deux espèces compétitrices sans restreindre la croissance en hauteur de l'épinette. En ce sens, le succès de recrutement des espèces arborescentes met en jeu un compromis entre l'ombre fournie par le couvert partiel, qui inhibe la croissance des plantes compétitrices, et la lumière transmise, qui permet le développement des plantules (Maundrell & Hawkins 2004).

1.3 Objectifs spécifiques et hypothèses de travail

Dans ce projet, le potentiel facilitant de jeunes plantations de peupliers hybrides vis-à-vis des essences forestières boréales est étudié en vue d'évaluer la capacité des plantations à accélérer la succession végétale sur pentes de stériles miniers recouvertes de sol superficiel. Le premier objectif spécifique de cette étude est d'éprouver ce potentiel facilitant et de déterminer comment l'espacement de plantation influence la levée et la survie initiale des plantules des essences forestières. L'influence de traitements d'espacement 1x1, 2x2, 4x4 m et d'un témoin sans arbres sur la levée et la survie initiale des plantules issues de la colonisation naturelle et d'un essai d'ensemencement est examinée. Nous avons émis l'hypothèse générale que l’utilisation des peupliers hybrides comme plantations-abris procure rapidement des conditions microenvironnementales plus propices au recrutement des essences forestières qu’un sol nu dans les pentes de stériles. Plus particulièrement, nous anticipons de meilleurs taux de levée dans les jeunes plantations sous couvert plus dense, en raison de l’augmentation des niveaux d’humidité. En revanche, les taux de mortalité des espèces arborescentes intolérantes à l’ombre devraient augmenter alors que la fermeture du couvert s’accentue et que la transmission de la lumière diminue.

Le deuxième objectif spécifique de cette étude est d’examiner si la présence d’un traitement conventionnel d’hydroensemencement herbacé contraint la levée et la survie initiale des plantules dans les plantations. Les performances des plantules seront comparées dans des parcelles d’espacement de plantation de 2x2 m, avec et sans hydroensemencement herbacé, afin de vérifier l’hypothèse suivante : la régénération des espèces arborescentes est contrainte par la présence d’un couvert herbacé hydroensemencé. Il est anticipé que le couvert herbacé accaparera les ressources en eau et en lumière, puis diminuera la réceptivité des lits de germination par accumulation de litière.

CHAPITRE 2

EARLY RECRUITMENT OF BOREAL FOREST TREES IN HYBRID POPLAR PLANTATIONS OF DIFFERENT DENSITIES ON MINE WASTE ROCK SLOPES

Early recruitment of boreal forest trees in hybrid poplar plantations of different densities on mine waste rock slopes

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2.1 Abstract

Mine wastes create harsh recruitment conditions for forest tree seedlings, especially waste rock piles where erodible slopes are prone to drought. Plantations using fast-growing tree species can potentially accelerate the conversion of degraded mine sites into forests through facilitation of tree recruitment, while contributing to the stability of slopes. In this study, hybrid poplars were tested as a means of achieving reclamation objectives by providing shelter for forest tree seedlings on waste rock slopes (3H:1V ratio) in the Canadian southern boreal region. Density effects of young hybrid poplars were assessed on the emergence and survival of early, mid and late successional species, naturally occurring or hand-seeded, and on the understory micro-environmental parameters in plantations of different spacings (1x1, 2x2, 4x4 m and control without planted trees). Results were also compared in 2x2-m plantations with and without a hydroseeded herbaceous cover, traditionally used to control erosion in slopes. During the 2nd growing season of the plantations, seedling emergence of naturally established *Salicaceae* (*Populus* and *Salix*) species followed a quadratic pattern along the density gradient, as emergence values were higher under an intermediary density. Nonetheless, decrease in light transmission emerged as a limiting factor of seedling survival for these early-successional, shade-intolerant species by the next summer. Following a spring sowing experiment in the 3rd growing season of the plantations, emergence rates for later-successional *Picea glauca* and *Abies balsamea* seedlings increased with hybrid poplar density. During their peak emergence period, in early season, higher soil moisture content was found under denser cover. However, at the end of the third year of the plantations, only *A. balsamea* showed moderate increase in early recruitment success rates under denser tree cover. In hydroseeded plots, a competitive effect of the herbaceous cover was observed on *Salicaceae* emergence and *A. balsamea* survival. These results suggest that planting of young plantations without a hydroseeded cover may offer a more suitable solution in order to quickly provide early recruitment opportunities for later-successional seedlings in waste rock slopes. Despite this, a significant decrease in moisture content recorded during the second half of the 3rd growing season under the 1x1-m cover, compared to the 2x2-m, likely signalled an increasing competitive effect from hybrid poplars, which may compromise their nursing potential in the longer term. Therefore, further monitoring is imperative for a better understanding of longer-term facilitation and competition interactions between nurse trees and understory seedlings in waste rock slopes, where competition for limited resources, such as water, may be severe.

Keywords: mine revegetation, afforestation, nurse plantation, hydroseeded cover, understory micro-environment, forest succession

2.2 Introduction

Understanding the processes involved in ecosystem recovery provides useful insights for re-establishing successional trajectories towards productive and self-sustaining ecosystems (Del Moral & Walker 2007; Walker & del Moral 2009; Polster 2011). There is growing scientific evidence that tree plantations can have a *catalytic effect* (Parrotta *et al.* 1997) on forest succession on severely degraded sites, where ecological barriers would otherwise impede recolonization by native species (Guariguata *et al.* 1995; Parrotta 1995; Carnevale & Montagnini 2002; Boothroyd-Roberts *et al.* 2013). In the boreal region, vast areas of land supporting forest ecosystems are rendered unproductive because of mining activities. Recruitment is often the stage that hinders the natural regeneration of native forest trees (Young *et al.* 2005). The facilitation successional theory (Connell & Slatyer 1977), as applied in restoration practice, suggests that planting of pioneer tree species able to grow on the newly exposed mine landform will assist the colonization of other species into the restored community (Nichols *et al.* 2010), and especially of later-successional species. The stress-gradient hypothesis predicts that positive interactions among plants increase with abiotic stress exposure (Bertness & Callaway 1994), hence hinting at the potential of facilitation in reclamation efforts because of the inhospitable nature of mining substrates.

When surface-mined, all the biotic components are removed from the forested area – including tree canopy, shrub layer, soil, rootstock and seed bank (Burger & Zipper 2002)– and replaced by accumulations of waste material. Waste rocks form one of the two main solid mine wastes along with mill tailings, and originate from rock material surrounding the ore, extracted by explosion and dumped in piles with steep slopes and flat tops (Brooks 1990). The main forest reclamation strategy on the flat areas consists in tree planting on a respread topsoil (Drake 1986; Kost & Vimmerstedt 1994; Ashby 1997; Emerson *et al.* 2009; Pietrzykowski 2010; Landhäusser *et al.*

2012; Sloan & Jacobs 2013). On the other hand, fast-growing herbaceous plants seeding with agronomic species is generally used on the slopes (Torbert & Burger 1994; Aubuchon 2010; Fields-Johnson *et al.* 2012), where soil erosion proves to be a significant barrier to plant establishment (Espigares *et al.* 2011). A ground cover of fast-growing herbaceous species allows the rapid stabilization of the soil surface and limits soil erosion on slopes (Helm 1995). However, species commonly used (mainly grasses and legumes) often compete with tree seedlings for water, nutrients and light resources (Rizza *et al.* 2007; Polster 2010; Franklin *et al.* 2012). Tree seedling establishment, survival and growth are thus often found to be very low on sites revegetated with herbaceous species (Andersen *et al.* 1989). Traditional reclamation treatments used in waste rock slopes to minimize short-term erosion may consequently hinder long-term recovery goals (Holl 2002).

As an alternative reclamation strategy, fast-growing tree plantations could benefit the regeneration of native species that can hardly grow in open environments or in competition with a herbaceous ground cover (Carnevale & Montagnini 2002). This nursing effect is first mediated by a *tree cover effect*. A number of mechanisms have been proposed to account for the better recruitment of native tree species under a plantation canopy, especially changes in understory microclimatic conditions (Lugo 1997; Otsamo 2000), reduction in competitive herbaceous species (Powers *et al.* 1997; Otsamo 2000) and improvement of soil fertility through readily decomposable litter (Filcheva *et al.* 2000). Secondly, fast-growing trees develop an extensive root system which rapidly colonizes the available soil volume (Wilkinson 1999; Douglas *et al.* 2010). Tree roots thus provide soil reinforcement that improves the stability of slopes (Abe & Ziemer 1991), where soil erosion could adversely affect tree colonization by reducing the availability of seeds, nutrients, and water in soil (Espigares *et al.* 2011).

While most trees can arguably exert a facilitating role, fast-growing broadleaf species are generally regarded as better catalysts (Parrotta *et al.* 1997). Hybrid poplar plantations were recently observed to accelerate the colonization of native species and the restoration of forest attributes on abandoned farmlands (Boothroyd-Roberts *et al.* 2013). Hybrid poplar cultivars have some of the most vigorous growth among trees available for reclamation (Guy & Bateman 1989; Casselman *et al.* 2006) and generally show good survival rates on mine sites (Czapowskyj 1978; Clark Ashby 1995; McGill *et al.* 2004). Some clones allocate a large proportion of their resources to roots (Larchevêque *et al.* 2011), which could foster the development of an extensive root system as well as a fast canopy closure to stabilize the soil and improve the understory micro-environment.

Tree spacing or density is regarded as an important factor of plantation design, potentially mediating facilitation performances in the restored community through its structuring effect on the understory micro-environment (Geldenhuys 1997; Paquette *et al.* 2008; Trindade & Coelho 2012). Denser tree covers generally offer less extreme temperatures and moisture deficiencies, but provide a more limiting light environment (Man & Lieffers 1999). If soil moisture is known to be the main limiting factor for the germination of boreal tree species (Greene *et al.* 1999), light quickly becomes limiting for the survival of shade-intolerant pioneer tree species (Karrenberg *et al.* 2002). Shading also hinders the development of light-demanding, weedy herbaceous species (De Keersmaeker *et al.* 2004). Dense weed layers not only compete for resources, but create a barrier to tree seedling establishment through leaf litter accumulation (Coates *et al.* 1994). The increased tree cover effect may thus maintain availability of favourable recruitment microsites and create opportunities for later-successional tree species (Boothroyd-Roberts *et al.* 2013), more vulnerable to desiccation than to constraints in light (Lieffers & Stadt 1994; Landhäusser & Lieffers 2001).

