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PERSPECTIVE ÉCOPHYSIOLOGIQUE DE L'ENVAHISSEMENT DES ÉRICACÉES DANS LE SOUS-DOMAINE DE LA PESSIÈRE NOIRE À MOUSSES DE L'EST DU QUÉBEC

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Résumé

Les arbustes éricacées sont réputés pour nuire à la croissance de l'épinette noire (*Picea mariana* (Mill.) [B.S.P.]) par une forte compétition pour les ressources. L'ouverture de la voûte forestière par la coupe peut intensifier cette compétition et mener à l'envahissement des plantes éricacées. L'objectif de ce projet de recherche était d'expliquer, par l'évaluation de la réponse des traits fonctionnels, le potentiel d'envahissement des éricacées et la stagnation de la croissance de la régénération naturelle d'épinette noire après coupe dans le domaine de la pessière noire à mousses de l'est.

Le premier volet de la thèse démontre que le thé du Labrador (*Rhododendron groenlandicum* [Oeder] Kron & Judd) s'acclimate rapidement à l'augmentation de lumière causée par la coupe, spécialement dans les coupes les plus intenses, par des modifications physiolgiques. De son côté, les traits morphologiques de l'épinette noire n'ont pas répondu au changement d'environement créé par la coupe, indicant soit une absence ou un délai d'acclimatation.

La deuxième expérience terrain a permis de constater que la photosynthèse de l'épinette noire était influencée négativement par la présence des plantes éricacées sur le parterre de coupe, et ce, peu importe la qualité de la station étudiée. Cette réduction du taux de photosynthèse serait attribuable à la plus faible disponibilité en azote minéral dans les parcelles témoin résultant d'une forte compétition souterraine des plantes éricacées pour les ressources nutritives du sol.

Une troisième expérience en serre a démontré que la masse foliaire par unité de surface (LMA) du *Rhododendron* et du *Kalmia* a diminué avec l'ombrage. L'épinette noire a montré une taux d'absorption et un taux d'absorption spécifique supérieurs à des niveaux d'azote plus élevés comparativement aux éricacées. La plasiticité envers la lumière fut supérieure pour le *Kalmia* (sauf pour la LMA) et celle envers l'addition d'azote fut supérieure pour le *Rhododendron* et l'épinette suggérant que la plasticité des traits est en accord avec le statut successionnel des espèces.

Abstract

Ericaceous shrubs are known to impair black spruce (*Picea mariana* (Mill.) [B.S.P.]) growth by creating a strong competition for below and aboveground resources. Opening of the forest canopy with harvest can intensify this competition and lead to enroachment of ericaceous shrub. Our objective was to explain, through evaluation response of functional traits, ericaceous potential enroachment after logging and stagnant growth of black spruce advance regeneration in the Quebec's eastern black spruce-feathermoss sub-domain.

The first chapter demonstrated the rapid acclimation of bog Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd) to higher light availability created by logging, especially in the more intense treatements, through a modification of both physiological leaf traits. On the other hand, black spruce leaf traits did not respond to changes in environement associated with logging; this may indicate either an absence or a delay in acclimation.

In a second field experiment, black spruce photosynthetic rate was negatively influenced by ericaceous shrub presence on the cutting area, regardless of the site fertility quality. The lower photosynthesis rate of black spruce, when associated with ericaceous shrubs, could be resulting of a lower mineral soil nitrogen availability created by a greater belowground competition for ressources form the ericaceous shrubs.

A third experiment under greenhouse conditions showed that *Rhododendron* and *Kalmia* leaf mass per unit of area (LMA) was reduced by shading, but was similar for black spruce. There were few differences in trait response to N addition among species. Black spruce showed higher absorption rate and specific absorption rate at higher N levels, compared to the two ericads. Plasticity to light was higher for *Kalmia* (except for LMA) and plasticity for nitrogen addition was higher for *Rhododendron* black spruce suggesting that trait plasticity is in accordance with successional status of these species.

Avant-Propos

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Plusieurs personnes ont contribué à l'accomplissement de mon cheminement académique jusqu'à l'obtention de ce diplôme de doctorat. J'aimerais tout d'abord remercier ma directrice de thèse, Alison D. Munson, professeure-titulaire de l'Université Laval, pour m'avoir soutenu tout au long de cette thèse, spécialement dans les moments difficiles. D'un point de vue professionnel, elle m'a donné un encadrement d'une qualité exceptionnelle, tout en me laissant assez de latitude pour développer mon autonomie et mon indépendance en tant que futur chercheur. D'un point de vue humain, Alison a fait preuve de beaucoup d'empathie et de compréhension et s'est toujours souciée de mon bien-être et je ne serai jamais assez reconnaissant envers elle. Elle m'a donné de précieux conseils qui m'ont facilité grandement la tâche au cours de ces études doctorales… et dans la vie en général. C'est aussi grâce à elle que je me suis ouvert sur le monde en me permettant de compléter ma formation dans d'autres pays.

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Structure de la thèse

Cette thèse est composée de trois articles scientifiques dont un qui un sous presse (Chapitre 1) dans le Journal canadien de recherche forestière et un autre publié dans Forest Ecology and Management (Chapitre 2). Par ma position d'auteur principal de chacun des articles, je suis le principal responsable de ces travaux de recherche allant de la planification de l'expérience jusqu'à la rédaction du manuscrit de chacun des articles. Les co-auteurs ont principalement agit comme conseillers et qui ont grandement contribué à la révision des manuscrits.

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Introduction générale

Contexte écologique et autécologie de l'épinette noire

Au Québec, le domaine de la pessière noire à mousses représente plus de 29 % du territoire total (412 400 km^2) et environ 62 % du territoire forestier commercial (MRNF, 2005). Ce domaine bioclimatique est caractérisé par des grands peuplements d'épinette noire (*Picea mariana* Mill. [B.S.P.]), le plus souvent monospécifiques mais parfois associés à des espèces compagnes comme le pin gris (*Pinus banksiana* Lamb.) et le sapin baumier (*Abies balsamea* L. [Mill.]). En strate arbustive, on y retrouve généralement des plantes de la famille des éricacées et en strate muscinale, on retrouve des mousses hypnacées (Brumelis et Carleton 1989, Viereck et al. 1990).

L'épinette noire, comme plusieurs espèces de conifères, est adaptée pour se régénérer après feu (Viereck et al. 1990). Les cônes semi-sérotineux de cette espèce permettent la libération des graines lorsque ceux-ci sont à maturité ou lors d'une chaleur intense comme un feu de forêt (Viereck et al. 1983). L'exposition du sol minéral, après le passage d'un feu de forte intensité, permet la création de lits de germination favorables à l'établissement de cette espèce (St-Pierre et al. 1991). En l'absence de feu, l'épinette noire se régénère de façon végétative par la formation de marcottes (Doucet 1988, Ruel et al. 2004), c'est-à-dire des branches vivantes qui s'enracinent lorsqu'elles entrent en contact avec le sol (Cooper 1911). En plus de répondre favorablement à l'ouverture du couvert forestier, la productivité des marcottes se compare favorablement à celle de la régénération par graines après feu (Lussier et al. 1992, Paquin et Doucet 1992 b, Paquin et al. 1999).

Les différences climatiques caractérisant ce domaine bioclimatique couvrant entièrement la province en longitude font en sorte que la partie Est est caractérisée par un cycle de feu plus long (Payette et al. 1989, Gauthier et al. 2000). La résultante de cette différence est une plus grande proportion de peuplements d'épinette noire de structure irrégulière à plusieurs cohortes d'âge, structure induite par l'établissement des marcottes lors de l’ouverture graduelle des peuplements (Bergeron et al. 1999, De Granpré et al. 2000, Ruel et al. 2004).

Sylviculture adaptée dans l’optique de l’aménagement écosystémique

À la lumière de ces connaissances, un nouveau type de coupe a fait son apparition à la fin des années 1980 et fait maintenant partie de la stratégie de protection sur les forêts du ministère des ressources naturelles et de la faune depuis 1994 (Anonyme 1994). La coupe avec protection de la régénération et des sols (CPRS) en pessière noire a pour objectif de protéger la régénération en place afin d’assurer un retour d’un peuplement productif, à condition que la quantité de régénération naturelle soit suffisante (Anonyme 2006). Par contre, en minimisant la perturbation des sols, la CPRS conserve le couvert de végétation arbustive présent avant la coupe, tout en augmentant la lumière disponible (Harvey et Brais 2002). Les coupes forestières sont souvent considérées au même titre que les perturbations naturelles puisqu’elles influencent les conditions environnementales qui ont un effet sur la croissance des plantes: la lumière, l’eau du sol, la température de l’air et de l’eau du sol (Holgen et Hanell 2000).

Par le prélèvement d’arbres matures, la coupe, qu’elle soit partielle ou totale, augmente la quantité de lumière disponible au niveau de la strate arbustive et réchauffe l’air et le sol (Tucker 1987, Burgess et Wetzel 2000, Prévost et Pothier 2003, Frey et al. 2003). La lumière disponible et la température du sol sont les deux variables qui sont les plus influencées par la densité de la strate arborescente (Brumelis et Carleton 1989 dans Bergsted et Milberg 2001, Lajzerovicz et al. 2004), même si le réchauffement du sol est moins fortement influencé que la lumière dans les coupes partielles (Barg et Edmonds 1999, Groot 1999). Les coupes influencent aussi la disponibilité de l’eau (Burgess et Wetzel 2000). Par contre, cet effet interagit avec la quantité de végétation résiduelle après coupe et la saison de croissance (Barg et Edmonds 1999, Burgess et Wetzel 2000, Granhus et al. 2003).

Enfin, la coupe a des effets positifs sur la disponibilité des nutriments, par une augmentation de la minéralisation de l'azote et une augmentation du taux de décomposition de la matière organique resultant d'une augmentation de l'activité microbienne (Binkley 1984, Frazer et al. 1990, Smethurst et Nambiar 1990, Keenan et Kimmins 1993, Prescott 1997, Barg et Edmonds 1999). L'activité microbienne, diminue graduellement avec la reconstitution du couvert du peuplement pour retourner à des niveaux semblables à ceux rencontrés avant la coupe (Frazer et al. 1990, Keenan et Kimmins 1993, Prescott 1997). Finalement, dans certains milieux, l'augmentation de la disponibilité en azote serait induite par une diminution de l'assimilation de l'azote (Prescott 1997).

L'augmentation de l'apport lumineux en strate arbustive favoriserait l'envahissement des éricacées dans certains peuplements au détriment des conifères. En effet, l'augmentation de lumière disponible stimule la croissance des éricacées (Messier 1992) et le taux photosynthèse des éricacées est supérieure à celle de l'épinette noire (Small 1972). Or, dans le domaine de la pessière noire à mousses de l'est, on dénombre de 10 à 15 % de peuplements d'épinette noire récoltés par CPRS où l'on note un une forte proportion d'éricacées (Warren 2009, communication personnelle). En présence de ce fort couvert d'éricacées, la croissance de la régénération d'épinette noire stagne et présente des signes de carence en nutriments. Des études réalisées dans la province Terre-Neuve ont démontré que l'occupation à long terme de ces éricacées menait, dans certains cas, à une conversion de forêt productive en une lande forestière dominée par le kalmia à feuilles étroites (*Kalmia angustifolia* L.) par des changements des propriétés physiques et chimiques du sol (Damman 1971, Mallik 1995). Présentement, aucune intervention sylvicole n'est préconisée dans ce type de peuplements si la quantité de régénération pré-établie est suffisante et correspond au même coefficient de distribution qu'avant coupe (Anonyme 2006). Cette approche pourrait potentiellement causer une perte de productivité forestière à moyen terme si la régénération stagne pendant un bon nombre d'années, et où une proportion de ces peuplements se convertissent en landes à éricacées (Warren 2009, communication personnelle).

Interaction éricacées-conifères en milieu boréal

Les effets néfastes des éricacées sur la croissance des conifères sont très variés et documentés, surtout pour le kalmia à feuilles étroites (Mallik 1987, Zhu et Mallik 1994, Yamasaki et al. 1998) et de façon limitée pour le thé du Labrador (*Rhododendron groenlandicum* [Oeder] Kron & Judd) (Inderjit et Mallik 1996) que l'on rencontre fréquemment en pessière noire à mousses de l'est. Ces mêmes effets sur la croissance des conifères ont aussi été mesurés en présence d'autres espèces éricacées comme la gaulthérie (*Gaultheria shallon* Pursh.) (Messier 1993, Fraser et al. 1993), *Calluna vulgaris* (L.) Hull. (Wheatherell 1953, Norberg et al. 2001), *Vaccinium myrtillus* (Jaderlund et al. 1997) et *Empetrum hermaphroditum* Hagerup. (Nilsson et al. 2000, Castells et al. 2005). On observe une réduction de croissance de l'épinette, provoquée par le kalmia à feuilles étroites, dans des milieux infertiles où la compétition pour l'eau et des nutriments semble être plus importante (Titus et English 1996, Thiffault et al. 2004). Le principal effet du kalmia à feuilles étroites sur la croissance de l'épinette noire est la compétition directe créée par cette espèce pour les nutriments (Yamasaki et al. 1998, 2002). La grande quantité de racines produites par le kalmia à feuilles étroites permet une plus grande assimilation de nutriments que l'épinette noire malgré une moins grande efficacité d'absorption par unité de biomasse racinaire (Damman 1971, Thiffault et al. 2004). De plus, le kalmia à feuilles étroites favorise l'accumulation d'humus, provenant de la mortalité des rhizomes et des racines, ce qui immobilise les nutriments en des formes organiques non disponibles pour l'épinette noire (Damman 1971, Titus et al. 1995, Titus et English 1996).

Même s'il n'y a pas de preuves directes d'effets allélopathiques du kalmia à feuilles étroites sur les conifères (Inderjit et Mallik 2002), Yamasaki et al. (2002) suggère que les mécanismes de compétition autres que nutritionnels (allelopathie) jouent un role important dans l'interférence du kalmia à feuilles étroites sur la croissance de l'épinette noire. En effet, les composés phénoliques contenus dans le feuillage de cette éricacée réduisent la minéralisation de l'azote, pouvant potentiellement nuire à la nutrition de l'épinette noire (Bradley et al. 2000). Ces substances créent des statuts nutritifs débalancés en augmentant la présence d'éléments minéraux autres que l'azote et en réduisant la quantité d'azote disponible pour les conifères par la formation de complexes avec des protéines et en diminuant l'activité enzymatique du sol (Mallik 2003, Castells et al. 2005, Joanisse et al. 2007, 2009). Les composés phénoliques sont aussi néfastes pour les communautés microbiennes du sol (Bradley et al. 1997), la germination (Zhu et Mallik 1994), la croissance des racines fines (Zhu et Mallik 1994, Yamasaki et al. 1998) et la mycorhization des racines de l'épinette noire (Mallik 1987, Titus et al. 1995). La présence du kalmia à feuilles étroites favorise la colonisation d'un pseudo-mycorhize *(P. dimorphospora*) sur les racines de l'épinette diminuant, par le fait même, l'absorption de nutriments de l'épinette (Yamasaki et al. 1998). Certains de ces effets néfastes sur l'épinette noire ont aussi été notés pour deux autres espèces d'éricacées présentes dans les pessières du Québec, soit le thé du Labrador et le bleuet (*Vaccinium sp.*) (Inderjit et Mallik 1996, Thiffault et al. 2004).

Dans le sous-domaine de la pessière noire à mousses de l'est, c'est le thé du Labrador qui est l'espèce d'éricacée la plus répandue. Cette éricacée est retrouvée principalement dans des peuplements ouverts d'épinette noire et aussi dans des peuplements un peu plus densément peuplés (Laberge-Pelletier 2007). Étant donné la fréquence des feux de forêts dans ce sous-domaine, on retrouve beaucoup de forêts de structure irrégulière (Ruel et al. 2007). Afin d'aménager ces forêts de façon écosystémique, un concept qui consiste à assurer le maintien de la biodiversité et de la viabilité des écosystèmes en diminuiant les écarts entre la forêt aménagée et naturelle, il est nécessaire de développer des stratégies sylvicoles particulières qui permetteraient de préserver les attributs structurels de ces forêts (Bergeron et al. 1999). La chaire CRSNG-Université Laval en Sylviculture et Faune a proposé différents types de coupes dans la pessière noire à mousses de l'est afin de respecter ce concept (Ruel et al. 2007). Or, il est essentiel d'étudier les mécanismes d'interactions entre le thé du Labrador et la régénération adventive de l'épinette noire afin de vérifier si les attributs structurels de ce forêt seront préservés dans le temps.

L'approche de compréhension par l'écologie fonctionnelle

Les mécanismes d'interaction entre les éricacées et les conifères au long de la succession en forêt boréale sont complexes et devraient être étudiés avec une vision plus large. L'écologie fonctionnelle, ou écologie comparative, nous présente une approche novatrice afin de mieux comprendre les relations éricacées-conifères. Cette approche passe par l'utilisation de traits de plantes comme variables explicatives et par la comparaison entre les traits des différentes espèces, ce qui permet de faire des comparaisons de ceux-ci à travers différents gradients environnementaux naturels ou anthropiques (Shipley 2007, Violle et al. 2007). Un trait fonctionnel est une caractéristique mesurable à l'échelle de l'individu, caractéristique ne requérant pas d'information venant de l'environnement de celui-ci ou de tout autre niveau d'organisation (Violle et al. 2007). On utilise les traits fonctionnels des individus (ou des espèces) afin de prédire des réponses à l'échelle de l'écosystème (p. ex. biogéochimie) et des communautés (p. ex. compétition entre espèces) face aux perturbations natruelles ou face aux changements créés par l'homme comme le changement d'utilisation des terres (Garnier et al. 2007, Violle et al. 2009) Dans notre cas, ce sont les modifications environnementales créées par la coupe des peuplements d'épinette noire à forte proportion d'éricacées qui nous intéresse comme vecteurs de modification des traits des plantes.

La compétition pour les ressources est un des processus écologiques les plus importants expliquant l'abondance des espèces dans les communautés. Ainsi, les traits fonctionnels qui influencent les changements en densité ou en biomasse des espèces sont ceux qui affectent le plus la disponibilité des ressources qui, en retour, aura une influence sur la performance des autres plantes (Viole et al. 2009). Les traits fonctionnels qui sont reliés à la contrainte d'aquisition-conservation des ressources sont souvent impliqués dans l'analyse des réponses aux changements environnementaux. Parmi ceux-ci, notons la masse foliaire par unité de surface, les contenus en nutriments foliaires et le potentiel hydrique pré-aube (Wright et al. 2004, Garnier et al. 2007, Viole et al. 2009). Nous étudierons spécifiquement la masse foliaire par unité de surface puisque ce trait varie selon la quantité de lumière disponible (Givnish 1988) et est positivement corrélé avec le contenu foliaire en azote (Wright et al. 2004); le contenu foliaire en azote ayant la caractéristique d'être module par la quantité d'azote disponible dans le sol (Munson et Timmer 1989) et qui semble être affecté, tout comme la lumière, par la coupe forestière (Titus et al. 2006).

La plasticité phénotypique est définie comme le changement de l'expression phénotypique d'un génotype à travers différents environnements induit par des modifications des traits fonctionnels morphologiques ou physiologiques (Weber et D'Antonio 1999, Baquedano et al. 2008). Les espèces ayant une grande plasticité phénotypique auront un avantage compétitif en comparaison d'espèces moins plastiques (Funk 2008).

L'approche de cette thèse, par la réalisation d'études expérimentales sur le terrain et en serre visait à mesurer la réponse des traits fonctionnels et évaluer la réponse de ces traits afin de mieux comprendre les relations de compétition entre l'épinette noire, la communauté d'espèces d'éricacées (terrain) et les espèces individuelles de cette famille de plante (serre). Pour la première expérience terrain, les ressources seront manipulés par des traitements sylvicoles, en visant un gradient de lumière et de fertilité. Quant à la deuxième expérience terrain, c'est plutôt la présence ou l'absence d'éricacée qui sera modulée afin de mesurer la réponse sur les traits de l'épinette. En serre, nous avons également manipulé directement la lumière et la fertilité, les deux ressources les plus importantes pendant la succession de la pessière noire à mousses de l'est. Pour cette expérience, nous avons aussi déterminé le niveau de plasticité des traits fonctionnels afin de vérifier la concordance avec le statut successionel des trois espèces à l'étude.