The restoration objective associated to this project was defined within a conceptual framework of community ecology (Naeem 2006) and aimed at reestablishing native boreal tree species to restore the structure of a forest community. The facilitating role of plantations in mining conditions was examined by few studies in relation to soil redevelopment process (Dutta & Agrawal 2002; Singh *et al.* 2004; Singh & Singh 2006; Singh & Zeng 2008) but remains largely unexplored regarding tree recruitment (Densmore 2005; Frouz *et al.* 2015), especially on waste rock slopes. This study aimed to test the facilitation hypothesis using young hybrid poplar plantations and to understand how nurse tree spacing influences the limiting factors for the recruitment of boreal tree species in a waste rock slope (3H:1V ratio). Three hybrid poplar spacings were compared to two control treatments: bare soil without planting or seeding, and soil with planted trees and a traditional hydroseeded cover treatment. Field experiments were carried out to evaluate the effects of these plantation designs on the understory micro-environmental parameters, and on the emergence and early survival of early, mid and late successional tree species. First, we monitored soil humidity and temperature conditions, available light at ground level, leaf litter accumulation and herbaceous biomass in the plantation understories. Second, we surveyed the naturally established pioneer seedlings in each plantation designs. Third, we surveyed later-successional *Picea glauca* and *Abies balsamea* seedlings following a seed-sowing experiment. We first hypothesized that planting of hybrid poplars as nurse trees would quickly exert a structuring effect on the understory micro-environmental parameters. Secondly, it was postulated that the nurse tree cover would benefit forest tree seedling performances compared to bare soil. More specifically, we predicted better seedling emergence under denser tree cover in the young plantations because of higher soil moisture content. However, seedling mortality rates are expected to increase during canopy closure for shade-intolerant pioneer species. Thirdly, we hypothesized that the presence of a hydroseeded cover would adversely affect the emergence and survival of forest tree seedlings.

2.3 Materials and methods

2.3.1 Mine site and waste rocks

The field experiments were conducted at the Canadian Malartic mine site, located in Northwestern Quebec, Canada (48°13’N, 78°12’W). Climate is cold-temperate continental with an average annual temperature of 1.5°C and a mean annual total precipitation of 929 mm (Government of Canada 2015). Average length of growing season ranges between 120 and 130 days with a mean frost-free period of 97 days (Agriculture and Agri-Food Canada 2014). The region belongs to the balsam fir-white birch bioclimatic domain in the southern portion of the boreal zone (MERN 2003). Forest stands surrounding the mine site includes balsam fir (*Abies balsamea* (Linnaeus) Miller), black spruce (*Picea mariana* (Miller) BSP), trembling aspen (*Populus tremuloides* Michaux), white birch (*Betula papyrifera* Marshall), balsam poplar (*Populus balsamifera* Linnaeus), jack pine (*Pinus banksiana* Lambert), white spruce (*Picea glauca* (Moench) Voss) and tamarack (*Larix laricina* (Du Roi) K. Koch).

The site is an active open-pit gold mine since 2011, where 55,000 tons of ore are being processed each day. Canadian Malartic ore is a mineralized greywacke. Waste rocks have low-sulphide content (around 1% S) and contain calcite. Mean trace metal concentrations in waste rocks are below Quebec regulatory thresholds for residential land use (Government of Quebec 2017).

2.3.2 Experimental setting, soil and plant material

The hybrid poplar plantations were established in May 2013 on a 50-cm overburden topsoil layer over a 3H:1V (33%) waste rock slope facing southwest and adjacent to a mature forest patch. Distance between the slope toe and the nearby forested area was slightly over 30 m. The overburden soil taken prior to ore excavation from the uppermost 30 cm (O- and A-horizons) of the partially wooded swamp above the pit was a luvic gleysol (Soil Classification Working Group 1998). The soil contained 20% organic matter and its mineral fraction was composed of 42% clay, 27% silt and 31% sand. The overburden soil was stockpiled in 7-m-high piles (2.5:1 slope) for 36 months before being respread.

Fifteen experimental plots of 8x12 m located along the lower half of the slope and separated by 4-m-wide buffer zones were treated according to a randomized complete block design. Five treatments within three replicate blocks were applied: (1) 1x1-m (10 000 stems/ha), (2) 2x2-m (2 500 stems/ha) and (3) 4x4-m (625 stems/ha) hybrid poplar spacing treatments, (4) a control treatment with an intermediary (2x2 m) poplar spacing and a traditional hydroseeded herbaceous cover, and (5) a control treatment without planting or hydroseeding (Figure 2.1).

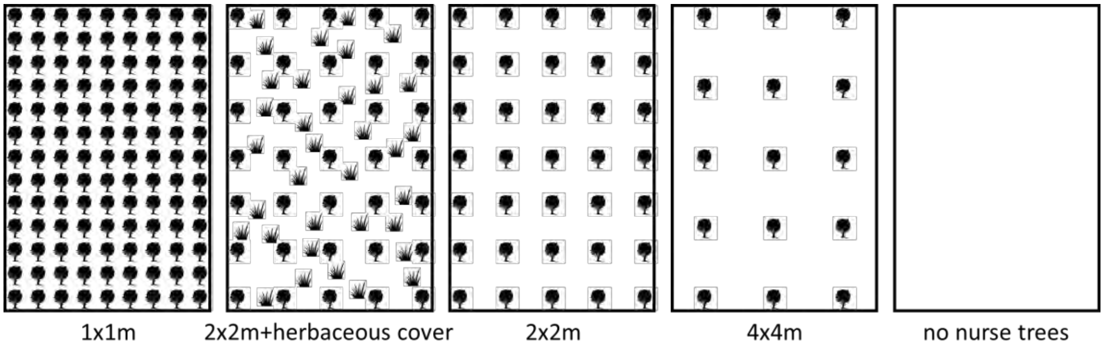


Figure 2.1 Hybrid poplar plantation designs grouped in each block of the experimental layout (not drawn to scale nor randomized).

The hybrid poplar stock consisted of clonally propagated one-year-old whips (1-m long cuttings) from *Populus maximowiczii* Henry × *P. balsamifera* L. (M×B, clone number 915319), locally produced by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) and well adapted to the local conditions. Grass and legume species in the hydroseeded plots included the following commonly used reclamation species: *Festuca rubra* Linnaeus (15%), *Poa pratensis* Linnaeus (15%), *Pennisetum* *glaucum* (Linnaeus) R. Brown (12%), *Lolium perenne* Linnaeus (12%), *Avena sativa* Linnaeus (11%), *Lotus corniculatus* Linnaeus (15%), *Trifolium pratense* Linnaeus (10%), *Trifolium repens* Linnaeus (7%) and *Trifolium hybridum* Linnaeus (3%). Seeding rate was 100 kg ha^{-1} while a fertilizer (8% N, 32% P, and 16% K, di- and mono-ammonium phosphates and potassium chloride) was applied once at seeding in May 2013 at 750 kg ha^{-1}.

A. balsamea and *P. glauca* seeds were also provided by the MFFP. The seed lots received a 48-hour-priming treatment followed by a 21-day cold moist stratification treatment to promote higher germination rates (Colas & Bettez 2014). A viability test was performed by placing 3x100 seeds of both species on wet paper in Petri dishes placed under controlled conditions at ~20°C for 20 days to assess the germination capacity of the seed lots before experimentation (Charron & Greene 2002; Johnstone & Chapin III 2006). The germination rates obtained were close to those reported by the MFFP: 72 and 92% respectively for *A. balsamea* and *P. glauca*.

2.3.3 Understory micro-environment measurements (2014-2015)

Three 1-m^2 microsites were placed systematically within each experimental plot for micro-environment measurements during the 2014 and 2015 growing seasons. Microsites were positioned at the intersection of the diagonals of the square formed by four adjacent planted hybrid poplars in each third of the plot along the slope (Figure 2.2). Continuous measures of soil water volumetric content were taken at 3-cm depth (ECH2O 5-cm probe, Decagon, calibrated for the soil type used) in the microsite located in the centre of each plot. From June to August 2014 and May to August 2015, hourly measurements were recorded to calculate weekly averages. Soil temperature at 3-cm depth (Acorn probe, Oakton Instruments) and photosynthetic photon flux density (PPFD) at ground level (Sunfleck Ceptometer, Decagon) were measured every two weeks in the three microsites of each plot during the same period. Measurements for these two parameters were taken around noon, under clear

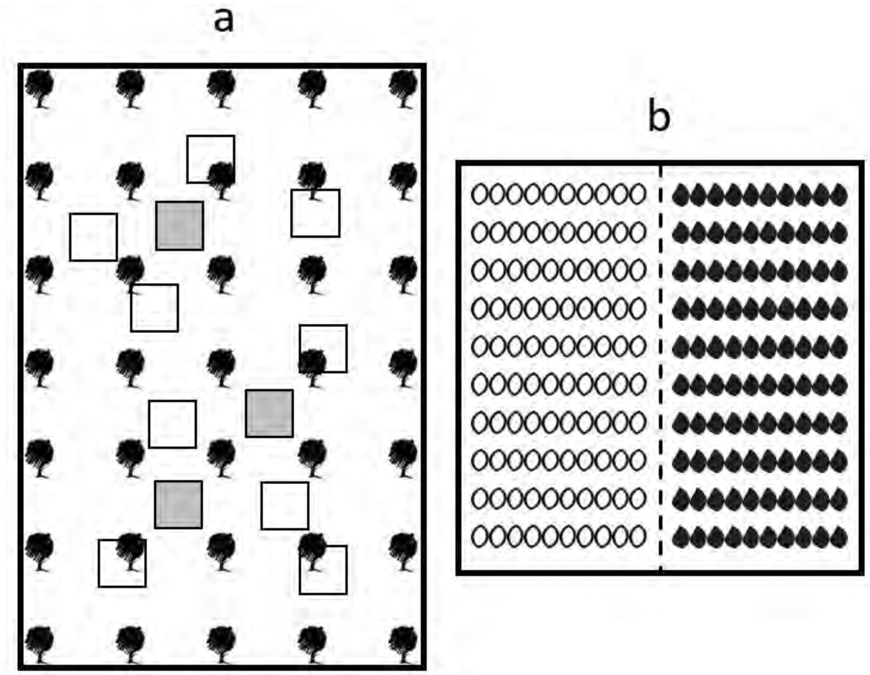


Figure 2.2 Sample units in individual experimental plot. a) Microsites for the micro-environmental measurements and the sowing experiment are symbolized by coloured squares; quadrats for the natural colonization survey, by blank squares. b) Magnified representation of microsites, sown with *Abies balsamea* and *Picea glauca* seeds (numbers shown are different to those in the experiment).

sky conditions. Aboveground herbaceous biomass was assessed during the period of maximal biomass (mid-July) in 2014 and 2015. A non-destructive point intercept method (Jonasson 1983; Jonasson 1988) was used to estimate the herbaceous biomass in the microsite located in the centre of each plot. A narrow rod placed perpendicularly to the soil surface was shifted along a 100 (10x10cm) intersection point grid which covered the microsite area. The number of contacts between the rod and each plant species was registered. In order to calibrate the method for biomass estimation, 12 1-m^2 quadrats (selected to include a wide range of biomass of the different species) were previously sampled in July 2014 using the same grid pattern. The vegetation within each of these quadrats was then clipped at ground level and dried in order to compute regression equations between contact points and dry biomass for the main herbaceous species. The summed number of contacts by species sampled in each experimental plot could then be used to estimate total herbaceous biomass per m^2. Finally, total leaf litter percentage cover (from hybrid poplars and herbaceous species) was measured in early and late summer 2014 and 2015. A 25 (20x20cm) point grid was used for this measurement in the three microsites for each plot. Each intersection point where the rod touched at least one leaf on the ground was noted as a litter occurrence to estimate the percentage cover as follows: number of occurrences/total number of measurement points x 100.