L'objectif de ce projet de recherche sera d'expliquer, par l'évaluation de la réponse des traits fonctionnels, le potentiel d'envahissement des éricacées et la stagnation de la croissance de la régénération naturelle d'épinette noire après coupe dans le domaine de la pessière noire à mousses de l'est. Le premier volet étudiera la réponse morphologique et physiologique de l'épinette et du thé du Labrador sous différentes modalités de coupes partielles dans le sous-domaine bioclimatique de la pessière noire à mousses de l'est. Les hypothèses étant que la réduction du couvert forestier, par la coupe, vont augmenter le niveau de disponibilité des ressources et que le thé du Labrador montrera une acclimatation physiologique, morphologique et une efficicité d'utilisation des ressources supérieure à l'épinette noire. Le deuxième chapitre analysera l'effet la végétation de compétition, selon un gradient écologique, sur les traits fonctionnels des marcottes d'épinette noire et des traits fonctionnels de l'écosystème, après CPRS dans des peuplements où la présence d'éricacées était substantielle. Les hypothèses de ce projet sont que les éricacées affecteraient négativement les paramètres physiologiques de l'épinette noire par les effets des éricacées sur les caractéristiques édaphiques et que ces effets seraient inversement proportionnels à la qualité de la station. Mon troisième volet comparera la réponse des traits fonctionnels des éricacées et de l'épinette noire face à différents niveaux de lumière et de fertilité du sol, les hypothèses étant que la plasticité des traits fonctionnels associés à l'acquisition de lumière et de nutriments expliqueraient la dominance successionnelle de chaque espèce. Mes résultats permettront de proposer, si possible, des approches sylvicoles adaptées afin de contrôler le phénomène d'envahissement des éricacées dans les peuplements jugés à risque, dans une optique d'aménagement écosystémique.

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Chapitre 1

Comparative physiological responses of *Rhododendron groenlandicum* and regenerating *Picea mariana* following partial canopy removal in northeastern Quebec, Canada.

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ABSTRACT

In boreal black spruce-dominated stands, careful logging around advance regeneration contributes to protect the shrub layer while increasing light availability. Therefore, it may promote expansion of bog Labrador tea (*Rhododendron groenlandicum*), which can impair black spruce (*Picea mariana*) growth by direct competition for nutrients and by alteration of soil biochemical conditions. Such harvesting approaches may not be suited for irregular, uneven-aged black spruce stands in the context of ecosystem-based management. Our objectives were to evaluate the effects of different intensities of partial harvest on critical resource availability, and to compare the physiological and morphological responses of black spruce and *Rhododendron* to different intensities of partial harvest treatments. Two years after harvest, photosynthesis rate of black spruce was unchanged and was lower than *Rhododendron*, which was 63 % higher after harvest. Nitrogen and water use efficiency were, respectively, 171 % and 42 % higher in *Rhododendron* than black spruce after logging. Following harvest, black spruce physiology appeared to be regulated by the atmospheric humidity deficit but for *Rhododendron*, physiology was regulated by light availability. The high plasticity of *Rhododendron* leaf traits could be indicative of the future advantage of this species in these stands following canopy removal associated with harvest.

RÉSUMÉ

Dans la forêt boréale résineuse, la coupe avec protection de la régénération et des sols (CPRS) contribue à protéger la strate arbustive tout en augmentant la quantité de lumière disponible. Cette situation peut promouvoir l'expansion du thé du Labrador (*Rhododendron groenlandicum* [Oeder] Kron & Judd), qui pourrait nuire à la croissance de l'épinette noire (*Picea mariana* [Mill.] BSP) en créant une compétition pour les nutriments et en altérant les conditions biochimiques du sol. Les objectifs étaient d'évaluer les effets de différentes intensités de coupe partielle sur la disponibilité des ressources et de comparer la réponse

physiologique et morphologique de l’épinette noire et du thé du Labrador soumis à un gradient de conditions créé par les traitements de coupe. Deux ans après coupe, le taux de photosynthèse de l’épinette noire est demeuré inchangé et était inférieur à celui du thé du Labrador, qui lui, a augmenté de 63 % après coupe. L’efficacité d’utilisation de l’azote et de l’eau étaient, respectivement, 171 % et 42 % plus élevés pour le thé du Labrador comparativement à l’épinette noire après coupe. La physiologie de l’épinette noire, après la récolte, semble être régulée par le déficit de pression de vapeur de l’air. De son côté, la physiologie du thé du Labrador semble être régie par les conditions de lumière disponible. La plus grande plasticité des traits du feuillage du thé du Labrador pourrait signifier un avantage futur de cette espèce dans ce type de peuplement après coupe.

1. Introduction

Bog Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd, previously referred to as *Ledum groenlandicum*) is a widely distributed, light intolerant, perennial understory shrub of the North American boreal forest (Jobidon 1995). In northeastern Quebec (Canada), Labrador tea (hereafter referred to as *Rhododendron*) is frequently found on coarse to medium-textured mineral soil with an acid, mor humus between 20-60 cm, where it is strongly associated with black spruce (*Picea mariana* [Mill.] BSP) overstories (Laberge-Pelletier 2007). *Rhododendron* cover increases mainly through vegetative growth after disturbances such as fire and harvest that open the canopy, often resulting in slow growth of black spruce regeneration (Inderjit and Mallik 1996). This shrub competes directly with black spruce for nutrients (Munson and Timmer 1989), due to a high root nutrient uptake (Chapin and Tyron 1983), and competes indirectly by: (i) enhancing nutrient immobilization in humus (Damman 1971); (ii) altering soil chemical conditions that reduce soil nitrogen (N) availability; and (iii) limiting mycorrhizal symbiosis, thus affecting black spruce growth (Inderjit and Mallik 1996).

Since 1994, careful logging around advance growth (CLAAG or CPRS in French) is the principal logging method used to harvest Quebec's boreal forest; the main objective of this approach is to favor black spruce advance regeneration while protecting soils (Anonymous 1994). However, by minimizing soil perturbation, CLAAG also contributes to protecting the shrub layer, while increasing light availability to the understory plants (Harvey and Brais 2002). Several authors hypothesize that higher light availability could lead to a long-term encroachment of ericaceous shrubs by eventual edaphic modifications (Damman 1971, Mallik 1995).

Sixty percent of the non-harvested area in northeastern Quebec is composed of stands characterized by an irregular structure (Côté 2006). In the context of ecosystem-based management, partial cutting is considered a promising "near-nature" silvicultural approach to perpetuate this stand type in Quebec's boreal forest (Bergeron et al. 1999, Ruel et al. 2007, Bouchard 2008). However, this approach can be problematic in stands that are susceptible to regeneration problems following canopy opening, such as black spruce-dominated stands with a significant cover of ericaceous species. Specifically, we do not know how the light conditions created by partial cutting affect the response of black spruce and *Rhododendron*, and how differential responses might impact subsequent succession on these sites.

Plants respond to changing light conditions by morphological and physiological modifications that directly affect primary growth, mainly through changes in photosynthetic capacity and leaf resource allocation (Sims and Pearcy 1994). For example, higher light availability contributes to increased leaf thickness, specific leaf weight and lower fine-root/foliar ratio of salal (*Gaultheria shallon* Pursh.), an ericaceous shrub of western Canada, ultimately resulting in increased growth and biomass (Messier 1992). Sheep laurel (*Kalmia angustifolia* L.) responds favorably to increased light availability by a rapid spread of rhizomes (Mallik 1993) and is also stimulated by a higher soil nutrient availability (another potential effect of harvesting; Titus et al. 2006), resulting in greater height growth and biomass accumulation (Mallik 1993). In the present study, we examined the physiological and morphological acclimation of *Rhododendron* to canopy disturbance by harvest, as this knowledge is essential to adequately adapt silvicultural strategies in northeastern boreal Quebec.

On the other hand, black spruce has a reduced physiological plasticity to changes in environmental conditions and resource availability (Zine El Abidine et al. 1994). Furthermore, black spruce advance regeneration in the understory develop shade tolerant needles with low leaf mass per unit of area (LMA), which leads to a lower photosynthesis rate. These needles can experience photoinhibition and water stress for the first few years after canopy removal, limiting the ability of black spruce to respond to the more favorable growth conditions created by harvest (Paquin et al. 1999).

Water and nutrient stress lead to convergent trait syndromes (higher resource efficiency) that allow resource conservation within well-protected tissues (conservative types) (Grime 1977, Diaz et al. 2004). Comparing resource efficiencies and strategies between two competing species in the same infertile habitat may help to understand how evergreen shrubs limit tree growth (DeLucia and Schlesinger 1991, Lebel et al. 2008). Small (1972) showed that sheep laurel and *Rhododendron* have higher photosynthetic rates and photosynthetic nitrogen use efficiency than black spruce growing in a peat bog. However, we do not know the potential of these species to respond to the environment created by tree harvest on mesic sites of commercial black spruce forests.

Our objectives were to evaluate the effects of different intensities of partial harvest on resource availability (light, water, nutrients) and to compare the physiological and morphological responses of black spruce and *Rhododendron* to the gradient of conditions created by these treatments. Based on previous studies of other ericaceous species, we hypothesized that reduced stand density following harvest improves resource availability, and that *Rhododendron* shows greater physiological acclimation (higher gas exchange, water potential, foliar nutrient concentration), higher resource use efficiency, and a more rapid morphological acclimation than black spruce.

2. Materials and methods

2.1 Study site

The study was conducted in three black spruce-feathermoss stands in the eastern part of Quebec's spruce-feathermoss bioclimatic domain (Saucier et al. 2009). The site is located 20 km northeast of Lac St-Pierre (50˚15'51.6''N, 68˚06'20.5''W), approximately 180 km north of Baie-Comeau, Quebec, Canada. This region has a cool climate with a mean annual temperature of 1.5˚C (±0.9˚C) and total precipitation of 1014 mm, with 361.5 mm (32.5 %) as snow (1971-2000 data from Baie-Comeau weather station (49˚7.8'N, 68˚12'W)) (Environment Canada 2008). Stands were selected based on several criteria:

comparable slope, topography, crown cover and tree species composition. The selected stands were, at least, 135 (site 1), 153 (site 2), and 187 (site 3) years old (age was evaluated on three dominant trees in a 400 m^2 circular plot) with no fire events since 1800 (Bouchard et al. 2008). The site indices (dominant height at age 50) were 12 m, 9 m, and 15 for sites 1, 2, and 3, respectively. The stands were dominated by black spruce with a small component of balsam fir (*Abies balsamea* (L.) Mill.). Crown cover was between 40 and 60 %. Advance regeneration in the understory layer was mainly black spruce, with a minor component of balsam fir with approximately 350 stems/ha (block 2), 825 stems/ha (block 3) and 950 stems/ha (block 4). The shrub layer was dominated by an extensive but patchy cover of *Rhododendron* (mean cover of 20 %), *Chamaedaphne calyculata* (L.) Moench., *Vaccinium myrtilloides* Michx., *Vaccinium angustifolium* Ait., *Kalmia angustifolia*, and *Gaultheria hispidula* (L.) Mühl. Ex Bigel. Herbs were dominated by *Coptis groenlandica* (Oeder) Fern., *Cornus canadensis* L. and *Clintonia borealis* (Ait.) Raf. The moss layer was composed mainly of *Sphagnum* spp. and *Pleurozium schreberi* (Brid) Mitt. with patches of lichen, including *Cladonia mitis* (Standst.) Hustich, *C. stellaris* (Opiz) Brodo, and *C. rangiferina* (L.) Nyl. Soils are humo-ferric podzols (Humods Spodosols), located on shallow (< 50 cm) to moderately deep (50-100 cm) coarse till glacial deposits with a mor humus (10-12 cm). The soils of all stands were characterized as well to moderately-well drained.

2.2 Experimental design and treatments

The experimental design consisted of three replicated blocks, arranged in a 5 × 2 × 3 × 6 split split split-plot design composed of five harvest methods (four harvest types and a control) per block, as the main factor, two species at the sub-plot level, sampling years (3) as the sub sub-plot factor, and sampling periods (nested in sampling years) (6) at the sub sub sub-plot level. Each block (5 ha) was divided into five 1-ha plots, to which one of the five following treatments was randomly applied using a harvester equipped with a multifunctional processing head. The first harvesting method was careful logging around advance growth (’’coupe avec protection de la régénération et des sols’’, or CPRS). In the

CPRS, all trees with a diameter at breast height (DBH) > 9 cm were harvested and 25 % or less of the area was disturbed by skid trails. The second harvest method (CPPTM) was similar to the CPRS, but the DBH of harvested trees was greater than 13 cm. The other two harvest types were designed to maintain the irregular age and height structure of the stands. For the first selection cut (TT), a 5 m-wide skid trail was established every 30 m. Two thirds of all trees with a DBH > 13 cm were harvested up to 5 m on each side of the skid trail (maximum reach of the machinery; Ruel et al. 2007). The second selection cut (PT) was similar to the TT. Five-meter skid trails were established every 35 m and secondary skid trails, perpendicular to the main trail, were established every 10 m. Secondary skid trails were 5 m wide and 5 m long; one third of all trees with DBH > 13 cm were harvested off these secondary trails. Residual % basal area from another study in the same region varied from 6.5 (CPRS) to 58.2 (PT) (Cimon-Morin, unpublished data).

2.3 Environmental measurements

Within each plot, available photosynthetic photon flux density (PPFD, 400-700 nm) was measured in the proximity of two black spruce advance regeneration layers and *Rhododendron* plants in 2006 (August 3-7), 2007 (July 23-25, August 22-30), and 2008 (July 26th, August 24th). Available PPFD both species was determined using a portable integrating radiometer (Sunfleck Ceptometer, model SF-80, Decagon Devices Inc., Pullman, WA, USA). Four PPFD readings for each plant or layer were taken under overcast conditions; these were averaged, and matched with a simultaneous reading from a nearby area with no canopy. Available PPFD was calculated as % of full PPFD (Messier and Puttonen 1995). Full PPFD readings were made using a portable integrating radiometer in 2006 and 2007, and with a quantum sensor (model LI-190SB, LI-COR Inc., Lincoln, NE, USA) in 2008.

Soil temperature at rooting depth (10 cm) was measured at five equidistant points (10 m) in the center of each plot, with individual dataloggers (Watchdog dataloggers, Spectrum technologies, Inc., IL, USA) (Figure 1). Temperature was monitored in 2007 with one measurement every 15 minutes, and data was downloaded at each sampling period. Growing degree-days at ≥ 5 °C were calculated in 2007 for each plot. Composite soil samples (organic and mineral) from five sampling points, concomitant to temperature readings, were collected, dried and ground to pass through a 2-mm mesh screen. Extraction of NH_4-N and NO_3-N was made on fresh soil samples, with a 2mol/L KCl solution and measured colorimetrically by spectrophotometry (Lachat Quickchem 8000, Zwellenger Instruments, Milwaukee, WI, Method No. 13-107-06-2-C). Extractable P, K, Ca and Mg were extracted with a Mehlich-III solution (Sen Tran and Simard 1993) and were measured by inductively coupled plasma analysis ICAP-OES (Inductively Coupled Argon Plasma-Optical Emission Spectrometry, Optima 4300 DV, Perkin-Elmer, Norwalk, CT, USA). Composite samples of organic and mineral soil were taken near the seedlings (one per species) to evaluate the volumetric soil water content (SWC) for each physiological measurement period in 2006 (one period) and 2008 (four periods) (Figure 1).

2.4 Physiological measurements

Physiological measurements were conducted before the application of the harvest treatments (August 3-7 2006) and for the two years following harvest. Three sampling periods were completed in 2007 (July 5-7 and 23-25, August 22-30) and data were collected at four sampling periods in 2008 (June 26th, July 26-28, August 7-8 and 22-25). Predawn and midday water potentials (Ψ_{pd}, Ψ_{md}), photosynthesis (A), transpiration (E) and stomatal conductance to water vapor (g_{wv}) were measured on one lateral shoot of a black spruce advance regeneration layer between 1 and 2 m in height (BS) and on a few leaves of *Rhododendron* (RG) on the upper third of the crown (Paquin et al. 1999). For black spruce, current and one year old needles were measured, but to ensure valid comparisons between black spruce and *Rhododendron*, only current needle results were used. For the first sampling periods of both 2007 and 2008, only water potential measurements were taken because current year foliage on black spruce was not sufficiently developed, and due to logistical constraints, only Ψ_{md} was measured at the August 7-8 period in 2008.

A, *E*, g_{wv} were measured *in situ* on current year foliage of one *Rhododendron* plant (RG), and on current needles of one black spruce advance regeneration layer (BS) in each plot (Figure 1). Needles and leaves were measured at the same phenological stage in all treatments for each measurment period. Measurements were made on sunny or partly cloudy days preceded by a day without rain. Gas exchange and vapor pressure deficit (VPD) measurments were carried out with a LI-6250 (2006 measurements) and a LI-6400 (2007-2008 measurements) portable photosynthesis systems (LI-COR, inc. Lincoln, NE, USA), both equipped with a 0.25 L cuvette. A halogen lamp was placed approximately 15 cm above the cuvette to provide saturating light (> 1200 µmol photons m^{-2} s^{-1}). Ambient CO_2 was fixed in 2007 and 2008 at 370 ppm. We measured *A* four times in one minute period after sample *A* saturation for at least a minute. Measurements were made between 8:30 and 13:00 E.T. Each experimental block was measured in less than two hours. Foliar surface area for BS was measured by the volume displacement technique (Brand 1987). For RG, foliar surface area was calculated by image analysis using WinFolia (Regent Instruments Inc., Quebec, Canada). Samples were oven dried at 65˚C for 48 hours and then weighed to determined leaf mass per unit of area (LMA).

For Ψ_{pd} and Ψ_{md}, measurements were taken on an excised shoot of two plants of both species put in open plastic bags and placed in a cooler filled with ice packs and water. Water potential was determined with the pressure chamber technique (PMS instruments, Corvallis, OR, USA) (Scholander et al. 1965). All shoots in the same block were sampled within 30 minutes, and measured within 45 minutes following excision. For Ψ_{pd}, all three blocks were measured during the same night, approximately 2-3 hours before dawn, and for Ψ_{md}, plants were measured during the same period as measures of *A*, *E* and g_{wv}.

2.5 Foliar nutrients

At each sampling period, current year foliage from plants (RG and BS) selected for *A*, *E* and g_{wv} was harvested to evaluate foliar nutrient concentration and content. Nutrient content was calculated by multiplying nutrient concentration × dry mass of 100 needles

(BS) or five leaves (RG). Samples were stored in a freezer until analysis and then oven-dried at 65˚C for 48 hours before grinding to a 40-mesh size screen. Total Kjeldahl N was analyzed colorimetrically by spectrophotometry, preceded by H_2SO_4-Se-K_2SO_4 digestion. P, K, Ca, Mg were measured by inductively coupled plasma analysis.

2.6 Nutrient and water use efficiency

Instantaneous water use efficiency (iWUE) was calculated by dividing photosynthesis by transpiration rate (*A*/*E*). Photosynthetic nitrogen and phosphorus use efficiency (NUE and PUE) were calculated by dividing *A* by the foliar nutrient content.

2.7 Statistical analyses

Analysis of variance (ANOVA) or analysis of variance for repeated measures (ANOVAR) for a split-split-split plot design were used for all variables, with harvesting treatment as the main plot level (TT, PT, CPPTM, CPRS, control (C)), species (BS, RG) at the subplot level, sampling year at the sub-subplot level, and sampling year nested in the sampling period (sub sub sub-plot level). An unstructured (UN) or autoregressive (AR) covariance structure was used if sampling dates were correlated with each other. Otherwise, a regular ANOVA was performed. ANOVA or ANOVAR were performed with the MIXED procedure of SAS 9.1 (SAS Institute, Cary, NC, USA).

We used a modified BACI design (Before-After-Control-Impact) following Underwood (1994), which includes a temporal replication in order to control for annual climatic variation (Figure 1). For any given variable, when a significant sampling year × species interaction was found, we performed *t* tests between year and harvest treatments to assess differences between the pre-harvest and post-harvest levels, the pre-harvest treatment considered as a control. A significant change in control plots between pre- and post-harvest years levels implied seasonal effects. With this approach, harvesting effects were not expected to be significant in 2006, as all plots were still undisturbed. Finally, a significant harvest × sampling year interaction implied varying harvest effects from one year to another. Differences among harvest treatments were determined by a priori contrasts (Steel and al. 1997) and Bonferroni correction of α was used when the number of contrasts exceeded the number of degrees of freedom (Chen et al. 2006).

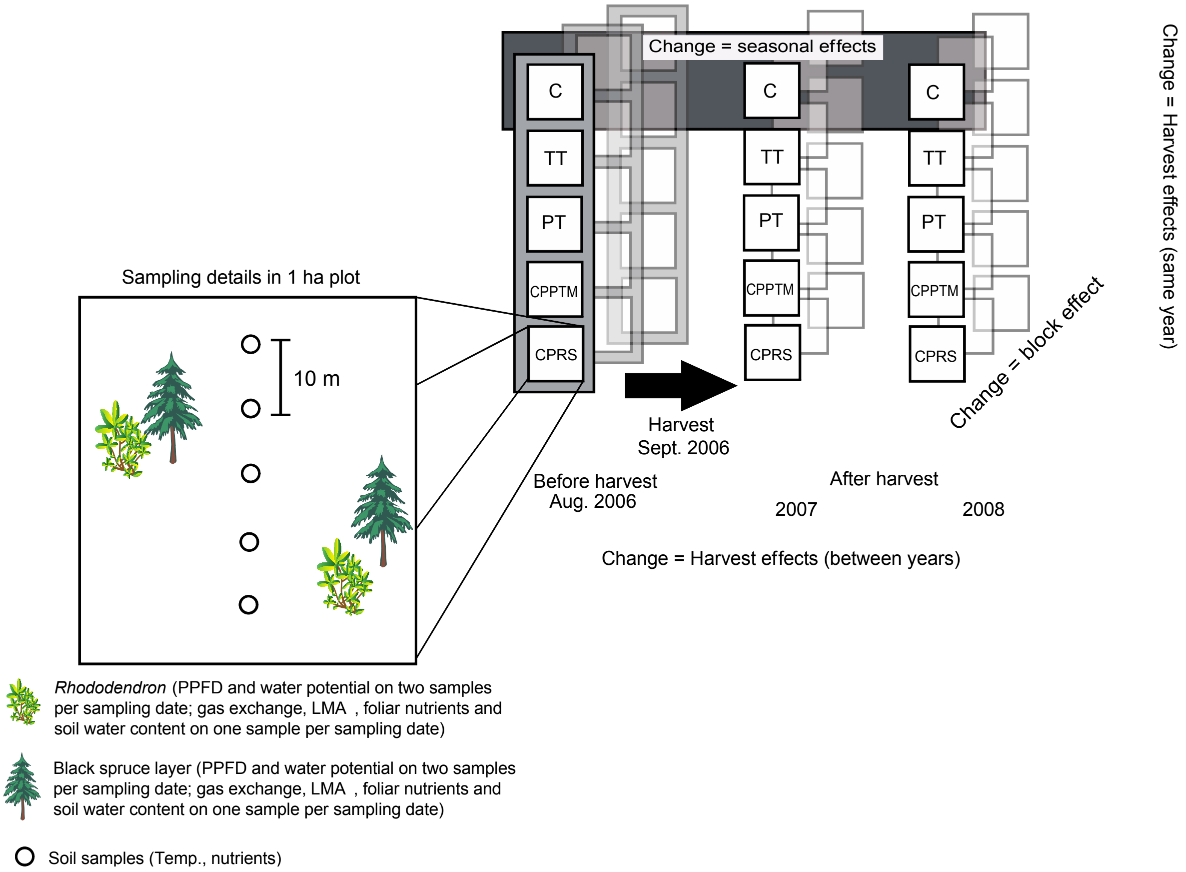

Figure 1: Conceptual representation of the BACI (Before-After-Control-Impact) design used for this study, and details of the sampling approach in one plot. Each box represents a harvest plot. C = control. TT = temporary skid trail harvest. PT = permanent skid trail harvest. CPPTM = careful logging around advance growth (dhb < 13 cm). CPRS = careful logging around advance growth (dhb < 9 cm).

Correlations among variables were tested with the REG procedure of SAS and significant correlations were used to make regression models by linear fitting. Analysis of covariance (ANCOVA) was performed to test differences between regression models for the two species with block effect taken in account ($P < 0.05$).

Normality and homoscedasticity of variance were verified for all data by examining visual distribution of data and by analysis of residues (Devore and Peck 1994). Natural logarithmic or square root transformations were made when necessary. Back-transformed means and confidence intervals with bias correction are presented (Ung and Végiard 1988, Végiard and Ung 1993).

3. Results

3.1 Environmental modification in response to harvest treatments

Seasonal soil temperature (average between May and September 2007) was higher by at least 23 % on the CPRS compared to other treatments (data not shown) but the sum of degree-days (597.8 ± 109.1) was similar between treatments in 2007. Soil water content (SWC) was not modified by any of the harvest treatments (constant before and two years after all harvest treatments); average SWC was 34.8 ± 13.5 % in the humus layer and 49.0 ± 9.8 % in the surface mineral horizon. Mean photosynthetic photon flux density (%PPFD) was the highest in the CPRS treatment, followed by CPPTM and the two partial harvest treatments (TT, PT). Percent PPFD in CPPTM was similar to that measured in the TT and PT treatments for three of the sampling periods; all harvest treatments were characterized by higher %PPFD than the control plots (Table 1, Figure 2). Forest floor and mineral soil variables (C/N, pH, total C, N, NH_4^+, NO_3^-, P, K, Ca, Mg, CEC) were not significantly influenced by harvest treatments in 2007 and 2008 (results not shown).

3.2 Morphology and physiology of Rhododendron and black spruce under harvest treatments

We noted a significant interaction among species and sample date (nested in years) affecting LMA (Table 1). *Rhododendron* LMA tended to be higher two years after harvest but this increase was not significant. Black spruce LMA was higher in 2007, but in 2008, LMA was similar to pre-harvest results (Figure 3a). Photosynthesis (A) was higher for *Rhododendron* after harvest (2007-2008); photosynthesis of black spruce decreased after harvest by 50 % but the difference was not statistically significant (Table 2, Figure 3b). The assimilation rate of *Rhododendron* was 63 % higher during the 2007 growing season compared to 2006, and remained constant in 2008. Stomatal conductance (Figure 3c) and transpiration (results not shown) were significantly higher for *Rhododendron* than for black spruce after harvest (Table 2). The g_{wv} of *Rhododendron* increased during the first year after harvest (2007) and again in the second year after harvest (2008); g_{wv} of *Rhododendron* was about three times higher than that of black spruce in 2007 and 2.5 times higher in 2008 (Table 2, Figure 3c). A similar trend between the two species was observed for E (results not shown). *Rhododendron* experienced higher predawn (Ψ_{pd}) and midday (Ψ_{md}) water potentials than black spruce, except Ψ_{pd} for two sampling periods (August 3-7 2007 and August 22-30 2008) where no difference between species was noted (Table 2, Figure 4).

Table 1: Summary of ANOVA results for selected physiological and morphological parameters measured on black spruce (BS) and *Rhododendron groenlandicum* (RG) under variable intensity of canopy removal in northeastern Quebec Canada. N = foliar nitrogen concentration P = foliar phosphorus concentration NUE = nitrogen use efficiency PUE = phosphorus use efficiency %PPFD = % of photosynthetic photon flux density, LMA = leaf mass per unit of area.

Source of variation (fixed)	ndf	N		P		NUE^{b}		PUE^{b}		% PPFD^{a}		LMA^{a}	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Harvest treatment (HT)	4	3.06	**0.030**	1.91	0.130	0.89	0.480	0.16	0.968	16.03	< **0.001**	2.51	0.065
Year (Y)	2	14.45	< **0.001**	13.58	< **0.001**	1.39	0.247	0.47	0.629	18.09	< **0.001**	3.21	0.055
HT *Y	8	1.93	0.087	1.44	0.210	3.67	**0.016**	0.64	0.741	1.98	0.104	1.24	0.312
Sample date(year) (SD(Y))	3	3.11	**0.038**	11.18	< **0.001**	3.79	**0.032**	4.47	**0.006**	17.81	< **0.001**	12.98	< **0.001**
HT*(SD(Y))	12	1.16	0.340	1.20	0.296	1.13	0.366	0.98	0.479	4.27	< **0.001**	0.31	0.981
Species (S)	1	925.85	< **0.001**	12.26	< **0.001**	2.26	0.100	35.75	< **0.001**	0.09	0.765	251.30	< **0.001**
S*HT	4	1.06	0.385	0.93	0.451	1.22	0.311	1.88	0.126	1.06	0.383	1.14	0.355
S*Y	2	6.15	**0.005**	1.06	0.350	56.48	< **0.001**	39.81	< **0.001**	0.32	0.571	7.75	**0.002**
S*Y*HT	8	1.31	0.272	1.05	0.407	1.54	0.193	1.04	0.420	0.11	0.977	0.63	0.751
S*(SD(Y))	3	0.65	0.589	0.62	0.601	0.14	0.934	0.04	0.987	0.66	0.520	1.36	0.274
S*HT*(SD(Y))	12	0.52	0.888	0.70	0.746	0.78	0.668	0.74	0.704	1.76	0.103	1.79	0.101

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

[b] Analysis performed on sqrt-transformed data.

Table 2: Summary of ANOVA results for selected physiological parameters measured on black spruce (BS) and *Rhododendron groenlandicum* (RG) under variable intensity of canopy removal in northeastern Quebec Canada. A = photosynthesis g_{wv} = stomatal conductance Ψ_{pd} = predawn water potential Ψ_{md} = midday water potential iWUE = instantaneous water use efficiency.

Source of variation (fixed)	ndf	A		g_{wv}^{a}		Ψ_{pd}^{a}		Ψ_{md}		iWUE^{b}	
		F	*P*	*F*	*P*	*F*	*F*	*F*	*P*	*F*	*P*
Harvest treatment (HT)	4	0.19	0.941	1.53	0.208	2.18	0.108	2.21	0.075	2.14	0.091
Year (Y)	2	1.26	0.294	4.92	**0.011**	14.93	**< 0.001**	18.26	**< 0.001**	12.08	**< 0.001**
HT *Y	8	1.09	0.388	1.31	0.260	0.63	0.745	0.66	0.721	0.25	0.978
Sample date(year) (SD(Y))	2^{d}	7.36	**0.003**	1.88	0.163	23.03	**< 0.001**	8.49	**< 0.001**	9.42	**0.003**
HT*(SD(Y))	8^{e}	0.70	0.685	0.56	0.802	1.13	0.335	0.63	0.877	0.77	0.620
Species (S)	1	180.97	**< 0.001**	187.29	**< 0.001**	98.65	**< 0.001**	203.17	**< 0.001**	27.66	**< 0.001**
S*HT	4^{f}	0.26	0.899	1.48	0.221	1.61	0.177	0.40	0.810	0.45	0.769
S*Y	2	15.80	**< 0.001**	38.32	**< 0.001**	0.42	0.661	0.56	0.574	0.00	0.996
S*Y*HT	8	0.87	0.554	1.04	0.420	1.35	0.228	0.81	0.594	1.15	0.350
S*(SD(Y))	2^{g}	2.99	0.084	0.39	0.682	6.43	**0.001**	2.80	**0.022**	2.10	0.133
S*HT*(SD(Y))	8^{h}	1.14	0.393	1.30	0.265	0.67	0.817	0.90	0.592	0.69	0.696

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

[b] Analysis performed on sqrt-transformed data.

[d] ndf = 5 (Ψ_{pd}. Ψ_{md}). [e] ndf = 16 (Ψ_{pd}). 20 (Ψ_{md}). [f] ndf = 5 (Ψ_{pd}). 4 (Ψ_{md}). [g] ndf = 4 (Ψ_{pd}). 5 (Ψ_{md}) [h] ndf = 16 (Ψ_{pd}). 20 (Ψ_{md}).

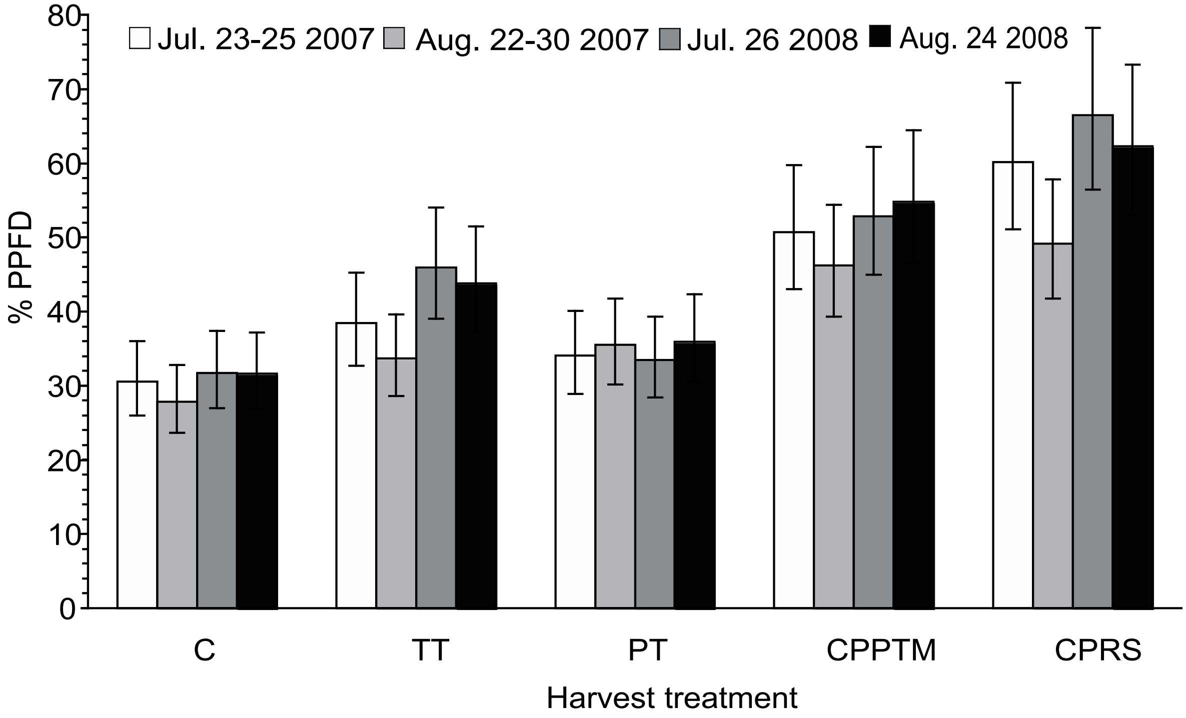

Figure 2: Harvest treatment effects on mean % photosynthetic photon flux density (%PPFD) in 2007 and 2008. Refer to Table 2 for treatment descriptions. Analysis performed on ln-transformed data; back transformed means and 95 % confidence interval approximates are presented (Ung and Végiard, 1988).

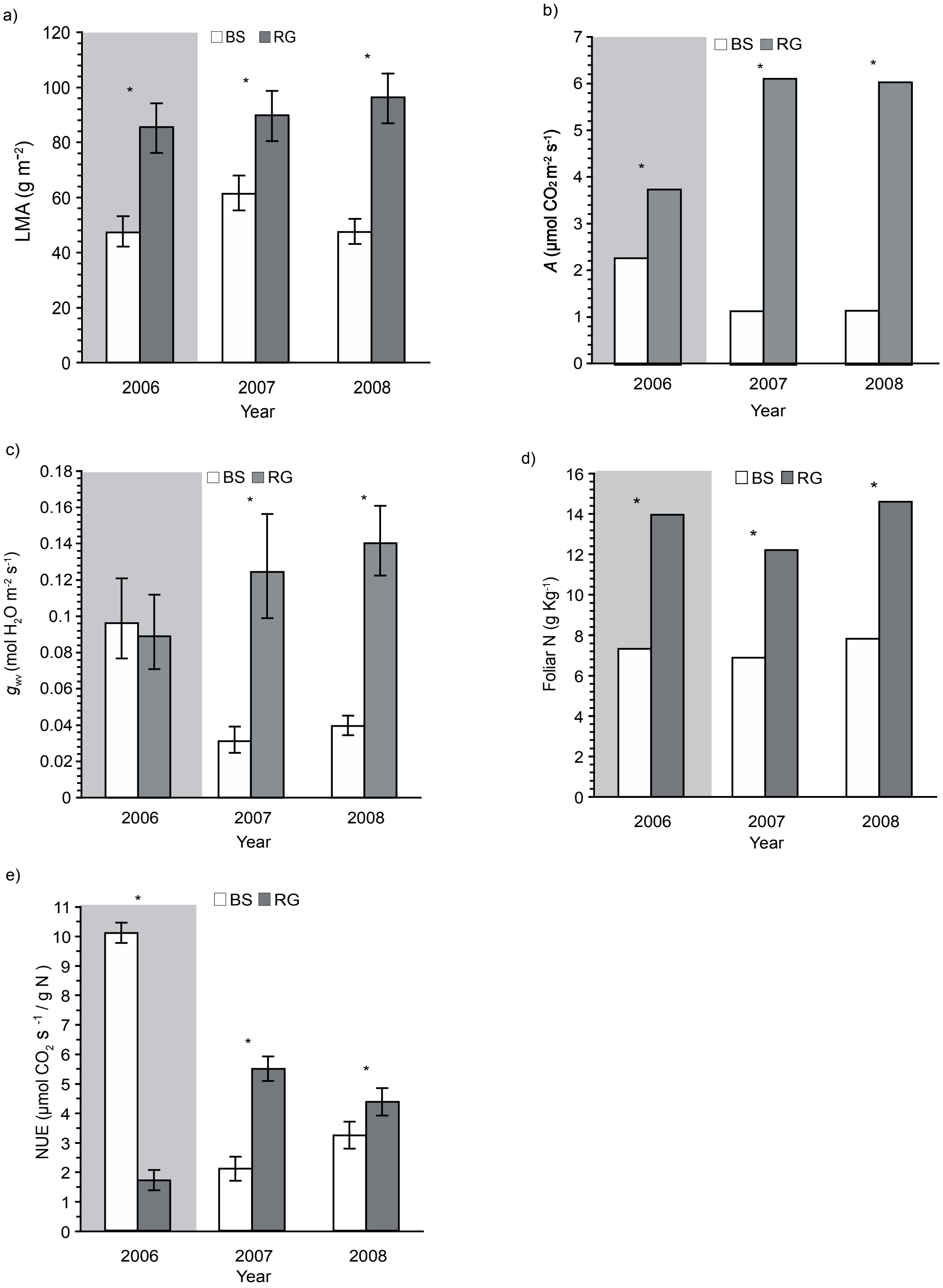

Figure 3: Growing season and species effects on selected physiological and morphological variables. Stars represent significant differences ($P \geq 0.05$) between black spruce (BS) and *Rhododendron groenlandicum* (RG). Grey area represents pre-harvest sampling period. Analysis performed on ln-transformed data (LMA, g_{wv}) or square-root transformed data (NUE and PUE); back transformed means and 95 % confidence interval approximates are presented (Ung and Végiard, 1988).