2.3.4 Natural colonization survey (2014-2015) and field sowing experiment (2015)

Naturally established pioneer woody (tree and arborescent shrub) seedlings were monitored in nine randomly positioned 1-m^2 quadrats in each plot (Figure 2.2). Seedling numbers were surveyed by species during early, mid and late summer 2014 and 2015. Data were used to quantify summer emergence (total number of new seedlings recorded during mid and late summer counts per m^2), summer mortality rates (total number of dead seedlings recorded during mid and late summer counts/total number of seedlings recorded during early, mid or late summer counts) and late-season abundance (total number of seedlings recorded during the late summer count per m^2) in each quadrat, for 2014 and 2015.

The sowing experiment was conducted in the three microsites already used for the micro-environment measurements in each of the 15 experimental plots. Each microsite was divided into two equal parts sown respectively with *A. balsamea* and *P. glauca* just after snowmelt in mid-May 2015. Seeds were sown by hand in tiny furrows (40 seeds x 10 rows for both species) at an interrow spacing of 10 cm and then partially covered to minimize the risk of loss by erosion on the slope (Figure 2.2). A total of 1200 seeds (400 seeds x 3 microsites) per species were sown this way in each plot. Seedling numbers were surveyed for each species every four weeks from June to August 2015. Data were used to quantify summer emergence rates (total number of emergences during the growing season/number of seeds), summer mortality rates (total number of dead seedlings/total number of emerged seedlings during the season) and first-year recruitment success rates (number of surviving seedlings at the end of the growing season/number of seeds) in each microsite.

2.3.5 Statistical analyses

Data from the natural colonization survey and the sowing experiment were analyzed according to a randomized complete block design using generalized linear mixed models. Models were fitted with the glmer function of the lme4 package of R (Bates *et al.* 2015; R Core Team –version 3.2.3– 2015). Maximum likelihood estimation was based on the Laplace approximation (Laplace 1986). A multiple regression analysis was used to test whether seedling emergence, mortality and abundance: (1) increased or decreased with planted hybrid poplar density (linear relation), (2) reached a minimum/maximum value under intermediate density (quadratic relation), and (3) differed between the 2x2-m-spacing treatments with and without a hydroseeded cover. Blocks and experimental units were treated as random effects with the latter nested in the former. That is, predictive models could be summarized as follows: seedling response variable ~ linear density + quadratic density + hydroseeding + random effects (block/experimental units).

Only the *Salicaceae* family was considered for the statistical analysis of the natural colonization survey, and tests were performed for all the species combined (pooled *Populus* and *Salix* species). Seedling emergence, mortality rates and late-season abundance were analyzed on a growing-season basis. For the sowing experiment, seedling emergence, mortality and recruitment success were analyzed separately for each species.

Data from the micro-environment measurements were analyzed with linear mixed effect models using the nlme package of R (Pinheiro *et al.* 2015). Model parameter estimates were based on the restricted maximum likelihood method. A multiple regression analysis was used to test the effects of hybrid poplar density, as linear and quadratic terms, and hydroseeding, as a binary variable, on: soil moisture, soil temperature, available light at ground level, herbaceous biomass and total leaf litter cover. The quadratic term was removed when not significant for a better estimate of the simple term of density. The analysis was conducted for key periods of seedling responses to experimental treatments, namely: (1) the highest emergence period of *Salicaceae* species (late June to late July 2014), (2) the highest emergence period of both *P. glauca* and *A. balsamea* (mid-May to mid-June 2015) and (3) the highest mortality period for any species (mid-July to mid-August 2015). Average value of micro-environmental variables registered in microsites within each time period was used for the analysis. A prior first order autoregressive analysis was conducted for repeated measures to confirm that the effect of treatments was constant within each period studied. Data were log-transformed when necessary to meet assumptions of normality and homogeneity of variance. The logarithmic value of hybrid poplar density was also used for all regression analyses, in order to get more regular intervals between treatment levels along the density gradient.

For all analyses, we considered a significance level equal to 0.10 to allow a broader effects-based analysis. For all models illustrated graphically, we used a Monte Carlo approach (Gelman *et al.* 2014) to estimate predicted values and 90% confidence intervals along the density gradient, from the median, the 5th and 95th percentiles of the posterior predictive distribution of model parameters.

Linear relationships between the micro-environmental variables and seedling emergence and mortality rates were explored using Pearson correlations for the determining periods mentioned above. A complementary analysis was conducted using the Hoeffding's D measure (Harrell Jr & Dupont 2006) to test for dependence structures beyond linear and monotonic associations but was not retained since no additional relationships between variables were detected. For both the natural colonization survey and the sowing experiment, we used the average value of each variable during the highest emergence and mortality periods recorded. The Bonferroni correction was applied to adjust for the significance level of multiple correlation tests, dividing the alpha level by the number of tests performed for each seedling response. Since five micro-environmental parameters were considered, p-value = 0.10/5 = 0.02.

2.4 Results

2.4.1 Tree cover effect on the understory micro-environment (2014-2015)

Variations in the understory conditions were observed along the hybrid poplar density gradient during key periods of seedling responses in the 2nd (2014) and 3rd (2015) growing seasons of the plantations (Table 2.1). The effect of the hybrid poplar density on herbaceous biomass was already noticeable in July 2014, while values measured during the period of maximal biomass decreased linearly with tree density (Figure 2.3). Mean dry herbaceous biomass was >3 times lower under the 1x1-m spacing treatment (45g·m^{-2}; CI limits: 25–70) compared to the control plots without nurse trees (150g·m^{-2}; CI limits: 100–225). Herbaceous biomass remained similarly related to poplar density in 2015, but was overall almost 2 times less important than that of the previous year under the developing canopies in the plantations (see appendix A for the list of inventoried herbaceous species).

Relationships between poplar density and soil moisture content followed a quadratic pattern from late June to late July 2014 (Table 2.1). The mean volumetric water content under an intermediary spacing treatment (26%; CI limits: 24–28) was higher than under the 1x1-m spacing treatment (22%; CI limits: 20–25) or the control without nurse trees (21%; CI limits: 19–23, Figure 2.3). For early season 2015, linear regression coefficients indicated a significant positive effect of poplar density on soil

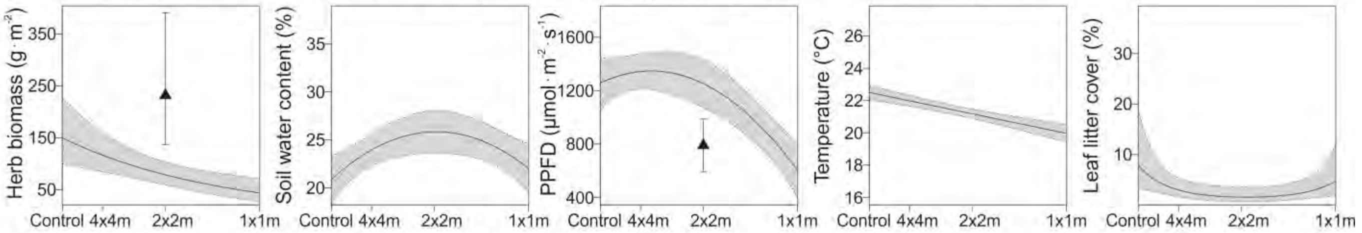
Table 2.1 Effect of hybrid poplar density and hydroseeded herbaceous cover treatments on herbaceous biomass, soil moisture, available light (PPFD) at ground level, soil temperature and leaf litter cover. Results are presented for the highest emergence period of *Salicaceae* (*Populus* and *Salix*) species (late June to late July 2014), the highest emergence period of *Picea glauca* and *Abies balsamea* (mid-May to mid-June 2015) and the highest mortality period for any species (mid-July to mid-August 2015) in the plantations. P-values are shown in bold when under the 10% significance threshold. N=15 for herbaceous biomass and soil moisture; N=45 for available light, soil temperature and leaf litter cover.

	Herbaceous biomass[a]			Soil moisture			Available light[b]			Soil temperature			Leaf litter cover[a]		
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
late June to late July 2014															
Intercept	4.451	0.272	<0.001	25.728	1.539	<0.001	1299.228	151.868	<0.001	21.357	0.624	<0.001	0.493	0.746	0.525
Linear density	-0.512	0.178	**0.018**	1.220	0.943	0.228	-215.925	76.068	**0.019**	-1.051	0.414	**0.029**	-0.447	0.354	0.239
Quadratic density	–	–	–	-3.047	1.269	**0.040**	-234.338	102.331	**0.048**	–	–	–	0.928	0.477	**0.084**
Hydroseeding	0.991	0.437	**0.049**	-3.105	2.065	0.167	-515.549	166.483	**0.013**	0.294	0.843	0.735	0.249	0.776	0.755
mid-May to mid-June 2015															
Intercept	NA	NA	NA	33.143	0.733	<0.001	7.395	0.083	<0.001	21.075	0.494	<0.001	25.555	1.394	<0.001
Linear density	NA	NA	NA	2.202	0.800	**0.020**	-0.166	0.049	**0.008**	-0.917	0.354	**0.029**	3.167	1.012	**0.011**
Quadratic density	NA	NA	NA	–	–	–	-0.236	0.065	**0.006**	-1.696	0.476	**0.006**	–	–	–
Hydroseeding	NA	NA	NA	-0.110	1.629	0.948	-0.044	0.106	0.690	-1.096	0.775	0.191	9.891	2.060	**0.001**
mid-July to mid-August 2015															
Intercept	62.660	5.024	<0.001	32.333	0.989	<0.001	1395.965	116.349	<0.001	26.438	1.055	0.000	47.662	5.841	<0.001
Linear density	-12.753	5.543	**0.044**	-0.132	0.640	0.841	-165.920	79.613	**0.067**	-1.205	0.275	**0.002**	3.707	4.080	0.385
Quadratic density	–	–	–	-3.253	0.861	**0.004**	-324.514	107.102	**0.014**	-0.841	0.370	**0.049**	–	–	–
Hydroseeding	65.541	11.287	**<0.001**	-1.104	1.400	0.451	-548.331	174.244	**0.012**	-1.305	0.602	**0.058**	9.689	8.307	0.271