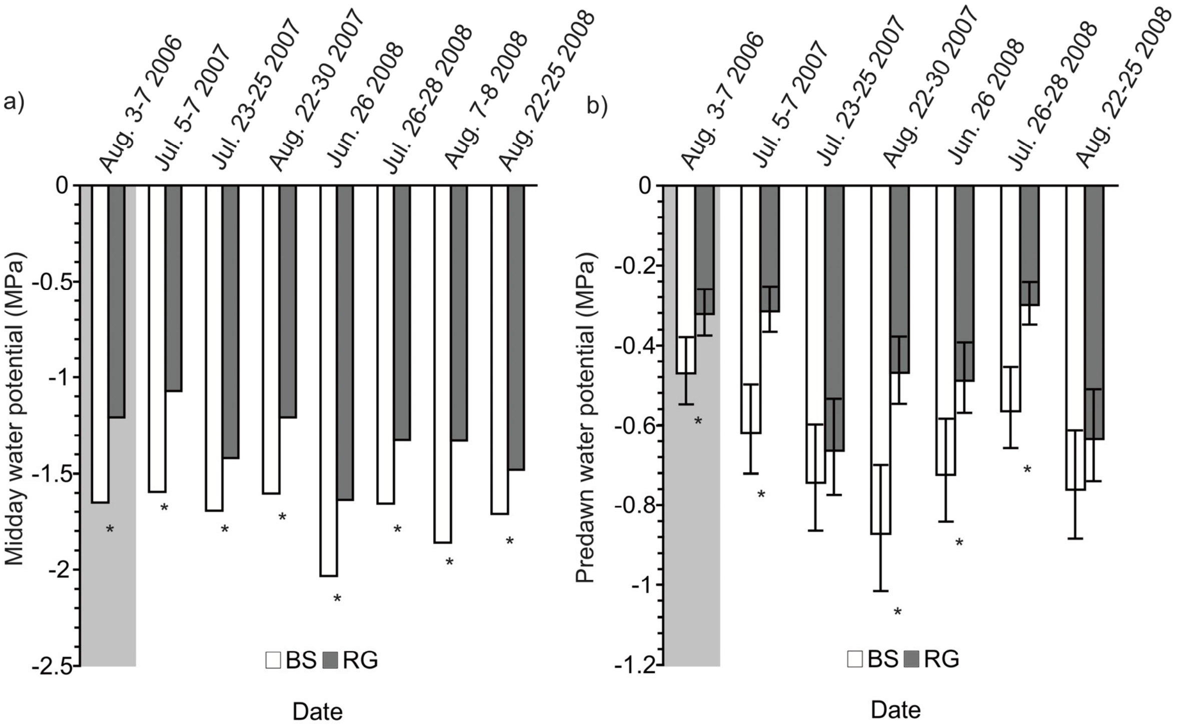

Figure 4: Sampling date and species effects on midday (a) and predawn (b) water potential. Stars represent significant differences ($P \geq 0.05$) between black spruce (BS) and *Rhododendron groenlandicum* (RG). Grey area represents pre-harvest sampling period. For predawn water potential, analysis was performed on ln-transformed data; back transformed means and 95 % confidence intervals approximates are presented (Ung and Végiard, 1988).

3.3 Foliar nutrients

A significant year × species interaction was noted for N concentration (Table 1) and content (results not shown). Foliar N concentrations of black spruce were similar in 2006, 2007, and 2008; these levels were lower than those for *Rhododendron* both before and two years after harvest (Figure 3d). Foliar N concentration of *Rhododendron* decreased in 2007 and then increased in 2008 to the levels measured before harvest (Figure 3d).

3.4 Resource use efficiency

Year × species interaction was significant for N and P use efficiency (NUE, PUE; Table 2). NUE was 3.8 times higher for black spruce than *Rhododendron* before harvest (2006), but the opposite effect was observed in 2007; NUE of *Rhododendron* was about 1.7 times higher than that of black spruce (Figure 3e). No difference was observed between species in 2008. The same trend was found for PUE (results not shown). Instantaneous water use efficiency (iWUE) was 42 % higher in *Rhododendron* throughout the duration of the measures (results not shown).

3.5 Relationships among physiological parameters

Photosynthesis declined with increasing C_i more steeply for *Rhododendron* than for black spruce, and the same trend was observed between iWUE and C_i, where the slope was steeper for black spruce (Figure 5a,c); the opposite trend was remarked between A and LMA (Figure 5b). We also found that LMA increased as foliar N concentration increased (Figure 5d).

Table 3: Summary of ANCOVA results for selected regression variables measured on black spruce (BS) and *Rhododendron groenlandicum* (RG), under variable intensity of canopy removal in northeastern Quebec, Canada A = photosynthesis, iWUE = instantaneous water use efficiency, C_i = intercellular CO_2 concentration, LMA = leaf mass per unit of area.

Source of variation (fixed)	ndf	A vs C_i		A vs LMA		iWUE vs C_i	
		F	*P*	*F*	*P*	*F*	*P*
Species (S)	1	41.40	**< 0.001**	0.05	0.829	3.50	0.063
X variable	1	69.90	**< 0.001**	18.14	**< 0.001**	119.69	**< 0.001**
S*X variable	1	18.46	**< 0.001**	5.47	**0.021**	5.02	**0.027**

Table 4: Regression equations for selected physiological parameters measured on black spruce (BS) and *Rhododendron groenlandicum* (RG), under variable intensity of canopy removal in northeastern Quebec, Canada A = photosynthesis, iWUE = instantaneous water use efficiency, C_i = intercellular CO_2 concentration, LMA = leaf mass per unit of area. Foliar N = foliar nitrogen concentration.

Species	Y variable	X variable	Slope	Intercept	*F*	*P*	R^2
BS	A	C_i	-0.011	4.525	39.31	**< 0.001**	0.3112
BS	A	LMA	0.015	0.397	5.12	**0.026**	0.0562
BS	iWUE	C_i	-0.014	5.436	118.12	**< 0.001**	0.5758
RG	A	C_i	-0.033	14.261	38.74	**< 0.001**	0.3081
RG	A	LMA	0.047	0.705	20.38	**< 0.001**	0.1916
RG	iWUE	C_i	-0.010	4.491	50.65	**< 0.001**	0.3680
Both	LMA	Foliar N	3.730	35.834	50.03	**< 0.001**	0.2233

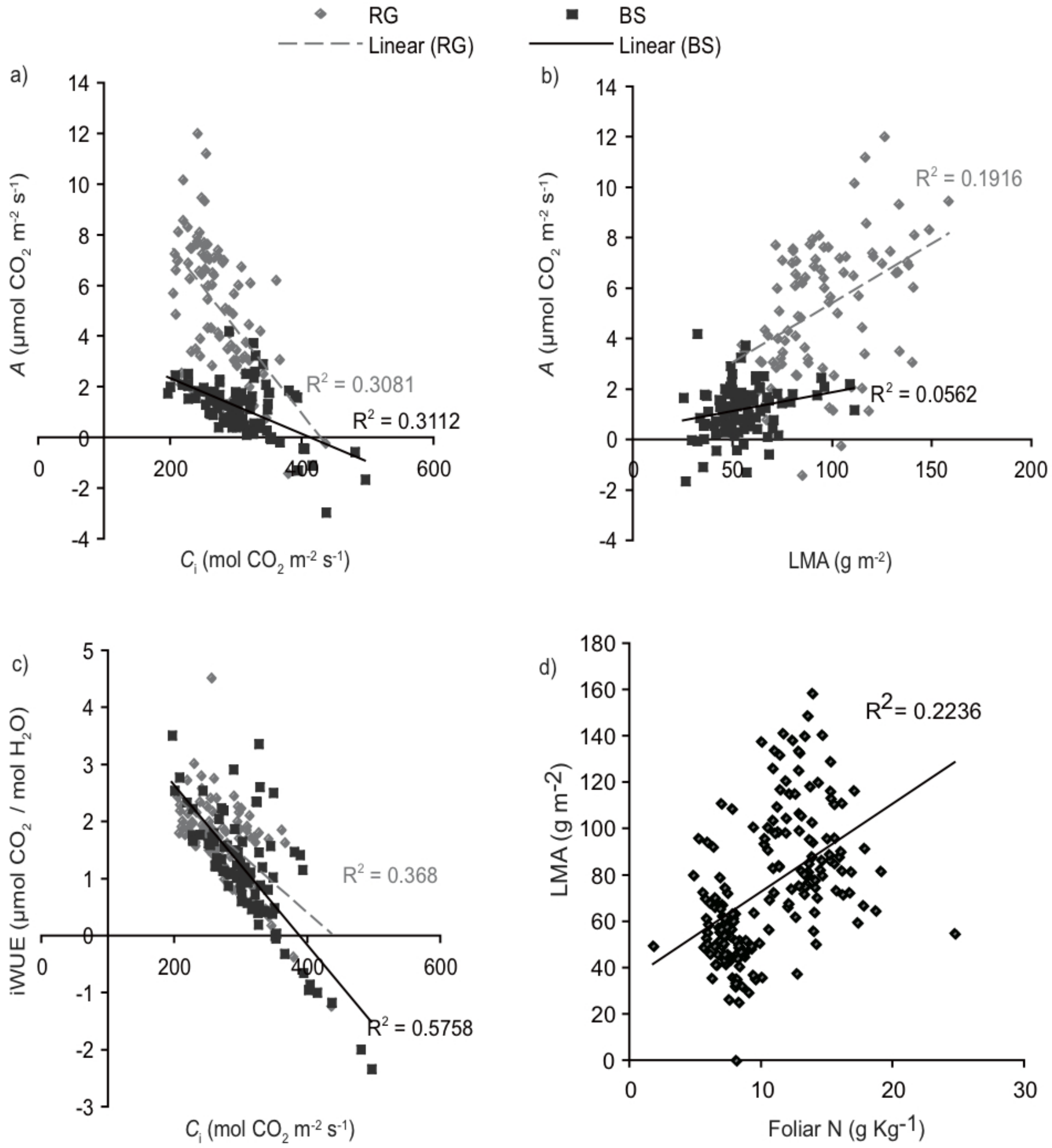

Figure 5: Relationship between selected physiological parameters for black spruce (BS) and *Rhododendron groenlandicum* (RG) (a,b,c) and on both species (d) established on a gradient of canopy removal treatments in northeastern Quebec, Canada. Refer to Table 4 for regression equations, *F* and *P* values.

4. Discussion

Light levels (%PPFD) measured in the harvest treatments were the result of differences in harvest intensity. Only in the CPRS treatment were the light levels sufficient for both species to achieve maximum photosynthesis rate (700 µmol m^{-2} s^{-1} for black spruce and 740 µmol m^{-2} s^{-1} for *Rhododendron*; Small 1972, Dang et al. 1991). Similar %PPFD between partially harvested and control plots was due, in part, to the pre-harvest stand structure and to the harvest prescription itself (see Ruel et al. 2007). The harvest treatments were designed to manage old, irregularly-structured mixed black spruce-balsam fir (*Abies Balsamea* L. [Mill]) stands with a wider range of DBH classes than that of the stands used in this study. Pre-harvest stand structures in the present study were characterized by a high proportion of trees with a DBH lower than 13 cm, restricting harvest levels.

We expected the harvest treatments to influence soil resource availability early after harvest (Titus et al. 2006), but the high frequency of precipitation events that occurred in this region in 2007 and 2008 could have masked the differences among treatments. Even if soil N availability measured punctually remained constant, harvest treatments could have accentuated N mineralization by increasing soil temperature, and contributing to higher foliar N. Black spruce foliar N concentration and the sum of growing degree-days revealed that it was not the case (Titus et al. 2006).

The higher photosynthesis rates of *Rhododendron* following harvest (in 2007 and 2008), result from the higher light availability created by canopy removal and by the leaf trait characteristics of this species. Humbert et al. (2007) classified *Rhododendron* as a relatively shade-intolerant species (light index of 7/9; 9 being shade-intolerant). Leafs traits measured on *Rhododendron* corroborate this classification; we measured a higher foliar N content, photosynthetic and stomatal conductance rate and leaf mass per area (LMA) than black spruce (Givnish 1988). This high plasticity of *Rhododendron* leaf functional traits, an important feature in the success of competitive species, allowed achievement of a higher water potential that could sustain increased stomatal conductance associated with the higher photosynthesis rate after harvest. Furthermore, the rapid acclimation of *Rhododendron* allows a maximal rate of water utilization when readily available, and a rapid adjustment in physiological performance if conditions become unfavorable (Stratton and Goldstein 2001).

Conversely, the new light conditions created by harvest did not reduce black spruce photosynthesis rate. The absence of morphological acclimation of black spruce, indicated by similar values of low LMA leaves before and after harvest, could result in damaged photosynthetic systems and diminished quantum efficiency with excess light availability following canopy removal (Osmond 1994). The lower stomatal conductance of black spruce after harvest does, however, indicate physiological acclimation. In accordance with Grossnickle and Blake (1986), we found that stomatal conductance of black spruce was regulated to a greater extent by vapor pressure deficit ($R^2 = 0.3299$, $P < 0.001$) than by water potential after harvest; vapor pressure deficit increased after harvest. However, this lower stomatal conductance did not result in a reduced photosynthesis rate after harvest, possibly because photosynthetic capacity was already at a maximum rate before harvest. Fifteen years after harvest, Paquin et al. (1999) reported values of A similar to those observed in our study. This implies that photosynthesis of black spruce needles (with low LMA) was limited by quantum efficiency rather than by stomatal closure.

Variation of instantaneous nutrient use efficiency for both species after harvest resulted from a change in photosynthetic rate rather than a modification of foliar nutrients. This is particularly true for black spruce needles, favoring N allocation to light-harvesting complexes, which could be damaged by photoinhibition (Osmond 1994, Rosati et al. 1999). Contrasting results for *Rhododendron* demonstrated a more efficient response to the changing environment. Nitrogen use efficiency increased after harvest due to a higher photosynthesis rate induced by a higher available %PPFD. Longer term NUE of black spruce could be higher if measured on a residence time basis (longer leaf life span), versus the lower instantaneous measurement of NUE measured for black spruce here.

Absence of a trade-off between NUE and WUE (both long-term and instantaneous) is an indication that: 1- harvest treatments created a light gradient that did not modify water and nutrient availability and, by extent, did not affect either plant water relations or nutrient foliar concentrations (Kranabetter and Simard 2008) or that 2- a higher NUE does not necessarily lead to lower WUE (Livingston et al. 1999). For black spruce, photosynthesis rate was not influenced by water or nutrient stress, but rather by a limitation of the photosynthetic apparatus of the low LMA leaves. This was also true for *Rhododendron;* higher light availability resulted in increased photosynthetic capacity with no significant change in resource availability.

In conclusion, we observed that *Rhododendron* showed more rapid physiological and acclimation than black spruce to increasing resources related to canopy removal (higher gas exchange parameters, water potential, resource use efficiency, nutrient foliar content and higher LMA). This faster acclimation is an important aspect in the success of invasive species to maximize their rates of resource utilization when resources are available (Stratton and Goldstein 2001). The acclimation of black spruce was limited to decreased photosynthesis rates and stomatal conductance, which was regulated more by quantum efficiency than by stomatal closure. This could be an indication of a future advantage of *Rhododendron* in these stands following partial harvest treatments that conserve irregular stand structure and protect black spruce advance regeneration. Therefore, we believe that partial cutting in this type of forest condition (black spruce-dominated with ericaceous shrub understory) will not contribute to regeneration success. More intensive, silvicultural treatments, imitating more severe disturbance (and therefore slowing shrub development) could potentially be used to manage these stands within a framework of to ecosystem-based management.

5. Acknowledgements

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Chapitre 2

Ericaceous shrubs affect black spruce physiology independently from inherent site fertility

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ABSTRACT

Vegetative layering of black spruce (*Picea mariana* [Mill.] BSP) is the principal mode of regeneration for over mature, uneven-aged stands subject to long fire cycles (> 300 years) in northeastern Québec, Canada. However, growth response of black spruce layers following disturbance by fire or harvest can be slow, due to a lag of morphological acclimation and potential nutrient limitation. This phenomenon can be accentuated if black spruce is associated with ericaceous shrubs such as *Kalmia angustifolia* and *Rhododendron groenlandicum*, which are known to interfere with conifer growth through direct and indirect competition. Such interactions can result in productive stands being converted to unproductive heathlands. It is not known whether these effects of ericaceous shrubs on black spruce are accentuated on low fertility sites, or if the impacts are independent of inherent site fertility. The objectives of this study were to evaluate the effects of ericaceous shrubs on both resource availability and on functional traits of black spruce advance regeneration across a gradient of site fertility (as defined by a site classification system). We monitored black spruce advanced regeneration physiology and soil nutrient availability over two growing seasons on a gradient of ecological site types in northeastern Québec (Canada). The eradication of competing vegetation favored higher soil NH_4-N and K availability, with increases of 67 % and 28 % compared to control conditions, respectively. Black spruce photosynthesis rate (*A*) and foliar K content were higher in plots where vegetation was eradicated, compared to the control plots, but did not vary among ecological site types. Photosynthesis did not appear to be limited by nitrogen or water relations, but was possibly limited by a deficit of foliar K^+, probably resulting from reduced availability following sequestration by the ericaceous root systems. The absence of interaction between inherent site fertility and the eradication of ericaceous shrubs suggests that vegetation management of ericaceous shrubs must be planned independently from the ecological site type.

RÉSUMÉ

Dans les peuplements inéquiens et irréguliers du sous-domaine de la pessière noire à mousses de l'Est du Québec, sujets à de longs cycles de feux (plus de 300 ans), le marcottage est le mode de reproduction principal de l'épinette noire (*Picea mariana* [Mill.] BSP). Par contre, la réponse de croissance des marcottes de cette espèce après coupe peut être lente et possiblement provoqué par un délai dans l'acclimatation morphologique et par une limitation en nutriments. Ce phénomène peut être accentué s'il y a présence d'arbustes éricacées comme *Kalmia angustifolia* et *Rhododendron groenlandicum* qui sont réputés pour nuire à la croissance des conifères par une compétition directe et indirecte. Ces interactions entre la régénération naturelle et les éricacées peuvent résulter en une conversion d'un peuplement résineux en une lande improductive. Il est difficile d'établir si les effets néfastes des éricacées sur l'épinette noire sont accentués dans les milieux moins productifs ou si les effets sont indépendants de la qualité intrinsèque de la station. Les objectifs de cette étude sont d'évaluer les effets des éricacées sur la disponibilité des ressources et sur les traits fonctionnels de la régénération naturelle de l'épinette noire, et ce, dans un gradient de fertilité de station (tel que défini par le système de classification écologique). Nous avons mesuré la physiologie des marcottes d'épinette noire et la disponibilité des éléments nutritifs du sol pendant deux saisons de croissance sur un gradient de fertilité de station. L'éradication complète de la végétation de compétition a augmenté la disponibilité en NH_4-N et K du sol, avec des augmentations de 67 % et 28 % comparativement aux parcelles témoin. Le taux de photosynthèse (*A*) et le contenu foliaire en K étaient plus élevés dans les parcelles sans compétition, peu importe la qualité de la station. La photosynthèse n'a pas semblé être limitée par la disponibilité de l'azote ou de l'eau, mais possiblement par un déficit en K foliaire, résultant possiblement d'une diminution provoquée par la séquestration du système racinaire des éricacées. L'absence d'interaction entre la fertilité de la station et l'éradication des éricacées suggère que le contrôle de la végétation éricacée doit être planifiée indépendamment de la qualité de la station.

1. Introduction

Under long fire cycles, black spruce (*Picea mariana* [Mill.] B.S.P.) regeneration in the eastern Canadian boreal forest mainly occurs by layering, i.e. rooting of low branches in the surface soil (Viereck et al., 1990). Black spruce layers respond positively to increased light availability created by canopy removal during harvest, with a lag of 5–8 years on mesic sites due to physiological acclimation and potential nutrient deficiency (Paquin et al., 1999; Prévost and Dumais, 2003). Following disturbance that opens the canopy, black spruce regeneration is often associated with the presence of ericaceous shrubs such as *Kalmia angustifolia* L. (hereafter referred as *Kalmia*) and bog Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd, or *Ledum groenlandicum*). *Kalmia* and bog Labrador tea (hereafter referred as *Rhododendron*) can establish and grow on a wide range of edaphic conditions in the eastern Canadian boreal forest, and their growth is stimulated by disturbances that increase light availability (Mallik, 1993; Laberge-Pelletier, 2007). Site encroachment by ericaceous shrubs can lead to decreased growth of black spruce regeneration (Mallik, 2001; Bloom and Mallik, 2004). Current harvest methods commonly applied that minimize soil disturbance, such as careful logging around advance growth, may be expected to stimulate rhizomatous growth of *Kalmia* and associated species through increased light availability.

Various mechanisms have been suggested to explain ericaceous interference with conifer growth. Stagnant growth of black spruce seedlings has been linked to direct nutrient competition (Inderjit and Mallik, 1996). Furthermore, mycorrhizae of *Kalmia* can assimilate sequestered forms of nitrogen that are not readily available to conifers (Yamasaki et al., 1998). *Kalmia* and *Rhododendron* litter is rich in secondary compounds that form stable complexes with proteins and in turn, reduce nitrogen mineralization and microbial activity (Inderjit and Mallik, 1996; Joanisse et al., 2007). As a result, long-term site occupancy by ericaceous shrubs can change soil physical and chemical properties, so that productive forests are converted into unproductive heathlands, a process that could be faster on poorer sites (Mallik, 1995; Bradley et al., 1997). Past studies on interactions between *Kalmia* and black spruce growth showed that site fertility ostensibly plays a significant role in the competitive ability of both species; *Kalmia* reduced humus N mineralization rate to a greater extent on lower fertility sites (Bradley et al., 1997; Yamasaki et al., 2002).

No study has yet investigated the effects of ericaceous shrub on conifer physiology across a gradient of inherent site fertility. Yamasaki et al. (2002) evaluated interference mechanisms between *Kalmia* and black spruce on a rich, wet site versus a dry site of lower fertility in Newfoundland (Canada). Proximity to *Kalmia* was associated with reduced humus extractable NH_4-N and reduced spruce growth on the wetter and richer site, while a direct negative effect of *Kalmia* on foliar N nutrition of spruce was observed on the drier and poorer site. However, the effects of ericaceous shrubs on conifer growth and, by extension, on ecosystem productivity, are difficult to evaluate under natural conditions, due to complex interactions between ecosystem components and due to the great variation of the environmental parameters (Nilsson, 1994). To overcome this difficulty, we decided to assess competitive impacts of ericaceous is by measuring the physiological response of the target species (in this case, black spruce advance regeneration) to its environment, with and without the presence of the competitors (Mallik, 2001; LeBel et al. 2008).

Consequently, our objective was to evaluate the effects of ericaceous shrubs (*Kalmia* and *Rhododendron*) on soil fertility and water availability across a site fertility gradient, and on the physiological and morphological responses of black spruce advance growth, 10 years after harvest. We hypothesized that ericaceous shrubs negatively affect tree physiological parameters (reduced rates of gas exchange, lower water potential and reduced nutrient foliar content) through their impacts on soil characteristics (lower soil nutrient availability), which in turn result in increased water and nutrient use efficiency. We also hypothesize that these negative impacts are aggravated when inherent site fertility is low.

2. Materials and methods

2.1 Study site description

This study was conducted in nine harvested stands of northeastern Québec (Canada), within the spruce-feathermoss bioclimatic domain (Saucier et al., 2009), ~175 km north of the city of Baie-Comeau (50°12’N, 69°36’W). All stands were harvested by the careful logging around advanced growth (’’coupe avec protection de la régénération et des sols’’, or CPRS) method between 1995 and 1996. The CPRS was carried out by a harvester equipped with a multifunctional processing head. This region has a cool climate with a mean annual temperature of 1.5˚C (± 0.9˚C) and a total precipitation of 1014 mm, of which 33 % fall as snow (Environment Canada, 2010). Three contrasting ecological site types (replicated three times each) were selected to represent an intrinsic fertility gradient typical of this region. Ecological site types were selected based on the governmental ecological classification system and characteristics are shown in Table 5.

Table 5: Site description for the three ecological site types selected in the eastern Québec's boreal forest.

Site fertility	Low	Medium	High
Ecological type[a]	RE21	RS20	RS22
Site index	12	12-15	15
% black spruce cover	> 50	> 50	> 50
% balsam fir cover	0	10-40	10-40
Deposit (texture)	Fluvioglacial outwash (coarse)	Organic or shallow till (medium)	Medium to deep coarse till (medium)
Soil profile (total depth)	Humo-ferric podzol on glacial outwashes	Humo-ferric podzol with mor humus (< 50 cm)	Humo-ferric podzol with mor humus (50-100 cm)
pH (forest floor)	2.9 ± 0.3	3.0 ± 0.1	3.1 ± 0.3
pH (mineral soil)	3.9 ± 0.5	3.5 ± 0.2	3.7 ± 0.4
Ca (mg/kg) (forest floor)	1445.00 ± 655.77	1503.42 ± 610.25	1982.50 ± 1035.13
Ca (mg/kg) (mineral soil)	47.53 ± 28.09	69.23 ± 25.83	105.96 ± 83.39
Mg (mg/kg) (forest floor)	367.29 ± 143.44	365.00 ± 135.85	375.22 ± 108.25
Mg (mg/kg) (mineral soil)	11.45 ± 4.28	19.26 ± 10.49	16.23 ± 7.92
C (mg/kg) (forest floor)	395.93 ± 125.61	425.52 ± 76.32	371.04 ± 80.86
C (mg/kg) (mineral soil)	29.83 ± 7.47	45.45 ± 21.50	32.40 ± 18.62
N (mg/kg) (forest floor)	7.08 ± 1.69	11.08 ± 2.37	9.16 ± 2.68
N (mg/kg) (mineral soil)	0.96 ± 0.23	1.60 ± 0.86	1.13 ± 0.54
C/N (forest floor)	54.61 ± 9.74	39.24 ± 6.79	41.53 ± 7.12
C/N (mineral soil)	31.18 ± 3.07	29.08 ± 3.75	27.77 ± 4.73
CEC (meq/100 g) (mineral soil)	22.87 ± 5.47	24.66 ± 8.69	20.95 ± 9.69
Drainage	Good to moderate	Good to moderate	Good to moderate
Advanced growth	Black spruce with small component of balsam fir	Black spruce with small component of balsam fir	Black spruce with small component of balsam fir
Shrub layer	Rhododendron groenlandicum [Oeder] Kron & Judd, Kalmia angustifolia L. and Vaccinium myrtilloides Michx. (about 20 % cover) associated with Vaccinium angustifolium Ait., Cornus canadensis L., Chamaedaphne calyculata (L.) Moench., Coptis groenlandica (Oeder) Fern., Gaultheria hispidula (L.) Mühl. Ex Bigel., Gaultheria procumbens L. and Maianthemum canadense Desf.	Rhododendron groenlandicum [Oeder] Kron & Judd and Chamaedaphne calyculata (L.) Moench. (about 20 % cover) associated with Kalmia angustifolia L., Vaccinium myrtilloides Michx., Vaccinium angustifolium Ait., Gaultheria hispidula (L.) Mühl. Ex Bigel., Coptis groenlandica (Oeder) Fern., and Rubus pubescens Raf.	Rhododendron groenlandicum [Oeder] Kron & Judd and Vaccinium myrtilloides Michx. (about 20 % cover) associated with Kalmia angustifolia L., Vaccinium angustifolium Ait., Gaultheria hispidula (L.) Mühl. Ex Bigel., Cornus canadensis L., Maianthemum canadense Desf. and Rubus pubescens Raf.
Moss layer	Pleurozium schreberi (Brid.) Mitt., Cladonia mitis (Standst.) Hustich, Cladonia stellaris (Opiz) Brodo, and Cladonia rangiferina (L.) Nyl. and small patches of Hylocomium splendens (Hedw.) B.S.G., Ptilium crista-castrensis (Hedw.) De Not., Rhythidiadelphus triquetrus (Hedw.) Warnst., Polytrichum spp., with some Sphagnum spp.	Pleurozium schreberi (Brid.) Mitt., and small patches of Hylocomium splendens (Hedw.) B.S.G., Ptilium crista-castrensis (Hedw.) De Not., Rhythidiadelphus triquetrus (Hedw.) Warnst., Polytrichum spp., with some Sphagnum spp.	Pleurozium schreberi (Brid.) Mitt., and small patches of Hylocomium splendens (Hedw.) B.S.G., Ptilium crista-castrensis (Hedw.) De Not., Rhythidiadelphus triquetrus (Hedw.) Warnst., Polytrichum spp., with some Sphagnum spp.

[a] As defined by Saucier et al. (2009).

2.2 Experimental design and treatments

The experimental design consisted of a split split split-plot, 3 × 2 × 4 (or 5) randomized design, replicated three times. Each replicate included three site types (one per stand), two vegetation management treatments, and four (or five) sampling periods. In each stand, a 0.25 ha square plot (50 m × 50 m) was established and a grid of 50 circular sampling points (2 m^2) was systematically distributed on five transects (10 sampling points per transect) laid out every 10 m. At each sampling point, % ericaceous cover for each species was estimated visually. In each plot, a 625 m^2 sub-plot was established in one of the four corners of the main plot (random selection of the corner). The sub-plot was subjected to complete ground vegetation eradication (except black spruce regeneration) in August 2006 with the application of a 2% (v/v) aqueous glyphosate herbicide solution (Monsanto Canada Inc., Winnipeg, Manitoba), combined with a 0.25% (v/v) Sylgard 309® silicone surfactant (Dow Corning Canada Inc., Mississauga, Ontario). Any resprouts of competitive vegetation were controlled with a second herbicide treatment in 2007.

2.3 Soil sampling

At three in each sub-plot, samples of organic forest floor (3) and mineral soil (3) (approximately 15 cm depth) were taken, and then pooled for one sample each per sub-plot. These composite samples were then used to evaluate the volumetric soil water content (SWC) and soil nutrient availability at the end of the season. Organic forest floor and mineral soil were mix with demineralized water to determine pH. Cation exchange capacity (CEC) was measured by the sum of exchangeable bases and the total acidity by a solution of $BaCl_2$ and triethanolamine. Samples were dried and ground to pass through a 2-mm mesh screen. Total Kjeldahl N (TKN) was analyzed colorimetrically by spectrophotometry (Quickchem 8000, Zwellenger Instruments, USA) preceded by H_2SO_4-Se-K_2SO_4 digestion (Sen Tran and Simard, 1993). P, K, Ca, Mg were extracted with a Mehlich III solution and measured by inductively coupled plasma analysis ICAP-61E (Inductively Coupled Argon Plasma-Optical Emission Spectrometry, Thermo Instruments, U.S.A.).

2.4 Physiological measurements

In 2007, two sampling periods were completed (17-22 July, 9-10 August) and in 2008, three measurement events were carried out (July 23rd (water potential only, see below), 5-6 August and 20-21 August). Each time, photosynthesis rate (*A*), transpiration (*E)* and stomatal conductance to water vapor (g_{wv}) were assessed on 1-year-old needles of an excised shoot located in the upper third of the crown (Paquin et al., 1999) of two black spruce layers (between 1 m and 2 m in height), in each sub-plot. Layers were selected following the quality index developed by Ruel et al. (1995); we selected only layers in the highest quality index (1), which corresponds to a layer with no stem wound, a lean angle < 60 %, a crown with a leader and more than 50 % of live foliage. Excised shoots were placed in a sealed bag with a wet sponge, and exposed to ambient light before measurements. Data were collected on sunny or partly cloudy days, preceded by at least a day without rainfall. Measurements were carried out with a LI-6400 portable photosynthesis systems (LI-COR, inc. Lincoln, NE, USA) equipped with a 0.25 L conifer chamber cuvette. A halogen lamp was placed at ~15 cm above the cuvette to provide saturating light conditions when necessary (> 1200 μmol photons m^{-2} s^{-1}). Ambient CO_2 was fixed at 370 ppm. We performed measurements between 0830 and 1300 eastern daylight saving time, within 30 minutes following excision. Foliar surface area was evaluated by volume displacement and length (Brand, 1987); samples were then oven dried at 65˚C for 48 hours, and weighed to determine leaf mass per unit of area (LMA). Predawn and midday water potentials (Ψ_{pd} and Ψ_{md}) were measured on an excised shoot of two layers on the upper third of the crown (Paquin et al. 1999), with a pressure chamber (PMS instruments, Corvallis, OR, USA) (Scholander et al., 1965). For predawn measurements, all shoots in the same block were sampled within 30 minutes, and measured within 45 minutes following excision. All three blocks were measured during the same night, approximately 1-2 hours before dawn. Midday measurements of Ψ were concomitant to A, E and g_{wv} .

2.5 Foliar nutrients

At each sampling period, seedling shoots used for A, E and g_{wv} measurements were collected to measure foliar nutrient concentration and content. Samples were stored in a freezer until analysis, and oven dried at 65˚C for 48 hours before grinding to a 40-mesh size screen. Total Kjeldahl N (TKN) was analyzed colorimetrically by spectrophotometry (Quickchem 8000, Zwellenger Instruments, USA) preceded by H_2SO_4-Se-K_2SO_4 digestion (Sen Tran and Simard, 1993). P, K, Ca, Mg were extracted with Mehlich III solution and measured by inductively coupled plasma analysis ICAP-61E (Inductively Coupled Argon Plasma-Optical Emission Spectrometry, Thermo Instruments, USA).

2.6 Resource use efficiencies

Instantaneous water use efficiency (iWUE) was obtained by dividing photosynthesis by transpiration rate (A/E). Photosynthetic nitrogen and phosphorus use efficiencies (NUE and PUE) were calculated by dividing A by the foliar nutrient content of the corresponding shoots.

2.7 Statistical analyses

Analyses of variance (ANOVA) or analyses of variance for repeated measurements (ANOVAR) for a split-split plot design were used for all variables with the ecological site type (low, medium, high fertility) as the main plot treatment, presence/absence of ground vegetation at the sub-plot level, and sampling date as the sub-sub-plot.

Based on the lower Akaike's information criterion (AIC), we selected an unstructured (UN) covariance structure if sampling dates were correlated with each other. Otherwise, a regular ANOVA was carried out. ANOVA or ANOVAR were performed with the MIXED procedure of SAS 9.2 (SAS Institute, Cary, NC, USA). Fisher's protected LSD tests (Steel et al., 1997) were performed when interactions were significant at a = 0.05. Differences between ecological site types were determined by *a priori* contrasts, whereas differences between vegetation control treatments and sampling dates were determined using pairwise *t*-tests on least square means.

We tested correlations among variables with the CORR procedure of SAS, and significant correlations were used to build regression models by linear fitting. Analyses of covariance (ANCOVA) were performed to compare differences between regression models for the site type or the vegetation control treatments ($P < 0.05$).

Normality and homoscedasticity were verified for all data using visual distribution of data and by analysis of residues (Devore and Peck, 1994). Natural logarithmic or square root transformations were made when necessary; we present back-transformed means and confidence intervals with bias correction when appropriate (Ung and Végiard, 1988; Végiard and Ung, 1993).

3 Results

3.1 Physiology and resource use efficiencies

Regardless of the ecological site type, photosynthesis rate (*A*) was 51 % higher in the eradication plots compared to the controls (Table 6, Figure 6a). Neither site fertility nor vegetation control influenced stomatal conductance, intercellular CO_2 concentration, LMA, phosphorus and iWUE (Table 6 and 7). On the medium fertility site type, black spruce experienced lower midday water potentials (Y_{md}) when vegetation was eradicated, compared to control conditions (Table 6, Figure 6b). We noted a significant ecological site type × vegetation control interaction for NUE; values were about 1.5 times higher when vegetation was eradicated, compared to control conditions, on the medium fertility ecological site type (Table 6, Figure 6c). Differences in NUE between vegetation control treatments were not significant in the low and high fertility ecological site types.

Table 6: Summary of ANOVA results for physiological variables measured on regenerating *Picea mariana* seedlings, across a gradient of ecological site type fertility in northeastern Québec (Canada) with, or without eradication of ericaceous vegetation. A = photosynthesis, g_{wv} = stomatal conductance to water vapor, Ψ_{pd} and Ψ_{md} = predawn and midday water potential, Ci = intercellular CO_2 concentration and VPD = vapor pressure deficit.

Source of variation (fixed)	ndf	A		g_{wv}[a]		Ψ_{pd}		Ψ_{md}		C_i		VPD	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ecological site type (EST)	2	0.82	0.451	0.33	0.724	2.13	0.129	0.24	0.795	1.25	0.302	2.93	0.069
Vegetation control (VC)	1	6.26	**0.019**	2.39	0.133	0.66	0.421	0.29	0.591	3.66	0.066	2.69	0.112
EST*VC	2	0.14	0.868	0.32	0.731	3.06	0.055	3.43	**0.040**	0.18	0.839	0.07	0.935
Date (D)	1[b]	2.37	0.135	2.42	0.132	12.66	< **0.001**	1.96	0.115	0.06	0.811	46.55	< **0.001**
EST*D	2[c]	2.66	0.088	0.70	0.507	0.86	0.559	1.53	0.170	3.60	**0.041**	8.77	**0.001**
VC*D	1[b]	2.40	0.133	0.72	0.405	0.30	0.880	1.56	0.199	1.57	0.221	3.23	0.083
EST*VC*D	2[c]	1.55	0.230	1.02	0.374	0.20	0.989	0.32	0.956	0.11	0.899	0.59	0.560
Contrasts (Aug-20-2008)												df	*P*
Low vs Med-High												25.4	0.787
Medium vs High												25.5	0.861

Bold indicate significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on sqrt-transformed data. [b] ndf = 4 (Ψ_{pd}. Ψ_{md}). [c] ndf = 8 (Ψ_{pd}. Ψ_{md}).

Table 7: Summary of ANOVA results for physiological variables measured on regenerating *Picea mariana* seedlings, across a gradient of ecological site type fertility in northeastern Québec (Canada) with, or without eradication of ericaceous vegetation. LMA = leaf mass per unit of area NUE = nitrogen use efficiency, PUE = phosphorus use efficiency (PUE) and iWUE = instantaneous water use efficiency.

Source of variation (fixed)	ndf	LMA[a]		NUE[a]		PUE		iWUE	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ecological site type (EST)	2	0.00	0.999	0.12	0.886	0.21	0.814	0.41	0.690
Vegetation control (VC)	1	0.05	0.823	9.95	**0.012**	3.39	0.089	2.79	0.146
EST*VC	2	2.34	0.115	5.34	**0.011**	1.17	0.342	0.10	0.910
Date (D)	1[b]	21.49	< **0.001**	11.63	**0.002**	7.20	0.018	3.79	0.078
EST*D	2[c]	1.66	0.161	0.89	0.424	0.56	0.582	2.71	0.112
VC*D	1[b]	2.02	0.134	3.34	0.076	1.75	0.207	2.40	0.150
EST*VC*D	2[c]	0.64	0.700	1.00	0.380	0.59	0.566	0.21	0.810

Bold indicate significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data. [b] ndf = 3 (LMA). [c] ndf = 6 (LMA).

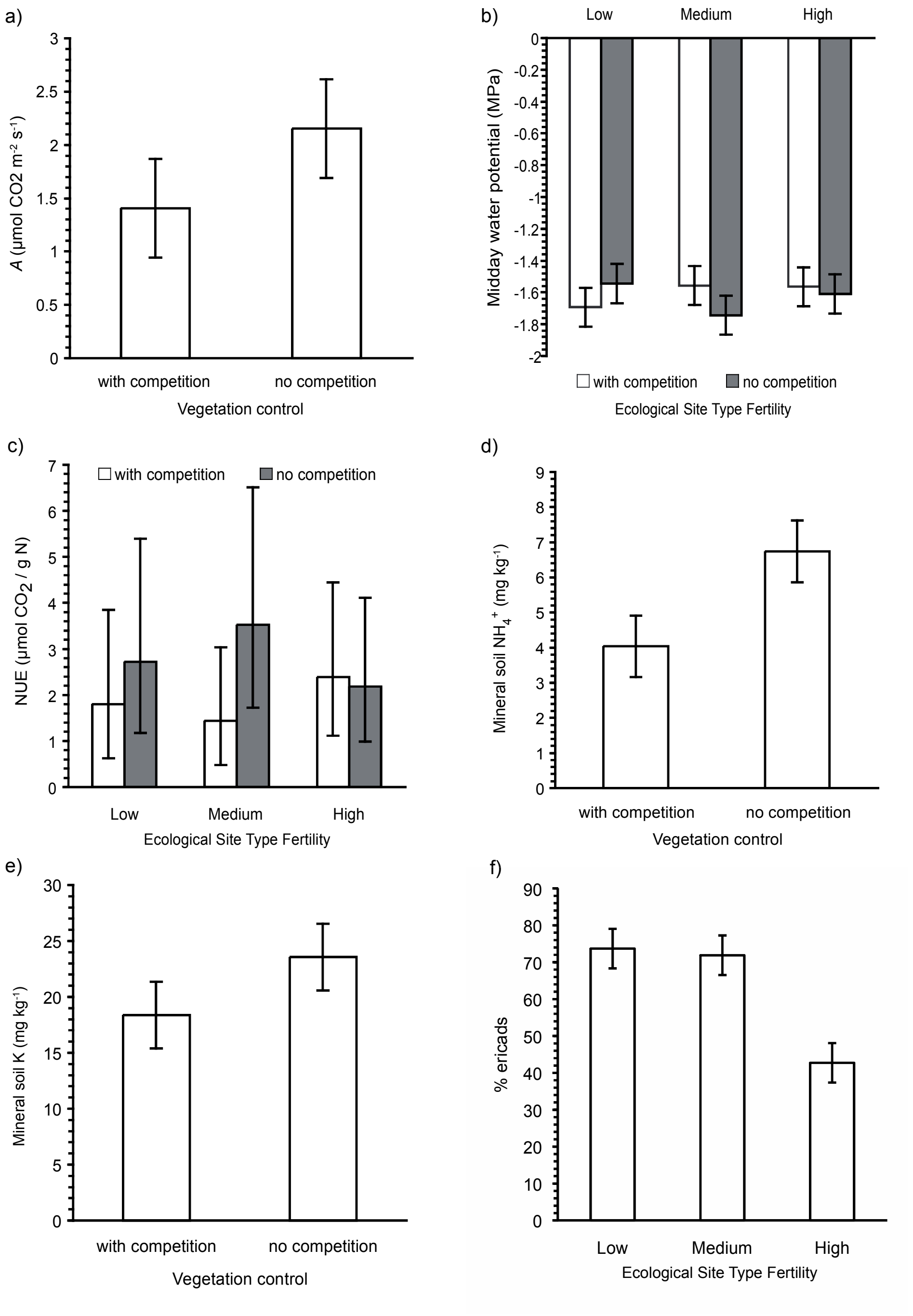

Figure 6: Vegetation control, ecological site type fertility and vegetation control × ecological site type fertility effects on photosynthetic rate (*A*) (a), midday water potential (b), NUE (c), mineral soil NH_4^+ and K (d,e), and % cover of ericaceous shrubs (f). Analysis performed on sqrt or ln-transformed data; back-transformed means and 95 % confidence intervals approximates are presented (Ung and Végiard, 1988).