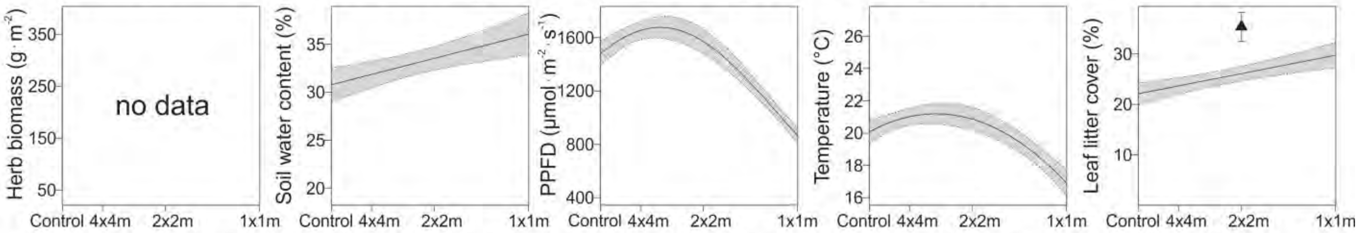
[a] Log transformed for late June to late July 2014

[b] Log transformed for mid-May to mid-June 2015

a) late June to late July 2014: highest emergence period of *Salicaceae*



b) mid-May to mid-June 2015: highest emergence period of *P. glauca* and *A. balsamea*



c) mid-July to mid-August 2015: highest mortality period for any species

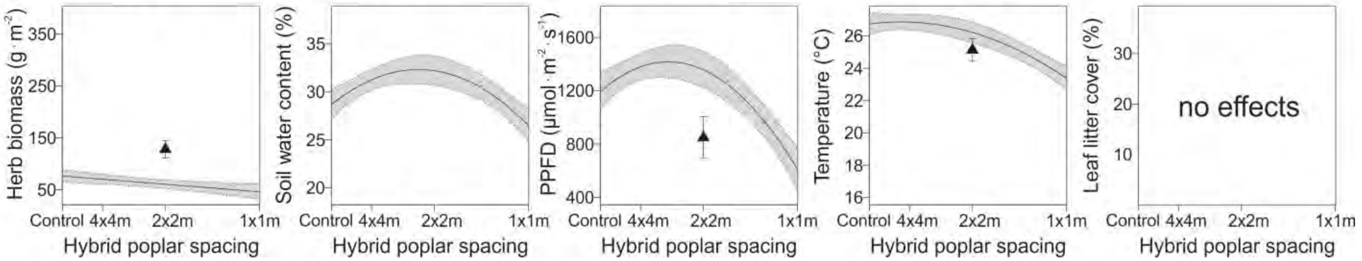


Figure 2.3 Influence of hybrid poplar spacing and hydroseeded herbaceous cover treatments on the understory micro-environmental parameters in key periods of seedling responses, during (a) the 2nd (2014) and (b, c) the 3rd (2015) growing seasons of the plantations. The solid line and grey margins symbolize predicted values and 90% CIs along the hybrid poplar gradient; the triangle and bars symbolize the predicted value and the 90% CI in the 2x2-m spacing treatment with a hydroseeded cover.

moisture conditions, while the highest mean volumetric water content was found under the 1x1-m spacing treatment (36%; CI limits: 34–38) and the lowest, under the control without nurse trees (31%; CI limits: 29–33). Similarly to 2014, the moisture content under denser cover dropped compared to intermediary spacing levels in the second half of the summer. The relation between poplar density and moisture content thus switched from a linear to a quadratic pattern, with lower mean values found at both ends of the density gradient (29%; CI limits: 27–30, and 27%; CI limits: 25–28, respectively for the control and 1x1-m treatments) from mid-July to mid-August 2015. Notwithstanding, soil volumetric water content remained higher than the wilting point measured (results not shown) for the soil material considered –with values over 18.5% for all types of cover treatment– during the whole growing season.

The influence of hybrid poplar density on available light at ground level and soil temperature was similar for the late June to late July 2014, mid-May to mid-June 2015 and mid-July to mid-August 2015 periods, showing significant linear or quadratic effects (Table 2.1). Mean values for these parameters were the lowest under the 1x1-m spacing treatment throughout the survey. The 1x1-m poplar cover intercepted on average ~70% of full sunlight (600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, CI limits: 400–810, compared to ~2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for full sunlight) during measurements from late June to late July 2014 (Figure 2.3). Light interception reached a maximum of ~80% during summer 2015, but was on average ~60% (870 $\mu mol \cdot m^{-2} \cdot s^{-1}$, CI limits: 820–930, compared to ~2180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for full sunlight) and ~70% (610 $\mu mol \cdot m^{-2} \cdot s^{-1}$, CI limits: 460–770, compared to ~2060 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for full sunlight) respectively for the early and late season periods considered. Comparatively, light interception for the 2x2m, the 4x4m and the control without nurse trees was roughly half that of the 1x1-m spacing treatment throughout the survey. Likewise, soil temperature was the lowest under the 1x1-m spacing treatment for every time period studied (Table 2.1, Figure 2.3). Mean temperature values for the 2x2m, the 4x4m and the control without nurse trees –as for available light– were generally more alike. Mean differences between the 1x1m plots and the other spacing levels were <2.5°C from late June to late July 2014, but increased to >4.3°C during both periods studied in 2015.

The density effect on total leaf litter cover (from hybrid poplars and herbaceous species) changed over the duration of the study (Table 2.1, Figure 2.3). A quadratic pattern was observed from late June to late July 2014, reflecting a stronger contribution from hybrid poplars and herbaceous species at opposite ends of the density gradient. However, regression coefficients indicate a positive linear effect of poplar density on leaf litter cover in early season 2015, but no significant effect in late season 2015, while mean values reached the 40-50% range.

2.4.2 Hydroseeded cover effect on the understory micro-environment (2014-2015)

The influence of the hydroseeded cover treatment on the herbaceous biomass was significant during the period of maximal herbaceous biomass both in 2014 and 2015 (Table 2.1). Mean herbaceous dry biomass in hydroseeded plots (235g·m^{-2}; CI limits: 140–390) was close to 3 times that of unseeded plots (80g·m^{-2}; CI limits: 60–105) in 2014 and slightly more than twice that of unseeded plots (130·m^{-2}; CI limits: 110–145 vs ~60g·m^{-2}; CI limits: 50–70) in 2015, with declining values from 2014 to 2015 (Figure 2.3). The hydroseeded cover treatment also significantly affected light availability. From late June to late July 2014, ~60% (790 µmol·m^{-2}·s^{-1}, CI limits: 590–990, compared to ~2000 µmol·m^{-2}·s^{-1} for full sunlight) of full sunlight was intercepted on average during measurements in hydroseeded plots compared to <35% (1250 µmol·m^{-2}·s^{-1}, CI limits: 1070–1430) in unseeded plots. Treatment effect on light conditions was not detected from mid-May to mid-June 2015 –before full early season regrowth– but increased later in the season, with % light transmission for the mid-July to mid-August period similar to those of 2014. Mean differences in soil temperature were not detected until mid-July to mid-August 2015 and remained marginal even during this period (~25.2°C, CI limits: 24.4–25.8, for hydroseeded plots; 26.2°C, CI limits: 25.6–26.8, for unseeded plots). The influence of the hydroseeded cover on leaf litter cover was not constant. Percentage leaf litter cover significantly differed only in early season 2015, while mean value was 36% (CI limits: 33–38) in seeded plots compared to 26% (CI limits: 25–28) for unseeded plots. Finally, soil moisture content was not impacted by the hydroseeded treatment during any of the period studied.

2.4.3 Natural colonization (2014-2015)

Abundance of colonizing woody (tree and arborescent shrub) species after three growing seasons was largely dominated by *Salicaceae*: *Populus* and *Salix* species accounted for 72 and 10% of total abundance respectively in the plantations. Other seedlings observed belonged to the genera (in order of decreasing abundance): *Picea* (10%), *Sorbus* (3%), *Abies* (2%), *Prunus* (1%), *Betula* (1%) and *Cornus* (1%) (see appendix B for the list of inventoried woody species). Mean abundance of seedlings in the quadrats for all genera combined was 1.3±0.2(CI)$\cdot$m^{-2} at the end of summer 2014, but 1.0±0.2(CI) seedlings per m^2 at the end of summer 2015, pointing to an overall emergence/mortality ratio switching from a >1 (2.7) to a <1 (0.4) value in the plantations. Variations in seedling emergence, mortality or abundance patterns were observed for the dominant *Salicaceae* species under both the hybrid poplar density and the hydroseeded cover treatments (Table 2.2). In 2014, mean seedling emergence was greater under the intermediary 2x2-m spacing treatment (~0.7$\cdot$m^{-2}; CI limits: 0.5–0.9) and lower under the control treatment without nurse trees (~0.3$\cdot$m^{-2}; CI limits: 0.2–0.4), following a significant quadratic pattern along the hybrid poplar density gradient (Figure 2.4). Mean emergences in 2014 were also significantly influenced by the hydroseeded treatment: nearly 3.5 times less seedlings emerged in hydroseeded plots (<0.2$\cdot$m^{-2}; CI limits: 0.1–0.3) compared to unseeded plots. In contrast, summer mortality in 2014 was not impacted by either treatment –the same applies for the

Table 2.2 Effect of hybrid poplar density and hydroseeded cover treatments on the emergence, mortality and late-season abundance of naturally established *Salicaceae* (*Populus* and *Salix*) seedlings. Results are presented for the 2nd and 3rd growing seasons of the plantations. P-values are shown in bold when under the 10% significance threshold. N=135.