3.2 Soil and vegetation variables

Vegetation control favored higher mineral soil NH_4-N concentration (an increase of 67 %), compared to control conditions (Table 8, Figure 6d). Vegetation control had no effect on all other soil variables except for mineral K availability, which was 28 % higher when vegetation was eradicated, regardless of site type (Table 8, Figure 6e). Soil water content (SWC) in the mineral soil was lower in the low fertility ecological site type compared to the medium and high fertility ecological site types (Table 8, Figure 7a). Extractable NH_4-N in the forest floor layer was 76 % higher on the medium and high fertility ecological site types compared to the low fertility ecological site type (Table 8, Figure 7b). Site type also affected C/N in the forest floor in 2007, and mineral soil extractable K (Table 8, Figure 7c,d). Ericaceous cover was 70 % higher on the low and medium fertility ecological site types compared to the high fertility ecological site type (Table 8, Figure 6f).

Table 8: Summary of ANOVA results for edaphic variables measured across a gradient of ecological site type fertility in northeastern Québec (Canada) with, or without eradication of ericaceous shrubs. % eri = % cover of ericaceous shrubs, SWC = soil water content.

Mineral soil

Source of variation (fixed)	ndf	NH_4^a		P		K		Ca		Mg^b		C/N		pH		SWC	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ecological site type (EST)	2	1.42	0.264	1.46	0.304	5.41	**0.012**	1.13	0.407	1.65	0.269	2.15	0.140	1.61	0.275	6.67	**0.026**
Vegetation control (VC)	1	9.10	**0.006**	0.72	0.407	5.47	**0.029**	3.11	0.128	1.90	0.185	0.57	0.458	0.30	0.588	2.91	0.116
EST*VC	2	0.96	0.398	0.78	0.475	2.29	0.125	0.20	0.632	1.03	0.376	0.01	0.990	1.47	0.257	1.38	0.291
Year (Y)	1[c]	0.00	0.962	24.38	**< 0.001**	0.08	0.778	0.00	0.999	1.59	0.224	0.13	0.726	26.49	**< 0.001**	3.33	0.068
EST*Y	2[d]	1.62	0.220	2.26	0.133	1.40	0.267	2.55	0.119	1.31	0.296	0.84	0.444	4.66	**0.024**	2.51	0.086
VC*Y	1[c]	1.02	0.323	0.00	0.962	0.80	0.380	0.08	0.787	0.03	0.855	1.31	0.265	0.61	0.445	1.20	0.361
EST*VC*Y	2[d]	1.34	0.282	0.70	0.512	1.26	0.305	3.68	0.057	1.37	0.281	0.70	0.505	2.17	0.143	1.06	0.441
Contrasts						df	*P*							df	*P*	df	*P*
Low vs Med-High						22	0.104									6.4	**0,012**
Medium vs High						22	**< 0.001**									6.71	0,247
Low vs Med-High (2007)														9.49	**0.026**		
Medium vs High (2007)														9.49	0.176		

Forest floor

Source of variation (fixed)	ndf	NH_4		P		K		Ca		Mg^b		C/N		pH		% eri	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ecological site type (EST)	2	5.33	**0.012**	0.67	0.562	0.78	0.499	0.69	0.539	0.08	0.923	6.95	**0.027**	1.90	0.200	18.78	**< 0.001**
Vegetation control (VC)	1	4.23	0.051	0.01	0.917	0.81	0.379	2.14	0.161	0.08	0.785	0.66	0.448	0.22	0.648		
EST*VC	2	1.64	0.215	0.95	0.406	1.72	0.208	0.03	0.968	1.51	0.248	0.14	0.876	0.69	0.526		
Year (Y)	1	4.28	**0.049**	60.57	**< 0.001**	2.17	0.158	0.64	0.433	0.74	0.398	0.00	0.976	0.40	0.540		
EST*Y	2	1.45	0.253	0.53	0.596	2.20	0.139	2.98	0.076	5.72	**0.012**	4.15	**0.043**	2.58	0.117		
VC*Y	1	0.08	0.777	0.94	0.344	1.63	0.218	0.31	0.585	0.00	0.975	0.01	0.944	0.01	0.939		
EST*VC*Y	2	0.64	0.536	2.76	0.090	0.74	0.491	1.25	0.310	0.44	0.654	2.11	0.165	0.66	0.534		
Contrasts		df	*P*									df	*P*			df	*P*
Low vs Med-High		24	**0.004**													1	**0.001**
Medium vs High		24	0.428													1	**< 0.001**
Low vs Med-High (2007)												10.5	**0.001**				
Medium vs High (2007)												10.5	0.569				

Bold indicate significance ($P < 0.05$. contrasts). ndf = numerator degrees of freedom.

[a] Analysis performed on sqrt-transformed data.

[b] Analysis performed on ln-transformed data.

[c] ndf (SWC) = 3.

[d] ndf (SWC) =6.

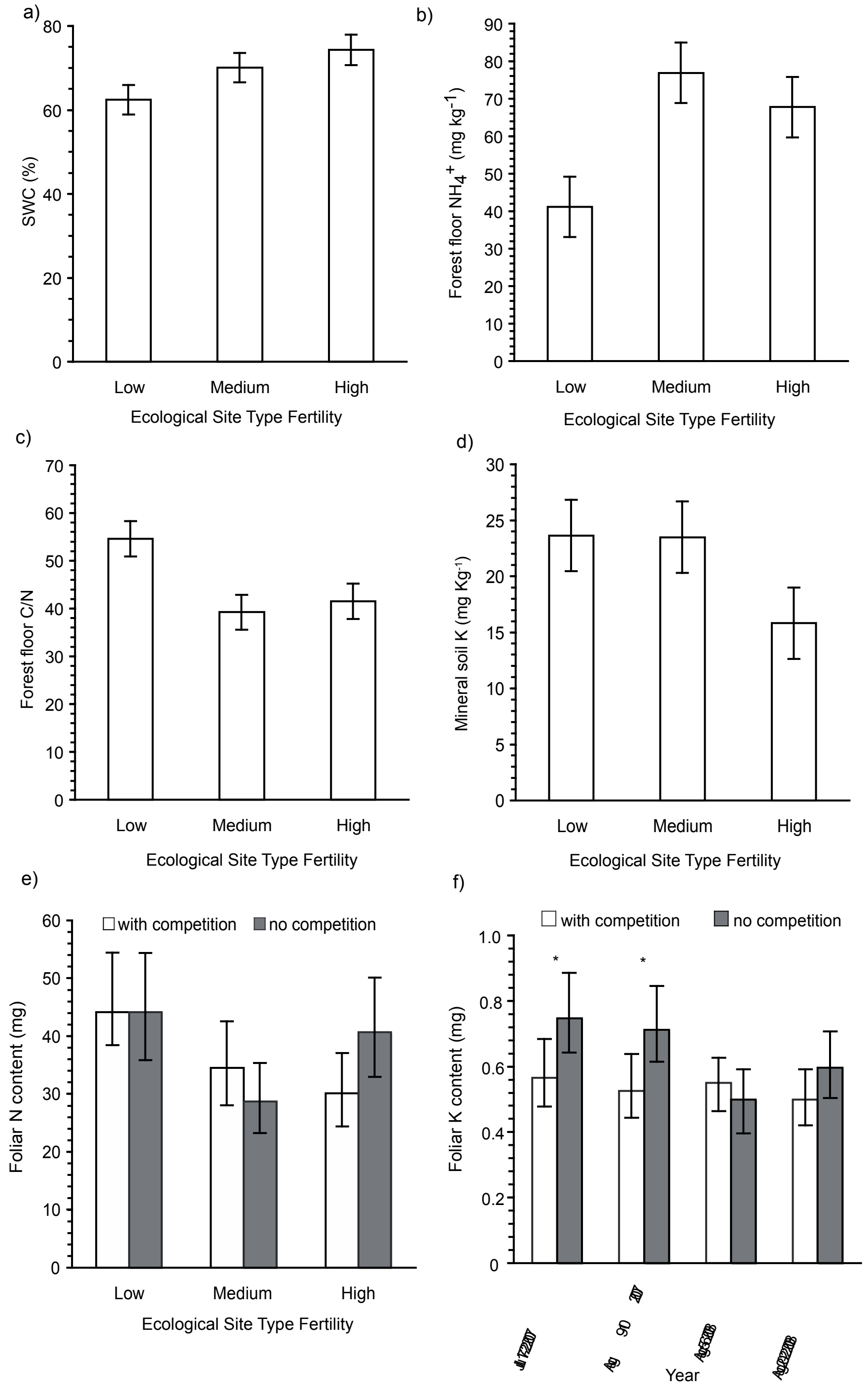

Figure 7: Vegetation control × ecological site type fertility, ecological site type fertility and vegetation control × sampling period effects on soil water content (SWC) (a) forest floor NH_4^+, C/N (b,c), mineral soil K (d), N and K foliar content (e,f). Analysis performed on ln-transformed data; back-transformed means and 95 % confidence intervals approximates are presented (Ung and Végiard, 1988).

3.3 Foliar nutrients

We observed a significant ecological site type × vegetation control interaction for foliar N content. When vegetation was eradicated, we found difference between ecological site types; foliar N was 47 % higher on the high and low fertility site types, compared to the medium fertility site type (Table 9, Figure 7e). The highest foliar N content was found on the low fertility site type when competing vegetation was present (Table 9, Figure 7e). We measured higher foliar K content when vegetation was eradicated the first year after treatment (Table 9, Figure 7f).

Table 9 Summary of ANOVA results for foliar nutrient content measured on regenerating *Picea mariana* seedlings, across a gradient of ecological site type fertility in northeastern Québec (Canada) with, or without eradication of ericaceous vegetation.

Source of variation (fixed)	ndf	N content[a]		P content[a]		K content[a]	
		F	*P*	*F*	*P*	*F*	*P*
Ecological type (EST)	2	4.82	0.566	4.70	0.059	6.83	**0.028**
Vegetation control (VC)	1	0.33	0.584	0.19	0.676	4.12	0.089
EST*VC	2	5.51	**0.044**	1.35	0.328	1.26	0.349
Date (D)	3	11861.30	< **0.001**	9146.82	< **0.001**	4.75	**0.004**
EST*D	6	0.48	0.825	0.61	0.722	0.35	0.907
VC*D	3	1.76	0.158	2.16	0.097	3.93	**0.010**
EST*VC*D	6	0.91	0.489	0.79	0.579	0.18	0.983
Contrasts		df	*P*			df	*P*
Low vs Med-High						6	**0.010**
Medium vs High						6	0.923
Low vs Med-High (no veg)		10.5	0.056				
Medium vs High (no veg)		10.5	**0.024**				
Low vs Med-High (with veg)		10.5	**0.020**				
Medium vs High (with veg)		10.5	0.319				

Bold indicate significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

3.4 Relations between physiological parameters

ANCOVA results show that increased NUE was associated with an increase in iWUE only when vegetation was present (Table 10,11 Figure 8a). Instantaneous water use efficiency (iWUE) was negatively related to intercellular CO_2 concentration, regardless of the vegetation or the ecological site type fertility (Table 11, Figure 8b). Finally, we found that leaf mass per unit of area was positively related to mineral soil P and K availability (Table 11, Figure 8c).

Table 10 : Summary of ANCOVA results for iWUE vs NUE.

Source of variation (fixed)	ndf	iWUE vs NUE	
		F	*P*
Vegetation control	1	9.03	**0.004**
X variable	1	24.31	< **0.001**
S*X variable	1	7.23	**0.009**

Table 11: Regression equations for selected parameters

	Dependant	Independant	Slope	Intercept	*F*	*P*	R^2
With vegetation	iWUE	NUE	0.5446	0.5913	22.99	< **0.001**	0.4181
All	iWUE	C_i	-0.0211	7.5488	170.96	< **0.001**	0.7276
All	LMA	P (min)	0.6132	54.4606	12.00	**0.003**	0.4286
All	LMA	K (min)	0.8187	55.2168	6.05	< **0.001**	0.2743

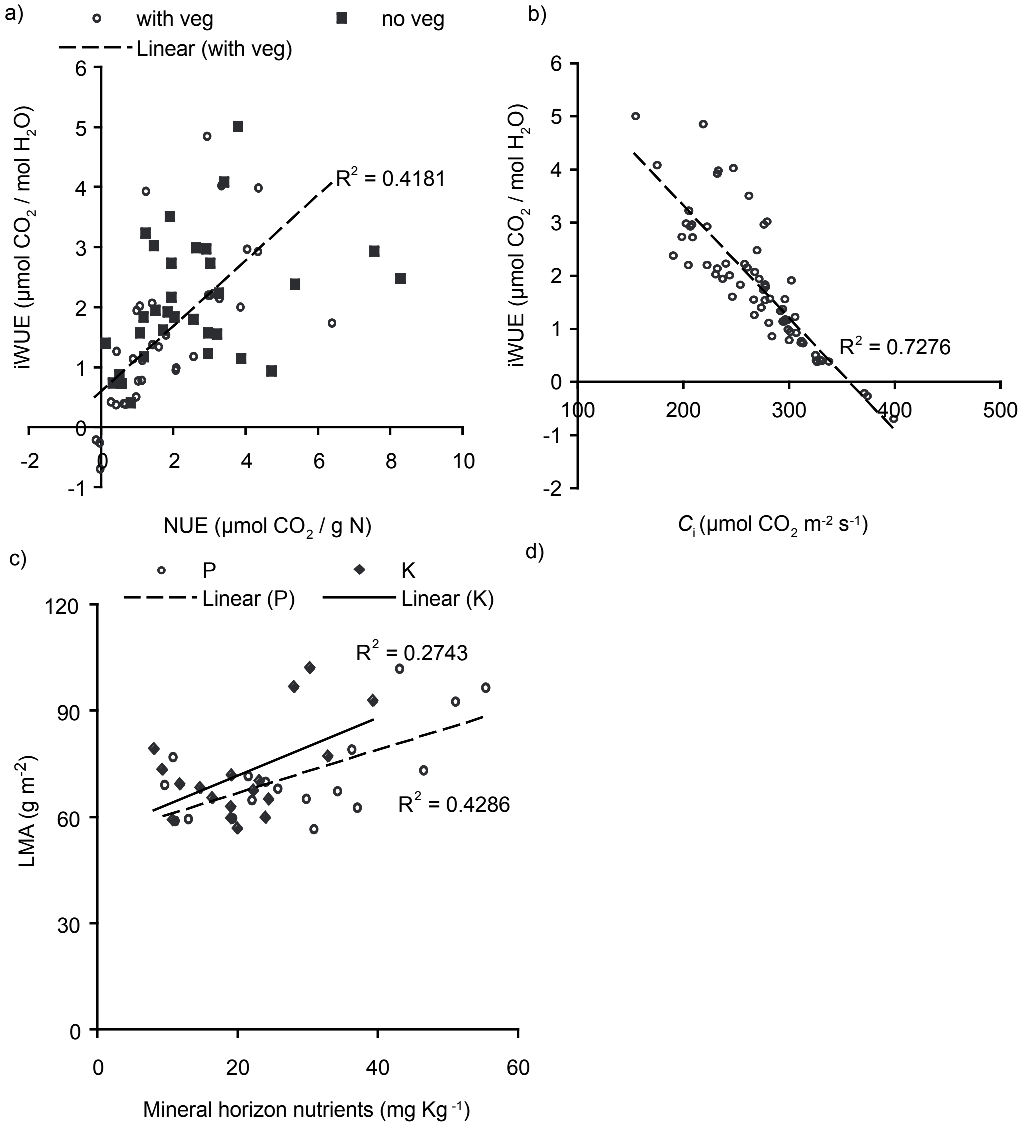

Figure 8: Relationship between selected physiological and edaphic parameters for black spruce advance regeneration in northeastern Québec, Canada. Refer to Table 7 for regression equations, *F* and *P* values.

4. Discussion

We found that regardless of the ecological site type fertility, ericaceous shrubs had a negative effect on black spruce advance regeneration after harvest, mainly by affecting the photosynthesis rate. Black spruce foliar K concentration in all treatments (0.37 % ± 0.09) was below the critical value (0.6 %) required to achieve saturating photosynthesis rate, even at full sunlight (Basile et al., 2003). Thus, a K deficiency – especially in the control plots– could have been responsible for reduced CO_2 assimilation rate, notably by lowering rubisco activity and other biochemical limitations in the chloroplasts (Basile et al., 2003; Cakmak, 2005). This interpretation is supported by the positive relationship we observed between LMA and soil mineral K; the higher LMA leaves were ostensibly able to sustain a higher level of Rubisco activity (Lusk et al., 2008). However, the relatively low R^2 of this relation, combined the absence of significant relations between LMA, foliar K content and photosynthesis, suggest that (i) LMA is less influenced by soil nutrient availability than by light availability (Lusk et al., 2008), and (ii) photosynthesis limitation in the control plots was due to factors other than limiting foliar nutrients.

On the other hand, the higher photosynthesis rate in the plots with vegetation control was not linked with water relations, as stomatal conductance and water potentials were similar in all treatments. Thus, black spruce photosynthesis was not regulated by stomatal closure, even in water stressed conditions, a phenomenon also observed by Hebert et al. in similar conditions (submitted). Furthermore, the difference in photosynthesis rate between the control plots and plots with vegetation control were not related to leaf morphological acclimation through changes in LMA. This trait is influenced mainly by light availability (Poorter et al., 2009), a condition that was constant across plots in our experiment, due to the greater height of black spruce layers compared to ericaceous shrubs. Neither was it related to nitrogen content, which is often positively related to LMA or to photosynthetic capacity (Rosati et al., 1999; Lusk et al., 2008). Higher photosynthesis rate could indicate a higher growth rate for black spruce, as noted for black spruce layers by

Paquin et al. (1999). Although relative growth rate is generally correlated with photosynthesis (Cernusak et al., 2008), we cannot draw conclusions for this study, since we did not measure biomass growth. Tremblay (2010) found growth difference between black spruce seedlings that was explained not by the photosynthesis rate, which was similar for all seedlings but it was probably because physiological measurements were made to late in the growing season.

Reduced mineral soil NH_4-N in ericad invaded plots did not significantly influence black spruce foliar N content. However, such an impact on soil NH_4-N is expected to have a long-term effect on black spruce photosynthesis, and possibly on growth, as conifers have a higher physiological capacity to process NH_4-N, compared to NO_3^- (Kronzucker et al., 1997). This absence of a short term effect of reduced mineral soil NH_4-N on foliar N content was also reported in other contexts (Munson and Timmer, 1989).