	Summer emergence			Summer mortality			Late-season abundance		
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
2014									
Intercept	-0.435	0.275	0.114	-2.047	0.258	<0.001	0.338	0.436	0.437
Linear density	0.244	0.193	0.207	0.295	0.303	0.329	0.165	0.162	0.309
Quadratic density	-0.450	0.232	**0.052**	–	–	–	-0.385	0.202	**0.056**
Hydroseeding	-1.322	0.511	**0.010**	0.529	0.688	0.442	-1.310	0.398	**0.001**
2015									
Intercept	NA	NA	NA	-1.713	0.294	<0.001	0.064	0.480	0.895
Linear density	NA	NA	NA	0.789	0.328	**0.016**	0.048	0.176	0.784
Quadratic density	NA	NA	NA	–	–	–	-0.466	0.206	**0.024**
Hydroseeding	NA	NA	NA	0.477	0.779	0.541	-1.387	0.437	**0.002**

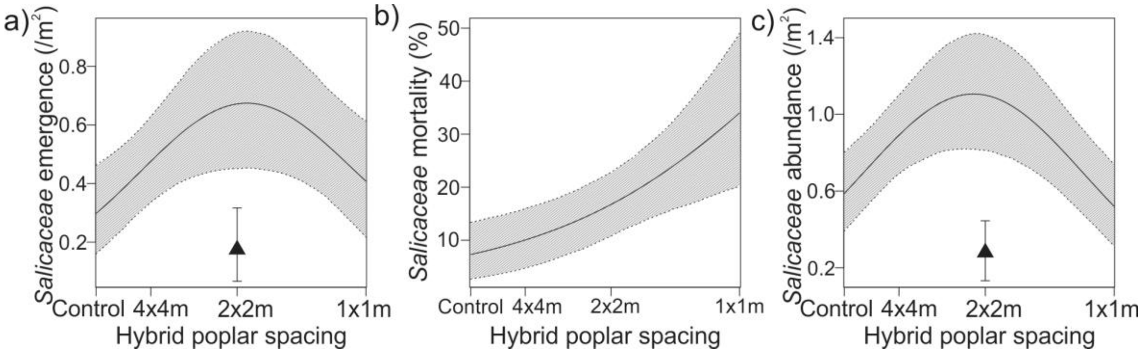


Figure 2.4 Influence of hybrid poplar spacing and hydroseeded herbaceous cover treatments on seedling response of naturally established *Salicaceae* (*Populus* and *Salix*) species during the 2nd and 3rd growing seasons of the plantations. Results summarize (a) summer emergence in 2014, (b) summer mortality in 2015 and (c) late-season abundance in 2015. The solid line and grey margins symbolize predicted values and 90% CIs along the hybrid poplar gradient; the triangle and bars symbolize the predicted value and the 90% CI in the 2x2-m spacing treatment with a hydroseeded cover.

2014-2015 winter mortality (results not shown). In 2015, seedling emergence was too low to test for effects. Summer mortality rates, on the other hand, increased linearly with hybrid poplar density in 2015: mean mortality rates were 34% (CI limits: 20–49) under the 1x1-m spacing treatment compared to 7% (CI limits: 3–13) in control plots without nurse trees. No effect of the hydroseeded cover treatment on the 2015 summer mortality was detected. At the end of the 2015 growing season, *Salicaceae* seedling abundance was greater under an intermediate level of hybrid poplar density (p=0.024 for quadratic relation) –with mean values up to $1.1 \cdot m^{-2}$ (CI limits: 0.8–1.4) in the 2x2m– and in plots without a hydroseeded cover (p=0.002) –with mean value as low as $<0.3 \cdot m^{-2}$ (CI limits: 0.1–0.4) in hydroseeded plots. In other words, differences in the pioneer seedling abundance observed after the emergence period in 2014 were still noticeable at the end of summer 2015. However, the lowest abundance values for the spacing treatment were now noted in the 1x1-m level at the end of summer 2015 ($\sim 0.5 \cdot m^{-2}$; CI limits: 0.3–0.7).

2.4.4 Field sowing experiment (2015)

The hybrid poplar spacing treatment significantly influenced the summer emergence of *P. glauca* and, more marginally, of *A. balsamea*, while rates increased linearly with poplar density for both species (Table 2.3). Mean emergence rates were 15.7% (CI limits: 13.7–17.7) and 6.4% (CI limits: 5.1–7.9) respectively for *P. glauca* and *A. balsamea* under the 1x1-m spacing treatment compared to 11.9% (CI limits: 10.6–13.2) and 4.4% (CI limits: 3.6–5.3) under the control treatment without nurse trees (Figure 2.5). On the other hand, emergence rates remained unaffected by the presence of a hydroseeded cover for both species. After one growing season, overall mean mortality rates in microsites were 30.5±3.8(CI) and 28.6±3.8(CI)% respectively for *P. glauca* and *A. balsamea*. Mortality rates for *P. glauca* were not significantly impacted by either treatments. *A. balsamea* mortality also remained unchanged by

Table 2.3 Effect of hybrid poplar density and hydroseeded cover on summer emergence, mortality and late-season recruitment success of *Picea glauca* and *Abies balsamea* seedlings following spring seeding in 3-year-old hybrid poplar plantations. P-values are shown in bold when under the 10% significance threshold. N=45.

	Summer emergence			Summer mortality			Late-season recruitment success		
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
Picea glauca									
Intercept	-2.004	0.107	<0.001	-1.194	0.086	<0.001	-2.367	0.131	<0.001
Linear density	0.116	0.057	**0.041**	0.149	0.092	0.108	0.029	0.067	0.660
Quadratic density	–	–	–	–	–	–	–	–	–
Hydroseeding	0.067	0.116	0.563	-0.061	0.189	0.749	0.076	0.134	0.568
Abies balsamea									
Intercept	-2.953	0.218	<0.001	-1.374	0.090	<0.001	-3.235	0.216	<0.001
Linear density	0.161	0.093	**0.085**	-0.122	0.100	0.225	0.184	0.100	**0.064**
Quadratic density	–	–	–	–	–	–	–	–	–
Hydroseeding	-0.163	0.187	0.384	0.375	0.187	**0.044**	-0.339	0.211	0.108

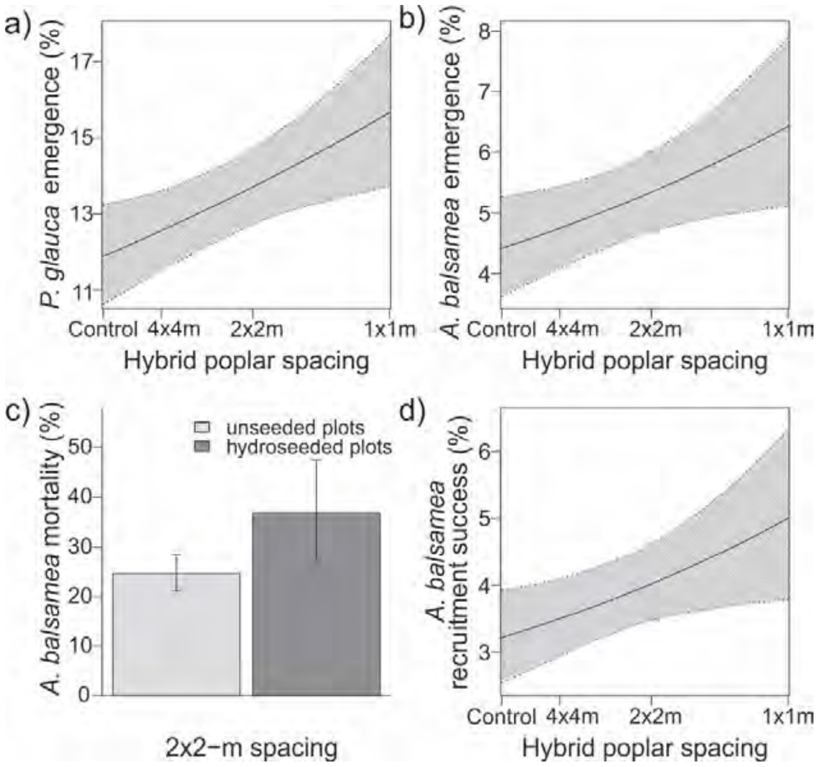


Figure 2.5 Influence of experimental factors on seedling responses of *Picea glauca* and *Abies balsamea* during the 3rd growing season of the plantations. Results summarize (a) *P. glauca* and (b) *A. balsamea* summer emergence rates in relation to hybrid poplar spacing treatment, (c) *A. balsamea* summer mortality rates in relation to hydroseeded cover treatment and (d) recruitment success rates for *A. balsamea* first-year seedlings along the poplar gradient. Fitted values are presented with a 90% CI.

the hybrid poplar spacing treatment, but significant differences were observed under the hydroseeded treatment (p=0.044), with higher rates registered in hydroeseeded plots (37%; CI limits: 27–48) compared to unseeded plots (25%; CI limits: 21–28). Overall recruitment success rates in microsites were 9.8±1.0(CI) and 4.0±0.7(CI)% respectively for *P. glauca* and *A. balsamea* first-year seedlings. The positive effect of density on recruitment success after one growing season was significant only for *A. balsamea* (p=0.064). Mean recruitment success rates for *A. balsamea* seedlings were ~5.0% (CI limits: 3.8–6.3) under the 1x1-m spacing treatment compared to 3.2% (CI limits: 2.5–3.9) under the control treatment without nurse trees. On the other hand, the resulting effect of the hydroseeded treatment on recruitment success at the end of the growing season was not statistically significant for either *P. glauca* or *A. balsamea*, notwithstanding the higher summer mortality rates registered for *A. balsamea* in plots with a hydroseeded cover.

2.4.5 Relationships between the understory micro-environment and seedling responses

The correlation analysis did not reach statistical significance regarding relationships between the micro-environmental variables and the *Salicaceae* seedlings emergence during the 2014 emergence period (Table 2.4). However, *Salicaceae* seedling mortality was negatively correlated with the available light variable (*r*=-0.398, p=0.013) during the main mortality period surveyed over the duration of the study, in late-season 2015. Diminution of light availability thus corresponded to increased seedling mortality rates for these species at the end of the third growing season in the plantations.

No significant relationships were identified between the micro-environmental variables and the seedling emergences of *P. glauca* and *A. balsamea* during the peak emergence period monitored in the 2015 growing season (Table 2.5). Strength of

Table 2.4 Correlations between naturally established *Salicaceae* (*Populus* and *Salix*) seedling emergence or mortality and micro-environmental variables. Results are based on the average value of each variable for the highest emergence (late June to late July 2014) and mortality (mid-July to mid-August 2015) periods. P-values are shown in bold when under the Bonferroni-adjusted significance threshold (p = 0.10/5 = 0.02). Confidence intervals (CI = 100 - 0.02 = 98%) excluding zero indicate a significant linear relationship at 2% probability of error.

	Emergence (2014)			Mortality (2015)		
	Coefficient	CI	P-value	Coefficient	CI	P-value
Herbaceous biomass	-0.538	-0.863 ; 0.099	0.047	0.403	-0.240 ; 0.800	0.136
Soil moisture	0.297	-0.350 ; 0.751	0.283	0.014	-0.596 ; 0.614	0.963
Available light	0.185	-0.170 ; 0.497	0.225	-0.399	**-0.672 ; -0.029**	**0.013**
Soil temperature	0.164	-0.191 ; 0.481	0.281	-0.075	-0.437 ; 0.308	0.655
Leaf litter cover	-0.388	-0.794 ; 0.256	0.153	-0.138	-0.670 ; 0.488	0.625

Table 2.5 Correlations between *Picea glauca* and *Abies balsamea* seedling emergence or mortality and micro-environmental variables. Results are based on average value of each variable for the highest emergence (mid-May to mid-June) and mortality (mid-July to mid-August) periods in 2015. P-values are shown in bold when under the Bonferroni-adjusted significance threshold (p = 0.10/5 = 0.02). Confidence intervals (CI = 100 - 0.02 = 98%) excluding zero (shown in bold) indicate a significant linear relationship at 2% probability of error.

	Emergence			Mortality		
	Coefficient	CI	P-value	Coefficient	CI	P-value
Picea glauca						
Herbaceous biomass	NA	NA	NA	0.013	-0.577 ; 0.595	0.962
Soil moisture	0.533	-0.077 ; 0.853	0.041	-0.182	-0.709 ; 0.475	0.533
Available light	-0.054	-0.391 ; 0.296	0.725	-0.092	-0.423 ; 0.261	0.549
Soil temperature	-0.248	-0.546 ; 0.105	0.100	0.158	-0.197 ; 0.477	0.299
Leaf litter cover	0.230	-0.124 ; 0.532	0.129	-0.490	-0.836 ; 0.135	0.064
Abies balsamea						
Herbaceous biomass	NA	NA	NA	0.440	-0.197 ; 0.816	0.101
Soil moisture	0.500	-0.122 ; 0.840	0.058	0.198	-0.463 ; 0.717	0.498
Available light	0.016	-0.330 ; 0.359	0.914	-0.018	-0.360 ; 0.329	0.908
Soil temperature	-0.144	-0.465 ; 0.211	0.345	-0.005	-0.350 ; 0.340	0.972
Leaf litter cover	-0.189	-0.501 ; 0.166	0.214	0.118	-0.503 ; 0.658	0.676

relationships for moisture conditions was the highest of all micro-environmental variables, both with *P. glauca* (*r*=0.533) and *A. balsamea* (*r*=0.500), but p-values (0.041 and 0.058) remained higher than the Bonferroni-adjusted significance threshold. Likewise, the correlation analysis did not detect any significant associations between the micro-environmental variables and *P. glauca* or *A. balsamea* seedling mortality.

2.5 Discussion

2.5.1 Nurse tree effect on the understory micro-environment

Young plantations of fast-growing trees on waste rock slopes rapidly exerted control over the understory conditions, in accordance with our first hypothesis. The micro-environment-modifying capacity of the nurse tree cover was observed for all understory parameters studied. However, the relationships between tree density and environmental conditions were often quadratic, indicating concurrent underlying mechanisms. The development of an overstory structure quickly reduced light availability in the young plantation understories, thereby driving changes in other micro-environment attributes. Stronger shading effect associated with denser hybrid poplar spacings likely contributed to decreasing herbaceous biomass –largely attributable to shade-intolerant species– along the density gradient. Light is often the most limiting resource affecting understory plant establishment and growth (Strengbom *et al.* 2004; Hart & Chen 2006). Conversely, light conditions can be modified by the understory vegetation, which in turn becomes a structural layer affecting the micro-environment (Burton & Bazzaz 1991; Hart & Chen 2006). Increased overstory light transmission is therefore frequently counterbalanced by increased light interception from the understory vegetation layer (Constabel & Lieffers 1996; Messier *et al.* 1998). In the plantations, the stronger structuring role played by the herbaceous cover under the widest spacing level and the control treatment without nurse tree was noticeable not only for available light at ground level, but also for other micro-environmental parameters, such as soil temperature and leaf litter cover. In other words, increased herbaceous biomass translated into a stronger contribution to light and heat interception and to litterfall.

The influence of a tree cover on surface soil moisture is known to be generally positive because of a reduced soil-to-air vapour pressure gradient and decreased wind movement, resulting in less evaporation from the soil surface (Geiger 1965; Burton & Bazzaz 1991; Man & Lieffers 1999). Nonetheless, a significant decrease in moisture content was recorded during the drier second half of summer 2015 under the 1x1-m cover compared to the 2x2-m cover, while the relationship between poplar density and moisture content switched from positively linear to quadratic. Competition for water on drought-prone sites like waste rock slopes may thus negate the facilitative effect of the nurse shelter at high densities (Dordel 2009). Moreover, fast-growing nurse trees may deplete soil water resources more rapidly than slower-growing species (Govindarajan *et al.* 1996, McIntyre *et al.* 1997). Rosenberg *et al.* (1983) noted that a fast-growing canopy can reduce soil moisture availability when transpiration rates exceed evaporation rates from bare soil. Thus, the trend observed in the plantations –that already started to appear in mid-summer 2014– likely reflected an offset of the beneficial tree cover shading effect by a transpiration effect for the highest planting density.

2.5.2 Nurse tree effect on forest tree seedlings

Our results partly support the hypothesis that planting of fast-growing nurse trees would benefit forest tree seedling performances (Lugo 1997; Parrotta *et al.* 1997) compared to bare soil, but indicate that facilitation and competition were driven by differential response patterns among species. The densest cover treatment (1x1m) promoted the highest emergence rates for *P. glauca* and *A. balsamea* seedlings. Sheltered conditions also improved the emergence of *Salicaceae* seedlings, while higher emergence rates were observed under the 2x2-m spacing treatment. The emergence patterns observed may compare with data collected in forested environments. For example, McLaren & Janke (1996) found *A. balsamea* emergence to increase as a function of tree cover in *Populus tremuloides*-dominated stands. Similarly, Calogeropoulos *et al.* (2004) observed greater *A. balsamea* emergence in partial cuts than in clearcut treatments in their study on the effects of harvest intensity. Sheltered sites were also noted to produce more germinants than open sites for earlier-successional tree species (Burns & Barbara 1990). Nonetheless, *Salicaceae* seedling mortality rates increased along the hybrid poplar density gradient during the final year of sampling (2015), likely pointing to an increasing exclusion of these species in the plantations, typical colonizers of more open habitats (Burns & Barbara 1990; Peterson & Peterson 1992).

The light-water model proposed by Holmgren *et al.* (1997) suggests that facilitation occurs when the improvement of plant-water relationships under the canopy exceeds the costs of decreased light availability, hence hinting at the potential of nurse plantations on drought-prone slopes, especially for shade-tolerant species. Our correlation analysis using a conservative significance threshold did not allow to clearly pinpoint the determining micro-environmentalal variables for seedling emergence. Nonetheless, the highest emergence rates for both *A. balsamea* and *P. glauca* coincided with the highest soil moisture contents found during the peak emergence period (mid-May to mid-June 2015), while moisture levels increased with plantation density. Greater emergence for *Salicaceae* species also occurred under the spacing treatment associated with the highest soil moisture content values during the 2014 emergence period, i.e. the 2x2-m spacing treatment. If soil moisture is known to be the most limiting factor for the germination of boreal tree species (Greene *et al.* 1999), light availability emerged as a driving factor of *Salicaceae* species abundance as soon as during the third growing season of the plantations. Decrease in understory light already became limiting for the survival of these shade-intolerant species, whose germinants lacking endosperm are more dependent on rapidly establishing photosynthetic leaf area to support development (Karrenberg *et al.* 2002).

Results for *Salicaceae* species showed that facilitation and competition mechanisms not only differ among plantation densities, but also change as plantations continue to develop and as seedlings grow. Pickett *et al.* (1987) remarked that early facilitation of a colonizer by a nurse plant often gives way to inhibition as the colonizer matures. Competition for light under denser cover started to outweigh facilitation and exerted a detrimental effect for *Salicaceae* seedlings in 2015. In this context, later-successional species such as *A. balsamea*, more sensitive to soil moisture than light limitations (Lieffers & Stadt 1994; Landhäusser & Lieffers 2001), may be better equipped to take advantage of opportunities in the understory. Nonetheless, the decrease in moisture content recorded at the end of the survey under the densest hybrid poplar spacing treatment suggests that their influence on soil water resources may become increasingly competitive over the next growing seasons, and compromise their nursing potential in the longer term.

2.5.3 Hydroseeded cover effect on forest tree seedlings

In accordance with our third hypothesis, the competitive effect exerted by the hydroseeded herbaceous cover limited seedling emergence and increased seedling mortality, although not all forest tree species were influenced in the same way. Dense herbaceous covers are known to reduce seedbed receptivity, especially for small-seeded species like poplars and willows, characterized by smaller radicles with limited ability to reach soil resources (Greene & Johnson 1998; Hesketh *et al.* 2009). Although we could only document the detrimental effect of the hydroseeded cover treatment on pioneer *Salicaceae* seedling emergence, we do not conclude that the hydroseeded cover would not affect the emergence of larger-seeded *P. glauca* and *A. balsamea* originating from seed rain. Our sowing method with direct positioning of seeds onto the mineral soil may have inflated emergence occurrences. Previous studies noted for instance that abundant herbaceous vegetation inhibits spruce regeneration: dense growth may intercept seeds before they reach the ground (Eis 1981), while germinants that do reach the soil are more easily shaded out, smothered by dead foliage or outcompeted for soil water (Coates *et al.* 1994). Increase in mortality rates in hydroseeded plots were, however, only registered for *A. balsamea* seedlings, which may be somewhat surprising given that fir seeds are four times larger than white spruce seeds and usually lead to more resistant seedlings able to develop their root system more rapidly (Bakuzis & Hansen 1965). Nonetheless, this result may reflect the difficulty for slower-growing seedlings to compete against aggressive herbaceous species in more open environments.

The understory vegetation can both act as a driver of tree succession (Hart & Chen 2006) and be determined by overstory structure (De Grandpré *et al.* 1993). The negative relationship between hybrid poplar cover and herbaceous biomass monitored in the young plantations suggests that the increasingly dense tree cover will eventually shade out the light-demanding (naturally established or hydroseeded) ground cover vegetation. Therefore, the competitive effect of the hydroseeded cover on seedlings may weaken as the plantations mature.

2.5.4 Forest-like recruitment rates?

It was suggested that the rapid redevelopment of a tree cover could accelerate the return of conditions beneficial to the regeneration of forest tree seedlings (Carnevale & Montagnini 2002; Boothroyd-Roberts *et al.* 2013). Under the densest tree cover treatment, recruitment success rate for *A. balsamea* first-year seedlings averaged 5%. This compares to results (4-4.5%) found in studies realized in aspen (*Populus tremuloides Michaux*)-dominated stands for seedlings less than two years old (McLaren & Janke 1996; Calogeropoulos *et al.* 2004). Regardless of tree cover treatment, recruitment success rate for *P. glauca* was higher (~10%) than for *A. balsamea*, and surprisingly high compared to studies in forested environment (2-4%)

(Purdy *et al.* 2002; Simard *et al.* 2003; Calogeropoulos *et al.* 2004; Wang & Kemball 2005). Although success rates of first-year seedlings may be promising, our sowing method could again limit the interpretation of our results –especially for smaller-seeded *P. glauca* seedlings, more dependent on seedbed receptivity–, since seed positioning in tiny furrows may have positively biased emergence rates. Concordantly, success rates in control plots without nurse trees remained relatively high for both *A. balsamea* (>3%) and *P. glauca* (~9%).