The rapid response in mineral soil NH_4-N and foliar K to vegetation eradication is seemingly a result of aggressive underground competition by the ericaceous shrubs in control plots. *Kalmia* and related species are characterized by a massive root system (Yamasaki et al., 1998), and have been demonstrated to reduce N mineralization and microbial activity (Inderjit and Mallik, 1996; Joanisse et al. 2009). Other studies observed K limitation related to competition by ericaceous shrubs, including higher K content in *Kalmia* compared to black spruce leaves (Damman, 1971; Mallik 2001). These studies also showed that only 20% of K in *Kalmia* plants was returned to the soil in leaf litter; a large proportion was presumably sequestered in the root system (Damman, 1971).

Our results contradict our research hypothesis concerning the interaction of ericaceous plant impact and site fertility. We found that the effects of *Kalmia* (and other ericads) on black spruce physiology and site productivity were not related to ecological site type fertility. Yamasaki et al. (2002) found that *Kalmia* had an effect on extractable NH_4-N pool but only on his richer site. In our study, neither higher forest floor NH_4 or lower foliar N content on the medium fertility site type was related to ericaceous cover. This result suggests that ericaceous shrubs seem to have the same influence on black spruce layers and on mineral soil nutrition regardless of the site fertility. From a management perspective, this suppose that the variation in fertility among ecological site types does not depend on ericaceous shrub cover or on plant interaction intensity (Mitchell et al., 2009). Differences in soil productivity variables between the medium and the high fertility ecological site types could have been due to a slightly higher variability of site conditions between replicates of the high fertility ecological site type.

The absence of a trade-off between NUE and WUE reveals that shrub eradication did not significantly modify the water relations or the N content of black spruce in the short-term, even if available soil N increased in the eradication plots (Kranabetter and Simard, 2008). The higher NUE we measured in the eradication plots of the medium fertility ecological site type also demonstrates that resource use efficiencies in these ecosystems were driven more by a change in the photosynthetic capacity, than by modifications of resource availability. It supports that higher NUE does not necessarily leads to lower WUE (Livingston et al., 1999), especially for black spruce when water is not limiting (Patterson et al., 1997).

To our knowledge, our study is the first to experimentally isolate the interactive effects of ericaceous competition and intrinsic site fertility on conifer physiology at such a scale in the field. We found that competition for belowground resources had a significant effect on spruce physiology. In the long term, this competition dynamic could have a determinant impact on species abundance and community structure. We also discovered that the impact of the ericaceous competition was independent from site type fertility, which suggests that vegetation management of ericaceous shrubs must be planned independently from the ecological site type. However, further monitoring, including assessment of growth of black spruce layers, would be required to confirm this interpretation.

5. Acknowledgements

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Chapitre 3

Does plasticity of three boreal nutrient-conserving species relate to their place in succession?

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ABSTRACT

Several mechanisms have been identified to explain the encroachment of ericaceous vegetation after natural or anthropogenic disturbance in boreal black spruce forests, leading to short or longer term dominance of these shrubs and stagnation of black spruce growth. Plant species with greater flexibility or plasticity in response to a changing environment may have a competitive advantage over species with less plasticity. The present study investigates potential differences in trait plasticity as an additional contributing mechanism explaining ericaceous shrub dominance during different periods of succession towards canopy closure. We evaluated several functional traits associated with light (leaf mass area – LMA; leaf nitrogen content; photosynthetic rate) and nutrient acquisition (nitrogen productivity; biomass allocation; specific absorption ratio), as well as allocation of newly acquired N (^{15}N) in order to verify our hypothesis. Two ericaceous species dominant in early versus late succession, respectively (*Kalmia angustifolia; Rhododendron groenlandicum*), and black spruce seedlings (*Picea mariana*), were submitted to combinations of three light levels and two levels of nitrogen addition during a simulated growing season of nine weeks under greenhouse conditions. For foliar trait response to light, only leaf mass per unit of area (LMA) of both ericaceous species was significantly reduced by shading; LMA of *Rhododendron* and *Kalmia* was, respectively, 54 % and 31 % higher in the highest light treatment, but LMA of black spruce was unchanged in response to light level. There were few differences in trait response to N addition among species. Black spruce showed higher absorption rate and specific absorption rate at higher N levels, compared to the two ericads. Plasticity to light was higher for *Kalmia* except for LMA and plasticity for nitrogen addition was higher for *Rhododendron* and black spruce. These results suggest that trait plasticity is in accordance with successional status of these species. Furthermore, plasticity of LMA may be a key trait explaining a competitive advantage of ericaceous species (especially *Rhododendron*) and potential encroachment on forested sites after disturbance.

RÉSUMÉ

Plusieurs mécanismes ont été identifiés afin d'expliquer l'envahissement de la végétation éricacée après les perturbations naturelles ou anthropiques dans la pessière noire à mousses. De telles perturbations mènent parfois, à court ou à long terme, à une dominance des éricacées et à une stagnation de la croissance de l'épinette noire. Les espèces végétales possédant une plus grande flexibilité, ou plasticité, en réponse aux changements des conditions environnementales pourraient avoir un avantage compétitif comparativement aux espèces ayant une plasticité moindre. Cette étude vise à évaluer les différences potentielles de plasticité des traits fonctionnels comme un mécanisme additionnel contribuant à expliquer la domination des éricacées durant différents stages successionnels tendant vers une fermeture de la voûte forestière. Afin de tester notre hypothèse, une expérience en serre a été réalisée en comparant deux espèces d'éricacées de début et de fin de succession (*Kalmia* et *Rhododendron*) et l'épinette noire (*Picea mariana*) soumis à trois niveaux de lumière (63, 19 et 8 %) et deux niveaux d'addition d'azote ^{15}N (100 kg/ha/an et 300 kg/ha/an) pendant une saison de croissance simulée. Nous avons mesuré différents traits fonctionnels associés à l'acquisition de lumière (masse foliaire par unité de surface ou LMA, concentration d'azote foliaire, photosynthèse) et à l'acquisition des nutriments (productivité d'azote, ratio d'absorption spécifique, absorption de ^{15}N). En ce qui a trait à la réponse à la lumière, seul la LMA des deux espèces éricacées a diminué avec l'ombrage; la LMA du *Rhododendron* et du *Kalmia* étant 54 % et 31 % plus élevée dans le traitement ayant la plus grande disponibilité lumineuse. Nous avons mesuré des différences entre les espèces entre terme de réponse des traits à l'addition d'azote. L'épinette noire a montré une taux d'absorption et un taux d'absorption spécifique supérieur a des niveaux d'azote plus élevés comparativement aux deux espèces d'éricacées. De son côté, la plasticité en réponse à la lumière a été supérieure pour le *Kalmia,* à l'exception de la LMA, et la plasticité en réponse à l'addition d'azote a été supérieure pour le *Rhododendron* et pour l'épinette noire. Les résultats suggèrent que la plasticité des traits est en accord avec le statut successionnel des deux espèces. De plus, la plasticité pour le LMA semble être le trait fonctionnel qui explique le plus l'avantage compétitif des éricacées (spécialement le *Rhododendron*) et un potentiel d'envahissement des peuplements après perturbation.

1. Introduction

Natural or anthropogenic disturbances in boreal forests open the forest canopy partially or completely, inducing changes in the availability of light, nutrient and water resources (Prescott 1997, Burgess and Wetzel 2000, Prévost and Pothier 2003). Under these conditions, plant species with higher flexibility or plasticity in response to changing conditions may have a competitive advantage over the less plastic species (Aerts et al. 1991). In nutrient-poor black spruce (*Picea mariana* Mill. BSP) forests of eastern North America, the understory vegetation is dominated by deciduous or evergreen ericaceous species (*Vaccinium* spp.; *Kalmia angustifolia* L., hereafter referred to as *Kalmia*; *Rhododendron groenlandicum* [Oeder] Kron & Judd, hereafter referred to as *Rhododendron*) that are well-adapted, as is black spruce, to low levels of soil nutrient availability. Canopy removal by natural disturbances (fire and windthrow) or forest harvest, creates light conditions that may favor the shrub understory, potentially contributing to a permanent opening of the canopy and development of heath-like conditions (Bloom and Mallik 2004), a situation observed in other ericaceous-dominated ecosystems in Scandanavia, New Zealand and western North America (Messier 1993, Nilsson et al. 2000, Feng 2008)

Although *Kalmia*, *Rhododendron* and black spruce can be considered resource-conservative in terms of nutrient use, understanding the plasticity of each species in response to changing light and nutrient availability may provide further insight into how each comes to dominate the community at different stages of succession. A recent study of boreal northeastern forests in Quebec (Canada) showed that *Kalmia* dominates early in succession after major disturbances, but is gradually replaced by *Rhododendron* as the canopy develops (Laberge-Pelletier 2007). Light and nutrient availability are expected to be higher at the beginning of succession, and to gradually decrease with the development of the canopy and the moss-dominated humus layer (Hart and Chen 2006).

Higher light availability induces plant trait modifications that maximize photosynthetic capacity, and therefore growth. It is often achieved through a change of leaf mass per unit of area (LMA), a trait related to light interception control and photosynthesis, and by higher leaf nitrogen content, which optimizes Rubisco regeneration (Wright et al. 2004, Violle et al. 2009). Previous studies showed that as light availability increases, *Kalmia* produces more belowground biomass (Mallik 1996) and has a higher leaf area index compared to individuals that grow in shaded habitats (Mallik 1994, Bloom and Mallik 2004). *Rhododendron* also responds relatively rapidly (compared to black spruce) to higher light availability by producing leaves with a higher LMA, which increases photosynthesis rate (Hébert et al. 2010, in press). Another North American ericaceous species, *Gaultheria shallon* Pursch, or salal, showed plasticity in response to fertilization by reducing its root to shoot ratio (Hawkins and Henry 2004). In contrast, black spruce shows a delay of photosynthetic and growth responses with increasing light availability (Zine El Abidine et al. 1994, Paquin et al. 1999). However no direct comparisons of these species have been made under the same light regimes, and relative responses of each species to nutrient availability have not been evaluated.

Studies of interference mechanisms between *Kalmia* and black spruce have identified that direct competition for nutrients by a massive hair-like root system (Inderjit and Mallik, 1996, Thiffault et al 2004) contributes to ericaceous domination of nutrient processes, even if black spruce shows higher nutrient absorption efficiency per unit root mass (Thiffault et al. 2004). Litter of *Kalmia* is rich in phenolics compounds that reduce nitrogen mineralization and microbial activity by forming stable complexes with proteins and affecting enzyme activity (Inderjit and Mallik 1996, Joanisse et al. 2007). Other mechanisms may involve an advantage of ericoid mycorrhizae to absorb organic N, associated with ericaceous shrubs compared to the ectomycorrhizae of black spruce (Reid and Perez-Moreno 2003).

We hypothesize that plasticity of functional traits associated with light and nutrient acquisition may also explain successional dominance of *Kalmia*, *Rhododendron*, and black spruce, and early dominance of the ericaceous shrubs in succession. A greenhouse trial using field transplants of the two shrubs and black spruce seedlings was set up to evaluate plasticity of specific physiological and morphological traits to three levels of light (imitating different levels of canopy opening) and two levels of nitrogen addition, over one artificially-induced growing season. We studied traits that are known to be the most important in response to each of these resources (leaf-level traits for light; biomass allocation, nitrogen productivity and absorption rate in response to nutrients) (Rozendaal et al. 2006, Miller and Hawkins 2007, Hernandez et al. 2009). As well, we used ^{15}N as a tracer in the N addition treatments, to evaluate N allocation in response to the different light and N levels.

As *Kalmia* dominates early in the succession, it should show greater plasticity to light, compared to *Rhododendron* and black spruce, which dominate later. *Rhododendron* is expected to demonstrate intermediate plasticity between *Kalmia* and black spruce in response to light. Nutrients being most limited at the end of succession, both *Rhododendron* and black spruce are likely to show greater response to changes in nutrient availability compared to *Kalmia* (eventually out-competed by *Rhododendron* in natural ecosystems).

2 Materials and methods

2.1 Experimental design and treatments

The experiment was conducted in a polycarbonate greenhouse at Université Laval, Quebec city, Canada (46°46’48’’N, 71°16’28’’W). We harvested transplants of *Kalmia* (KA) and *Rhododendron* (RG) in October 2007 near the town of Chibougamau (49°16’08’’N, 73˚53’42’’W), in the Quebec’s black spruce-feathermoss bioclimatic domain described by Saucier et al. (2009). Transplants between 20 and 30 cm high with the intact root system were put in 15.3 L plastic containers (IPL plastics, inc. St-Damien, Qc. Canada, square opening of 645 cm^2) half-filled with sand collected near-site. In order to collect the proper underground biomass, rhizomes were conserved and rolled into the container. *Kalmia* and *Rhododendron* were compared to two-year-old black spruce (BS) container-grown seedlings (root plug volume of 110 cm^3), produced in nursery from a seed source located near the collecting site. At the end of the production, seedling had a mean nitrogen concentration of 1.73 % with a mean height of 16.6 cm (± 4.86) and a mean diameter of 2.7 cm (± 0.14). In late fall 2007, seedlings and transplants were placed outside the greenhouse on a plastic sheet to induce dormancy while avoiding rooting outside the containers.

On February 5th, 2008 (Julian Day 36), we transferred the seedlings and transplants in the greenhouse, where they were submitted to 14/10°C cycles with a 12 h photoperiod for three weeks (Wallstedt et al. 2002). During the third week, all the material was transplanted in new 15.3 L containers filled at half height with sand. Seedlings and transplants were rooted in the upper half, in a mix of organic soil composed of 1/3 of organic horizon collected at the original collecting site, and 2/3 of a standard sphagnum peat moss mix (Lambert Peat Moss Inc. Riviere-Ouelle, Quebec, Canada).

The greenhouse had a light transmission capacity of ~ 63 % of full photosynthetic photon flux density (PPFD). Individuals of each species were randomly selected to be submitted to one of the following three light regimes created with use of shade cloths: low light level (LL) (two layers of shade cloth), medium light level (ML) (one layer of shade cloth) and high light level (HL) (no shade cloth). We attached the shade cloth above and on the side of the selected seedlings or transplants with steel rod inserted at each corner of the container. Each rod was cut to allow about 30 cm of free space between the plant and the cloth.

Seedlings and transplants were randomly selected to receive one of two levels of N addition, that was the equivalent of either 100 kg N ha^{-1} $year^{-1}$ (100) or 300 kg N ha^{-1} $year^{-1}$ (300). As ericaceous shrubs are devoid of nitrate reductase (Pasche et al. 2001, Krywult et al. 2002), we used 5 % ^{15}N enriched ammonium sulfate $(^{15}NH_4)_2SO_4$ (Icon Services Inc., Summit, New Jersey, USA) diluted in 100 ml of water.

The resulting experimental setup was a fully randomized design with four replicates, composed of three species, three light levels, two nitrogen addition levels and two sampling dates (a total of 144 plants). We disposed the containers on a 12 × 12 grid, with 0.5 m between each other. In order to avoid shading between the experimental units, containers were placed according to a checkerboard design. The 12 × 12 grid was surrounded by a line of containers of the three species (randomly selected), which served as a buffer layer.

2.2 Experimental conditions

The experimental growth conditions were set on February 26th (JD 57) and corresponded to 20/16°C temperature cycles with a photoperiod of 16 hours. We monitored PPFD in the greenhouse with a reference quantum sensor (model LI-190SB, LI-COR, Inc., Lincoln, NE, USA) placed at the level of apical shoot of the highest plant. Using quantum sensors and portable light meters (model LI-250, LI-COR, Inc., Lincoln, NE, USA), we measured seedling and transplant available PPFD on two dates, simultaneously on six individuals (two by species) per light regime, three times a day (morning, midday and afternoon). Relative to HL conditions (63 % PPFD), light levels obtained and used for this study were 30.31 ± 4.01 % for ML, and 13.21 ± 8.32 % for LL, that is 19 % and 8 % of full PPFD, respectively. We monitored air temperature in the greenhouse with thermistors (model 107BAM, Campbell Sci., Edmonton, AB, Canada); data were recorded every minute and averaged every 15 min with a CR10X datalogger (Campbell Sci. Inc., Edmonton, AB, Canada). Air temperature at the soil surface was monitored every 15 minutes for six seedlings (one per species × light regime) with individual dataloggers (Watchdogs dataloggers model 100, Spectrum technologies, Inc., IL, USA).

We applied N fertilizer once a week during four weeks (March 13-19-26 and April 2nd) (JD 73, 79, 86, 93); irrigation was done twice a week with about 100 ml of deionized water to limit N loss. After the fertilization period, seedlings were watered at soil saturation capacity (between 500-1000 ml, twice a week).

2.3 Gas exchange measurements

Photosynthesis (*A*), and other gas exchange variables (results not shown), were measured on current year foliage of four individual of each species, during two periods in the secondary growth period (April 14-16, April 29th-May 1st) (JD 105-107, 120-122). We performed the measurements with a LI-6400 portable photosynthesis system equipped with a 0.25 L conifer cuvette (LI-COR, inc. Lincoln, NE, USA). A halogen lamp was placed ~15 cm above the cuvette to provide saturating light conditions (> 1200 µmol photons m^{-2} s^{-1}). Seedlings were subjected to saturating light for a minimum of 15 min before measurement. Cuvette CO_2 was fixed to 380 ppm. We fixed the atmospheric relative humidity of the chamber to 30-35 % for the first sampling period, and 45 % during the second sampling period. Air temperature was 25°C during the two sampling periods. We performed measurements between 8:50 and 14:10 E.T. Each replicate was measured within 150 min. We determined foliar surface area for BS with the volume displacement technique (Brand 1987). For RG and KA, foliar surface area was calculated by image analyzing using WinFolia (Regent instruments Inc., Québec, Canada). The samples were oven dried at 65°C for 48 hours and then weighed to determine LMA.

2.4 Morphological and nutrient measurements

At the end of the experiment (nine weeks), all seedlings were measured for length of apical shoots (mean of all shoots for KA and RG) and total height from soil level. We separated the plant belowground biomass (roots and rhizomes) from the growing media by gentle washing, based on their color and their attachment to aboveground parts (Thiffault et al. 2004). Plant biomass was separated in five compartments: current shoot (foliar, stem), 1+ year shoot (foliar, stem) and belowground biomass. Samples were stored in a freezer until analysis; they were oven-dried at 65°C for 48 hours before weighing and ground to pass a 40-mesh size screen. Nitrogen isotope mass and atomic percent were measured on

10-mg samples with an Isotope Ratio Mass Spectrometer (Europa Scientific Integra, PDZ Europa, Cheshire, UK) at the Davis Stable Isotope Facility (University of California, Davis, California). Total ^{15}N uptake and percent of ^{15}N recovery by unit of belowground biomass were calculated for all species on a 1-m^2 basis. We present the % ^{15}N recovery of the new foliage per unit of belowground biomass (%^{15}N F0), the % ^{15}N recovery for the entire plant per unit of belowground biomass (%^{15}N total) and the % ^{15}N recovery of belowground biomass (%^{15}N root).

Using dry biomass data, we calculated the following ratios: root to shoot ratio (root:shoot), leaf-mass ratio (LMR; the leaf dry mass to the total aboveground dry mass) and root-mass ratio (RMR; root dry mass to the total dry mass). Nitrogen productivity (NP) of new shoots produced during the experiment was calculated as the inverse of the nitrogen concentration in the current foliage by the current foliage biomass (Miller and Hawkins 2007). The specific absorption rate (SAR) of roots was determined by the N content of current foliage divided by the belowground biomass (Osone et al. 2008).

2.5 Plasticity index

To assess plasticity of each species to light and nutrient treatments, we calculated the phenotypic plasticity index (PI) following Valladares et al. (2000), as the difference between the minimum and the maximum mean values between the two levels of each treatment divided by the maximum mean value.

2.6 Statistical analyses

We performed analysis of variance (ANOVA) for a completely randomized design with the MIXED procedure of SAS 9.2 (SAS Institute, Cary, NC, USA). Fisher's protected LSD tests were made (Steel et al. 1997) when interactions were significant at $\alpha = 0.05$.