Results from the natural colonization survey showed that *A. balsamea* (2%) and *P. glauca* (10%) seedlings accounted for a small proportion of colonizing seedling abundance after three growing seasons. This translates into a rather marginal density of 0.02 and 0.10 seedlings per m^2 respectively for each species. While context-dependent and based on a limited period of time, these results may suggest that seed availability for species most likely to benefit from the understory conditions could be unreliable on uphill rock slopes. White spruce seeds are known to disperse up to 300 m (Sims *et al.* 1990), but as low as 7, 4 and 0.1% of them generally reach 50, 100 and 200 m (Nienstaedt & Zasada 1990). The distance is even smaller for the heavier fir seeds, many of which fall with their scales near the parent tree (Sims *et al.* 1990). Consequently, since successful seedling recruitment requires sufficient availability of seeds, management practices may have to include seeding work depending on the vicinity of seed bearers and site topography.

2.6 Conclusion

Natural processes such as succession provide a framework for the implementation of sustainable restoration practices. Plantations may act as accelerators of natural succession through rapid canopy re-establishment. Compared to the traditional anti-erosion treatment, results in the young plantations of hybrid poplars suggest that fast-growing plantations rapidly provide opportunities for the early establishment of later-successional boreal tree seedlings in waste rock slopes. This novel assemblage

(Hobbs *et al.* 2006) relying on a semi-exotic tree species accelerated canopy redevelopment and already exerted a structural influence on the forest tree recruitment conditions in the first years after planting. Nonetheless, soil moisture monitoring results may imply that influence on soil water resources will become increasingly competitive as fast-growing hybrid poplars continue to develop.

Waste rock pile topography, characterized by erodible slopes, increases the importance of rapid tree establishment. Hybrid poplars have the advantage of growing more quickly than other nurse tree species available for reclamation (Guy & Bateman 1989). However, high soil water consumption may compromise longer-term nursing potential of hybrid poplars in waste rock slopes where competition for limited resources, such as water, may be severe. Therefore, competition mechanisms in the young plantations could rapidly outweigh facilitation in the developing interactions between nurse trees and understory tree seedlings.

2.7 Acknowledgements

This study was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Fonds de recherche du Québec – Nature et technologies (FRQNT) and the Canadian Malartic Partnership. The authors are indebted to the research technician and undergraduate students who have contributed to the collection of field data, namely Avril Jobin, Yoan Goudreau, Charles Frenette-Vallières, Sara Gervais, Paulo-Bernardo Neves-E-Castro, Antoine Beaulieu, Maguelonne Rajot and Liam Boivin. We are also grateful to Brian Harvey, Guy LaRocque, Yves Bergeron and Jean-François Boucher for providing valuable comments.

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CHAPITRE 3

CONCLUSION

Il a été suggéré que la mise en œuvre de pratiques cherchant à faciliter le processus de succession naturelle pouvait améliorer significativement le succès de revégétalisation des sites dégradés (Polster 1989; Walker & del Moral 2009). Dans cet esprit, un nombre grandissant d'études ont signalé que les plantations pouvaient jouer un rôle catalyseur vis-à-vis de la succession forestière par l'intermédiaire du redéveloppement rapide d'un couvert arborescent (Guariguata *et al.* 1995; Parrotta 1995; Carnevale & Montagnini 2002; Boothroyd-Roberts *et al.* 2013). Le potentiel facilitant des plantations a par ailleurs été étudié en contexte minier en lien avec les processus de reformation du sol (Dutta & Agrawal 2002; Singh *et al.* 2004; Singh & Singh 2006; Singh & Zeng 2008), mais demeure néanmoins largement inexploré en regard du recrutement des essences forestières (Densmore 2005; Frouz *et al.* 2015), notamment sur les pentes de stériles.

Cette étude visait à examiner le potentiel facilitant de jeunes plantations de peupliers hybrides vis-à-vis du recrutement des essences forestières boréales sur pentes de stériles miniers. Dans le cadre de ce projet, l'effet de la densité de plantation a été mesuré sur la levée et la survie initiale des plantules d'essences forestières de début, mi et fin de succession ainsi que sur le microenvironnement du sous-étage. La performance des plantules a également été examinée dans des parcelles avec hydroensemencement herbacé, soit le traitement conventionnel utilisé dans les pentes pour minimiser l'érosion. Cette étude testait donc l'hypothèse de facilitation écologique en contexte boréal et examinait des pistes de solutions à l'égard des défis rencontrés par les gestionnaires de projets de réhabilitation sur pentes de stériles.

Notre suivi de la colonisation naturelle a révélé un nombre significativement plus élevé de levées de plantules de *Salicaceae* sous un couvert de densité intermédiaire (2x2 m), lors de la 2^e^ saison de croissance des plantations. Cependant, les conditions d'éclairement du sous-étage se sont avérées limitantes pour la survie de ces plantules intolérantes à l'ombre dès l'année suivante. Notre essai d'ensemencement réalisé pendant la 3^e^ saison de croissance des plantations a, quant à lui, généré des taux de levées plus élevés chez *Picea glauca* et *Abies balsamea* sous le traitement d'espacement le plus dense (1x1 m), soit celui où les conditions d'humidité printanières les plus favorables ont été enregistrées. Au terme de la saison de croissance, une augmentation modérée de l'abondance des plantules en fonction de la densité du couvert demeurait observable seulement chez *A. balsamea*.

Nos résultats tendent à indiquer un effet facilitant vis-à-vis des levées de plantules par l'intermédiaire d'une amélioration des conditions d'humidité sous le couvert des jeunes plantations. Cependant, un effet compétitif grandissant pour la lumière est observé, alors que la fermeture du couvert s'accentue rapidement. De la sorte, nos résultats suggèrent non seulement que l'effet du couvert varie en fonction de la densité de plantation, mais que des changements s'opèrent dans les mécanismes de facilitation/compétition entre arbres-abris et plantules au fur et à mesure que les jeunes plantations se développent et que les plantules croissent. Pickett *et al.* (1987) observe que la facilitation précoce par une plante-abri vis-à-vis de l'établissement d'une espèce colonisatrice donne souvent lieu à une inhibition quand le colonisateur grandit. De cette manière, les plantules d'espèces typiques de stades plus avancés de la succession comme *A. balsamea*, plus sensibles aux contraintes d'humidité que de lumière (Lieffers & Stadt 1994; Landhäusser & Lieffers 2001), sont celles qui pourraient mieux tirer profit des modifications du microenvironnement dans le sous-étage des plantations à moyen terme. Néanmoins, la baisse des teneurs moyennes en humidité enregistrée sous le niveau d'espacement 1x1 m comparativement au 2x2 m, dans la 2^e^ moitié de l'an 3 des plantations, laisse présager une influence de plus en plus compétitive des peupliers sur les ressources en eau au cours des prochaines saisons de croissance. Dans des milieux vulnérables à la dessiccation comme les pentes de stériles, la compétition pour l'eau pourrait rapidement s'avérer limitante et supplanter l'effet facilitant d'un couvert de moindre densité (Dordel 2009). De surcroît, les arbres à croissance rapide comme le peuplier hybride, qui se caractérisent souvent par des taux de transpiration élevés, peuvent exacerber plus vitement les contraintes liées à la disponibilité en eau du sol (Boothroyd-Roberts *et al.* 2013).

D'autre part, dans le cadre de nos suivis dans les parcelles avec hydroensemencement herbacé, l'incidence négative du traitement traditionnel sur les performances des plantules a été observée de deux manières, soit par une diminution des levées de plantules issues de la colonisation naturelle et une hausse des mortalités des plantules d'*A. balsamea*. L'effet compétitif d'un couvert hydroensemencé, susceptible de mener à une stagnation successionnelle (Kimmins 1987), avait déjà été décrit en contexte minier (Rizza *et al.* 2007). Il est également pertinent de mentionner que, dans nos plantations, les parcelles sans hydroensmencement ont été colonisées naturellement par les herbacées, mais avec une biomasse plus faible que dans les parcelles hydroensemencées. Une relation négative entre la densité de plantation et la biomasse herbacée a été observée dans ces parcelles. Ce résultat pourrait ainsi suggérer une régression progressive des herbacées intolérantes à l'ombre (hydroensemencées ou issues de la colonisation naturelle) au fur et à mesure que la fermeture du couvert s'intensifie. En d'autres mots, l'effet compétitif du couvert hydroensemencé dans les plantations pourrait faiblir alors que les plantations continuent de se développer. De cette manière, nos résultats laissent entrevoir le potentiel de l'utilisation conjuguée des arbres-abris et d'un traitement hydroensemencé en vue d'harmoniser les visées à court et plus long termes de la revégétalisation en pentes de stériles abruptes, au sol érodable. La présence d'un couvert hydroensemencé permettrait de limiter l'érosion pendant les premières années d'implantation de la jeune plantation-abri (Remaury 2017). À moyen terme, sa disparition progressive sous le couvert arborescent créerait des opportunités d'établissement pour les espèces arborescentes tolérantes à l'ombre. Néanmoins, les recherches en vue d'identifier les mélanges herbacés compatibles avec la survie des arbres-abris demeurent cruciales.

L'examen des taux de recrutement enregistrés au terme d'une saison de croissance lors de l'essai d'ensemencement indique des résultats plutôt élevés. Sous le couvert le plus dense (1x1 m), le taux de recrutement moyen d'*A. balsamea* avoisine 5%, ce qui se compare à des résultats observés (4-4.5%) dans des peuplements de *Populus tremuloides pour des plantules de <2 ans* (McLaren & Janke 1996; Calogeropoulos *et al.* 2004). Peu importe la densité de couvert, le taux de recrutement moyen chez *P. glauca* était plus élevé (~10%) que chez *A. balsamea,* et étonnamment élevé comparé à ceux (2-4%) rencontrés dans certaines études réalisées en milieu forestier (Purdy *et al.* 2002; Simard *et al.* 2003; Calogeropoulos *et al.* 2004; Wang & Kemball 2005). Bien que ces taux de recrutement paraissent prometteurs, la méthode d'ensemencement pratiquée pour diminuer les pertes par érosion –dans de légers sillons avec recouvrement partiel des graines– a pu entraîner un biais positif à l'égard de l'émergence des plantules. De plus, des taux de recrutement relativement élevés ont été observés même dans les parcelles témoins sans arbres. En outre, la bonne qualité du sol et un taux d'érosion relativement faible dans les pentes (Remaury 2017) ont pu contribuer au succès de recrutement. Néanmoins, les résultats du suivi de la colonisation naturelle ont indiqué des densités marginales pour *A. balsamea* ($0.02 \cdot m^{-2}$) et *P. glauca* ($0.10 \cdot m^{-2}$), bien loin des densités recommandables de $2 \cdot m^{-2}$ pour ces jeunes plantules après perturbation en milieu forestier (Calogeropoulos *et al.* 2004). Bien que circonstancielles et échelonnées sur une brève période, ces observations tendent à démontrer que la disponibilité des graines des espèces plus aptes à tirer avantage du couvert des arbres-abris peut s'avérer limitante dans les pentes de stériles surplombant le milieu forestier environnant. Toutefois, puisque notre méthode d'ensemencement est difficilement applicable à l'échelle industrielle, il serait hasardeux d’émettre des recommandations aux gestionnaires de projet de restauration à l’égard des nombres de graines à ensemencer par hectare pour obtenir les densités d’arbres forestiers convoitées. Par ailleurs, et bien que cette pratique concurrente excède la portée du présent projet, la plantation d’arbres indigènes dans le sous-étage des plantations-abris pourrait s’avérer avantageuse, notamment en pente abrupte.

À la lumière de nos résultats, l'utilisation des plantations de peupliers hybrides semble une stratégie plus avantageuse, comparativement au traitement anti-érosion traditionnel, en vue de maximiser rapidement les mécanismes de facilitation et de diminuer la compétition herbacée. Ce nouvel assemblage (Hobbs *et al.* 2006) reposant sur une espèce semi-exotique a permis le redéveloppement rapide d’un couvert arboré et la modification des conditions de recrutement dès les premières années d’implantation. Dans le cadre de cette pratique, la densité de plantation utilisée devrait viser à optimiser le bilan positif des interactions entre arbres-abri, plantes herbacées et plantules ligneuses du sous-étage à plus long terme, soit permettre une fermeture suffisante pour limiter la compétition herbacée et l’évaporation directe à la surface du sol tout en limitant les pertes en eau liée à la compétition par les arbres-abris. Néanmoins, les caractéristiques inhérentes aux peupliers hybrides pourraient rapidement compromettre leur potentiel facilitant en pentes de stériles. Les plantations-abris à croissance rapide vont notamment réduire plus rapidement la disponibilité en eau du sol que des plantations à croissance plus lente (Govindarajan *et al.* 1996; McIntyre *et al.* 1997). De la sorte, il demeure incertain que les essences forestières puissent tirer profit du couvert des peupliers hybrides lors de leur développement subséquent dans un environnement où la compétition pour les ressources, notamment en eau, peut être sévère. D’autre part, des observations récentes (Remaury 2017) dans nos plantations, sur pente de 33%, indiquent des taux d’érosion relativement faibles – entre autres grâce à la colonisation naturelle des herbacées –, mais une contribution limitée des peupliers au contrôle de l'érosion dans les trois premières années d'implantation. Ces résultats pourraient mettre en cause l'étendue des gains engendrés par l'utilisation des peupliers hybrides, qui comptent parmi les espèces capables de s'établir sur les sites dégradés les plus vigoureuses (Guy & Bateman 1989), par rapport à des espèces indigènes pionnières à croissance plus lente. Enfin, d'autres critiques ont été formulées à l'égard de l'utilisation de telles monocultures – notamment leur utilisation peu efficace des ressources du sol, leur faible stabilité ou résilience, leur biodiversité déficiente, leur potentiel invasif dans un ensemble forestier indigène (Lugo 1997; Kelty 2006; Forrester *et al.* 2010) – qui pourraient témoigner de limites importantes de leur utilisation en contexte de restauration écologique.

Il faut toutefois mentionner que les résultats présentés ne peuvent être extrapolés à tous les clones de peupliers hybrides. Le clone de peuplier hybride sélectionné (M × B, 915319) se caractérisait par une productivité élevée (DesRochers & Tremblay 2009) ainsi qu'une forte allocation de sa biomasse vers les racines (Larchevêque *et al.* 2011a). Les différences de croissance, d'allocation de biomasse ainsi que de taux de transpiration qui caractérisent les différents clones influenceront différemment le développement des arbres-abris dans les pentes de stériles, et donc les effets du couvert arboré sur les conditions de recrutement. Par ailleurs, des limites inhérentes à la méthodologie utilisée pour la prise des données microenvironnementales sont à souligner, notamment à l'égard du suivi de l'éclairement disponible et de la température du sol superficiel. Des mesures simultanées avec acquisiteurs de données auraient permis une précision accrue par rapport aux mesures consécutives prises d'une parcelle à l'autre, plus vulnérables aux fluctuations rapides des conditions atmosphériques pendant la séance d'échantillonnage. De même, l'utilisation d'une seule sonde à humidité et d'un seul quadrat d'échantillonnage de la biomasse herbacée par parcelle permettait plus difficilement de pallier une éventuelle hétérogénéité des conditions mesurées. Enfin, l'inclusion d'autres facteurs aurait pu contribuer à élargir le spectre d'analyse des mécanismes de facilitation et compétition étudiés, notamment la hauteur des arbres-abris pour chaque niveau d'espacement, la composition spécifique du couvert herbacé formé par les plantes adventices, les associations mycorhiziennes reliant peupliers plantés et semis forestiers, et l'aspect qualitatif de la lumière (ratio rouge clair/rouge sombre).

Les études subséquentes pourraient s'intéresser aux plantations-abris multispécifiques, en vue d'examiner les associations d'arbres-abris qui permettent une utilisation complémentaire des ressources disponibles dans les pentes de stériles par les différentes espèces. De même, ces études pourraient examiner les associations d'arbres-abris qui permettent une complexité structurale du couvert arborescent susceptible d'augmenter l'hétérogénéité des conditions biotiques et abiotiques du sous-étage afin de bénéficier au recrutement d'espèces forestières d'exigences écophysiologiques variées.

Pour récapituler, nos résultats tendent à démontrer que, comparativement au traitement anti-érosion traditionnel, les plantations de peupliers hybrides étudiées procurent rapidement des opportunités d'établissement pour des espèces plus typiques des stades avancés de la succession par l'intermédiaire du redéveloppement accéléré d'un couvert arboré dans les pentes de stériles. Néanmoins, les arbres-abris à croissance rapide comme les clones étudiés, qui se caractérisent par des taux de transpiration élevés, pourraient exacerber les contraintes liées à la disponibilité en eau du sol dans des milieux vulnérables à la dessiccation comme les pentes de stériles. Ainsi, un suivi à plus long terme s'avère nécessaire afin de vérifier que les mécanismes de compétition ne supplantent pas rapidement ceux de facilitation dans les interactions entre arbres-abris et plantules du sous-étage au cours des prochaines saisons de croissance. De la même manière, l'avantage de l'utilisation des peupliers hybrides comme plantations-abris comparativement à celle d'espèces forestières pionnières indigènes demeure à démontrer dans un contexte de restauration écologique. De la sorte, les recommandations en faveur de leur utilisation par les gestionnaires de restauration de haldes à stériles miniers s'avéreraient prématurées.

ANNEXE A

LIST OF HERBACEOUS SPECIES INVENTORIED DURING THE 2ND AND 3RD GROWING SEASONS IN THE HYBRID POPLAR PLANTATIONS

Common name	**Scientific name**
Alsike clover	*Trifolium hybridum* Linnaeus
Bull thistle	*Cirsium vulgare* (Savi) Tenore
Canada goldenrod	*Solidago canadensis* Linnaeus
Canada thistle	*Cirsium arvense* (Linnaeus) Scopoli
Coltsfoot	*Tussilago farfara* Linnaeus
Common dandelion	*Taraxacum officinale* F.H. Wiggers
Common kochia	*Bassia scoparia* (Linnaeus) Voss
Common lamb's-quarters	*Chenopodium album* Linnaeus
Common mullein	*Verbascum thapsus* Linnaeus
Common plantain	*Plantago major* Linnaeus
Common timothy	*Phleum pratense* Linnaeus
Common yarrow	*Achillea millefolium* Linnaeus
Curled dock	*Rumex crispus* Linnaeus
Field sow-thistle	*Sonchus arvensis* Linnaeus subsp. *arvensis*
Fireweed	*Chamaenerion angustifolium* (Linnaeus) Scopoli subsp. *angustifolium*
Garden bird's-foot trefoil	*Lotus corniculatus* Linnaeus
Grass-leaved goldenrod	*Euthamia graminifolia* (Linnaeus) Nuttall
Heart-leaved aster	*Symphyotrichum cordifolium* (Linnaeus) G.L. Nesom
Horsetail sp.	*Equisetum* sp.
Large-leaved aster	*Eurybia macrophylla* (Linnaeus) Cassini
Narrow-leaved blue-eyed-grass	*Sisyrinchium angustifolium* Miller
Orange hawkweed	*Pilosella aurantiaca* (Linnaeus) F.W. Schultz & Schultz Bipontinus
Oxeye daisy	*Leucanthemum vulgare* Lamarck
Red clover	*Trifolium pratense* Linnaeus

Red fescue	*Festuca rubra* Linnaeus subsp. *rubra*
Red raspberry	*Rubus idaeus* Linnaeus
Reed canarygrass	*Phalaris arundinacea* Linnaeus
Rough cinquefoil	*Potentilla norvegica* Linnaeus
Rough-stemmed goldenrod	*Solidago rugosa* Miller
Sedge sp.	*Carex* sp.
Smartweed sp.	*Persicaria* sp.
Tufted vetch	*Vicia cracca* Linnaeus
Urled dock	*Rumex crispus* Linnaeus
White clover	*Trifolium repens* Linnaeus
White sweet-clover	*Melilotus albus* Medikus
Wild strawberry	*Fragaria virginiana* Miller
Yellow sweet-clover	*Melilotus officinalis* (Linnaeus) Lamarck

ANNEXE B

LIST OF NATURALLY ESTABLISHED WOODY (TREE AND ARBORESCENT SHRUB) SPECIES INVENTORIED DURING THE 2ND AND 3RD GROWING SEASONS IN THE HYBRID POPLAR PLANTATIONS

Common name	**Scientific name**
American mountain-ash	*Sorbus americana* Marshall
Balsam fir	*Abies balsamea* (Linnaeus) Miller
Balsam poplar	*Populus balsamifera* Linnaeus
Bebb's willow	*Salix bebbiana* Sargent
Black spruce	*Picea mariana* (Miller) BSP
Paper birch	*Betula papyrifera* Marshall
Pin cherry	*Prunus pensylvanica* Linnaeus f.
Prairie willow	*Salix humilis* Marshall
Pussy willow	*Salix discolor* Muhlenberg
Red-osier dogwood	*Cornus sericea* Linnaeus
Trembling aspen	*Populus tremuloides* Michaux

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