Differences between sampling dates were determined using pairwise *t*-tests on least square means.

Aboveground relative growth rate (RGR_{aerial}) was used to analyze treatment or species effects on aboveground growth, using the Poorter and Lewis method (1986), based on analysis of variance, with ln-transformed dry mass as the dependent variable. A significant treatment or species × time interaction indicates a difference in relative growth between treatment or species.

We tested correlations among variables with the CORR procedure of SAS and significant correlations were used to make regression models by linear fitting. Analyses of covariance (ANCOVA) were performed to compare differences between regression models for the three species ($P < 0.05$).

Normality and homoscedasticity of variance were verified for all data by visual analysis of residues (Devore and Peck 1994). When necessary, we made natural logarithmic, square root or arcsin transformations. Back-transformed means and confidence intervals with bias correction are presented (Ung and Végiard 1988, Végiard and Ung 1993).

3. Results

3.1 Light acquisition

Photosynthesis rate of both ericaceous species, for both sampling periods, was more than four times higher than that of black spruce (by 420 % for date 1; by 330 % for date 2) (Table 12, Figure 9a) but was not influenced by the shading or N addition treatments. The shading treatment significantly reduced LMA for both ericaceous species, but not for black spruce (Table 12, Figure 9b). LMA of *Kalmia* was 31% higher under HL (63 % PPFD) compared to the two shaded treatments. The same trend was observed for *Rhododendron*;

LMA was 54 % higher under the HL treatment compared to ML and LL treatments (Figure 9b). All species grown at 8 % of light availability (LL) had a 64 % lower percentage of absorption of ^{15}N of current foliage by unit of root biomass (% F0 ^{15}N), compared to the HL and the ML light treatments (Table 13, Figure 9c). Conversely, absorption of ^{15}N of 1+ year old foliage by unit of root biomass (% F1 ^{15}N) was higher in the LL treatment, but only for black spruce (Table 13, Figure 9d) Aboveground relative growth rate (RGR_{aerial}) differed among the three species (Table 12, Figure 9e); RGR_{aerial} was highest for *Rhododendron* followed by *Kalmia*. Black spruce RGR_{aerial} was significantly lower than the two ericad species (Figure 9c). Significant differences in water use efficiency (WUE) were observed among species (Table 12); WUE was 34 % higher for *Rhododendron* compared to the two other species (Figure 9f).

Foliar N concentration of current foliage was influenced by the light treatment; N concentration was 13 % higher in the LL treatment compared to the ML and HL treatments (Table 14, Figure 10a). Foliar N concentration was higher for black spruce compared to the ericaceous species, for both current and one year-old foliage (Figure 10b,c). Differences between the two ericads depended on foliage age; foliar N of current leaves was slightly lower for *Kalmia* compared to *Rhododendron*, but higher in the one year-old foliage (Figure 10b,c).

A significant interaction between species and light treatments was noted for nitrogen productivity (NP) (Table 13). NP increased with decreasing light for black spruce, but not for the ericaceous species (Figure 10d). At HL, *Kalmia* had the highest NP but at LL, black spruce had the highest NP (Figure 10d).

3.2 Nutrient acquisition

Kalmia was characterized by the highest root to shoot ratio; the ratio was 70 % and 367 % higher compared to *Rhododendron* and black spruce, respectively (Figure 11a). Root mass ratio (RMR) was the highest for *Kalmia*, which was 100 % and 21 % higher than black spruce and *Rhododendron*, respectively (results not shown).

Belowground N concentration followed the same pattern as that observed for foliar N (1+ year old), with a 170 % and 217 % higher concentration in black spruce roots compared to *Kalmia* and *Rhododendron.* We also measured a significant effect of N addition on belowground N concentration with a slightly higher concentration (5 %) observed at the higher N addition level (Table 14).

Nitrogen addition had a consistent effect on the percentage of ^{15}N absorption (% abs ^{15}N) for all biomass compartments, with the exception of the current foliage, F0 (Table 13). For the current foliage, we found no difference between the two N addition treatments for ericaceous species. Black spruce had a higher foliar absorption capacity than the ericaceous species, and absorption was higher at the lower level of N addition, 100 kg/ha/year (Figure 11b). Percentage of absorption of ^{15}N by the entire plant (%^{15}N total) was more than two times higher for black spruce compared to the ericaceous species and the difference was ~ 2.5 times higher in the lowest fertility treatment, regardless of species (Figure 11c,d).

Specific absorption rate (SAR) was similar for all light treatments and was consistently higher for black spruce compared to the two shrub species (Figure 11e).

We noted a significant relationship between LMA and % of ^{15}N absorbed by the entire plant (%^{15}N total) (Table 15, Figure 12a). LMA was also positively related to photosynthesis rate, but only for black spruce (Table 15,16; Figure 12b).

3.3 Plasticity of the three species

In general, there was a tendency to higher plasticity in physiological traits versus biomass allocation traits (Figure 13a). As well, plasticity tended to be higher in response to the light gradient (3 levels) compared to the nutrient gradient (2 levels; Figure 13a,b).

Kalmia tended to have higher plasticity in response to light than other species in photosynthesis, WUE and LMR, while *Rhododendron* plasticity tended to be higher for LMA and root:shoot (Figure 13a). Black spruce showed slightly higher plasticity in RMR in response to light.

Species differences in response to the fertility levels were less evident. *Kalmia* tended to have the lowest plasticity for LMA, WUE and RMR, while black spruce PI was lower for LMR (Figure 13b).

Table 12: Summary of ANOVA results for selected physiological parameters measured on black spruce, *Rhododendron* and *Kalmia* under variable intensity of shading and nitrogen addition.

Source of variation (fixed)	ndf	A^a		LMA		RGRaerial^a		WUE^b	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Light (L)	2	0.16	0.856	16.29	**< 0.001**	10.29	**< 0.001**	0.40	0.674
N addition (A)	1	0.85	0.360	0.47	0.494	4.00	**0.047**	0.69	0.409
L*F	2	0.49	0.617	0.24	0.786	0.76	0.469	0.50	0.610
Species (S)	2	63.86	**< 0.001**	175.22	**< 0.001**	195.06	**< 0.001**	5.63	**0.005**
L*S	4	0.96	0.441	3.48	**0.011**	3.57	**0.008**	0.04	0.997
A*S	2	1.10	0.342	0.48	0.618	4.88	**0.008**	0.67	0.512
L*A*S	4	0.24	0.917	0.14	0.966	1.74	0.141	0.42	0.793
Date (D)	1	68.84	**< 0.001**	6.80	**0.011**	39.19	**< 0.001**	15.75	**< 0.001**
D*L	2	2.66	0.078	0.19	0.827	0.65	0.523	0.38	0.685
D*A	1	2.21	0.142	0.32	0.582	0.42	0.516	0.02	0.899
D*L*A	2	1.10	0.339	0.98	0.378	0.02	0.980	0.79	0.457
D*S	2	8.41	**0.001**	2.40	0.096	6.04	**0.003**	0.14	0.871
D*L*S	4	1.97	0.115	0.42	0.793	0.72	0.578	0.53	0.715
D*A*S	2	0.41	0.664	0.25	0.783	0.01	0.991	0.31	0.736
D*L*A*S	4	1.92	0.124	0.41	0.803	0.02	0.991	1.89	0.485

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

[b] Analysis performed on sqrt-transformed data.

Table 13: Summary of ANOVA results for selected physiological parameters measured on black spruce, *Rhododendron* and *Kalmia* under variable intensity of shading and nitrogen addition.

	ndf	% F0^{15}N [b]		% F1^{15}N[b]		% S0 ^{15}N[b]		% S1 ^{15}N[a]	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Light (L)	2	4.12	**0.019**	3.23	**0.043**	3.03	0.054	1.47	0.234
N addition (A)	1	41.22	**< 0.001**	22.89	**< 0.001**	26.69	**< 0.001**	33.67	**< 0.001**
L*A	2	0.85	0.431	0.49	0.615	1.81	0.171	0.58	0.561
Species (S)	2	96.12	**< 0.001**	149.54	**< 0.001**	82.75	**< 0.001**	29.10	**< 0.001**
L*S	4	2.08	0.088	3.03	**0.020**	2.44	0.054	1.50	0.207
A*S	2	3.09	**0.049**	1.28	0.281	2.42	0.096	0.25	0.782
L*A*S	4	0.51	0.729	0.55	0.697	0.95	0.440	0.56	0.695

	ndf	% Root ^{15}N[a]		%^{15}N Tot[a]		NP[a]		SAR[a]	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Light (L)	2	2.17	0.119	1.48	0.236	3.14	0.047	0.44	0.645
N addition (A)	1	230.91	**< 0.001**	70.37	**< 0.001**	1.56	0.215	3.23	0.075
L*A	2	0.08	0.920	2.05	0.137	1.24	0.294	1.95	0.148
Species (S)	2	53.61	**< 0.001**	77.99	**< 0.001**	6.70	0.002	147.49	**< 0.001**
L*S	4	1.43	0.228	1.28	0.287	7.29	**< 0.001**	2.61	**0.039**
A*S	2	2.47	0.089	0.72	0.491	0.15	0.862	1.77	0.175
L*A*S	4	0.50	0.730	1.48	0.219	1.02	0.402	1.24	0.300

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

[b] Analysis performed on sqrt-transformed data

Table 14: Summary of ANOVA results for selected plant traits measured on black spruce, *Rhododendron* and *Kalmia* under variable intensity of shading and nitrogen addition.

	ndf	Root:shoot		Leaf mass ratio		Root mass ratio	
		F	*P*	*F*	*P*	*F*	*P*
Light (L)	2	0.71	0.495	0.20	0.819	0.63	0.533
N addition (A)	1	0.05	0.815	2.42	0.123	0.10	0.756
L*A	2	0.05	0.954	0.11	0.892	0.09	0.914
Species (S)	2	66.06	**< 0.001**	65.68	**< 0.001**	76.61	**< 0.001**
L*S	4	1.36	0.251	1.13	0.345	1.36	0.253
A*S	2	0.29	0.747	1.59	0.208	0.41	0.662
L*A*S	4	0.28	0.893	0.30	0.878	0.33	0.859

	ndf	Foliar N (year 0)		Foliar N (year 1+)^{a}		Root N	
		F	*P*	*F*	*P*	*F*	*P*
Light (L)	2	10.90	**< 0.001**	0.71	0.495	0.83	0.439
N addition (A)	1	0.69	0.409	0.17	0.680	4.06	**0.046**
L*A	2	0.39	0.679	0.48	0.621	1.07	0.345
Species (S)	2	37.01	**< 0.001**	41.74	**< 0.001**	1004.99	**< 0.001**
L*S	4	1.84	0.125	1.38	0.245	1.40	0.237
A*S	2	0.21	0.815	0.73	0.483	0.61	0.543
L*A*S	4	1.45	0.221	0.15	0.961	0.80	0.525

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

Table 15: Regression equations for selected physiological parameters measured on black spruce, *Rhododendron* and *Kalmia* under variable intensity of shading and nitrogen addition

Species	Y variable	X variable	Slope	Intercept	*F*	*P*	R^2
BS	A^a	LMA	0.082	-1.975	14.04	**0.001**	0.2461
All	$\%^{15}N$ Tot^a	LMA^a	0.746	-0.793	50.58	**< 0.001**	0.3934

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

Table 16: Summary of ANCOVA results photosynthesis rate (*A*) of black spruce, *Rhododendron* and *Kalmia* under variable intensity of shading and nitrogen addition

Source of variation (fixed)	ndf	A^a	
		F	*P*
Species (S)	1	9.16	**0.001**
LMA	1	9.38	**0.003**
S*LMA variable	1	4.55	**0.013**

Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom.

[a] Analysis performed on ln-transformed data.

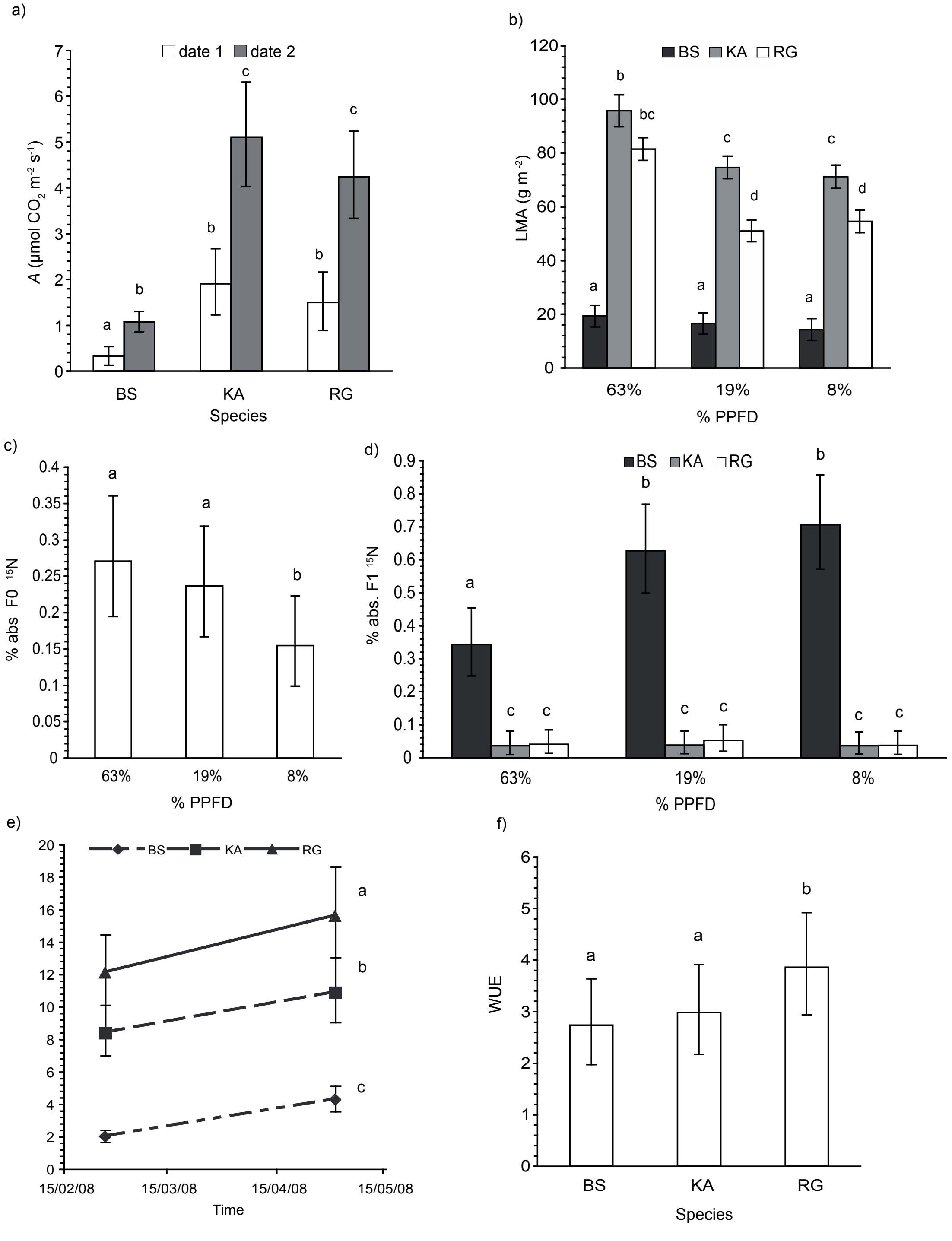

Figure 9: Species*date (a), light*species (b,d), light (c), species (f) effects for light-related relative growth rate, physiological parameters and foliar ^{15}N absorption plant traits. *A* = photosynthesis, LMA = leaf mass per unit of area, % abs. F0 ^{15}N: % current leaves foliar ^{15}N absorption, % abs. F1 ^{15}N: % 1+ year old leaves foliar ^{15}N absorption RGR aerial = relative growth rate for aboveground biomass, WUE = water use efficiency. Letters represent Fisher protected-LSD results. Analysis performed on ln-transformed data (LMA, *A*, RGRaerial) or square-root transformed data (% abs. ^{15}N F0, F1 and WUE); back transformed means and 95 % confidence interval approximates are presented (Ung and Végiard, 1988).

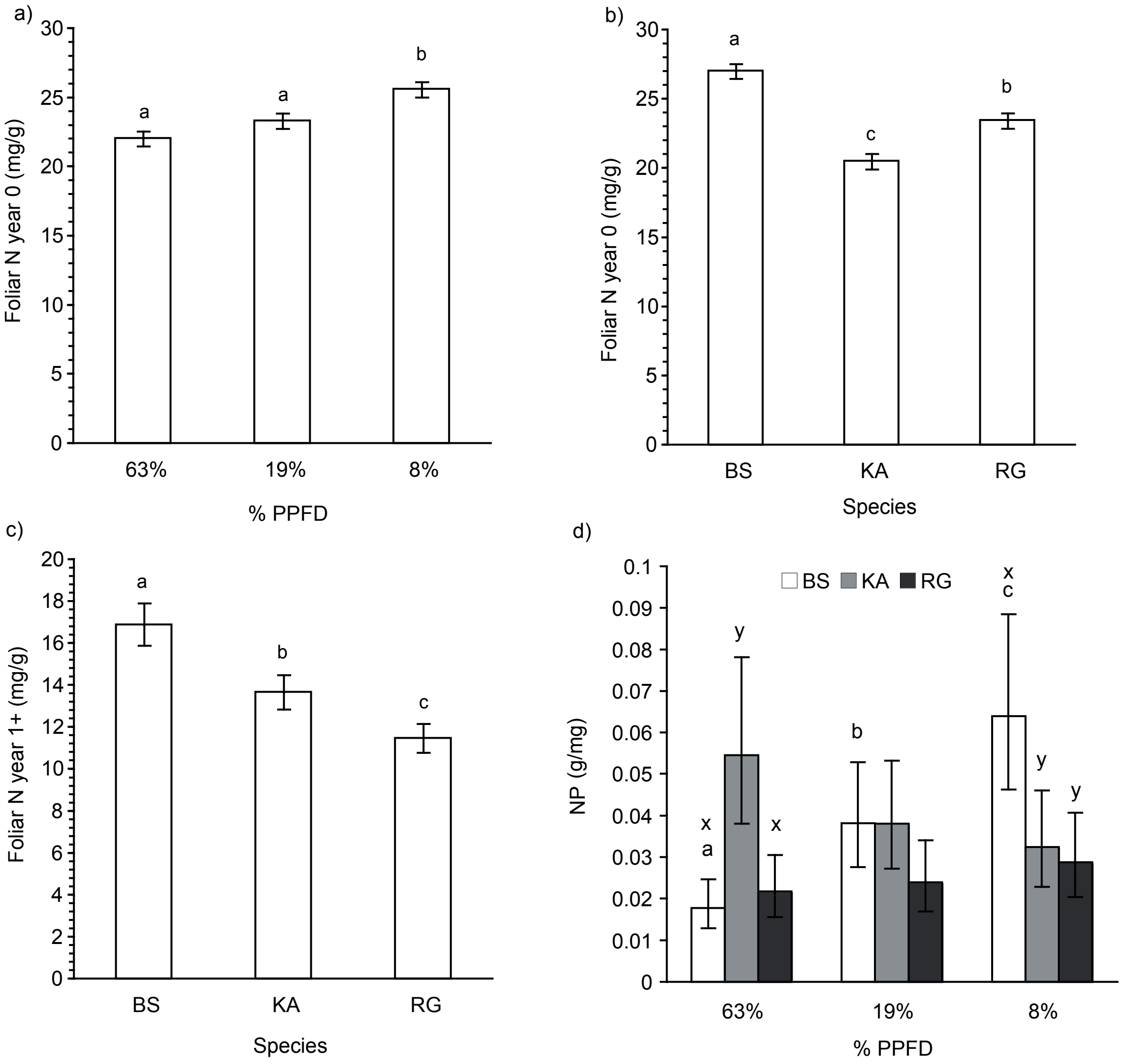

Figure 10: Light (a), Species (b,c) and light*species effects for nutrient-related plant traits. Letters represent Fisher protected-LSD results. Analysis performed on ln-transformed data (Foliar N 1+ year); back transformed means and 95 % confidence interval approximates are presented (Ung and Végiard, 1988).

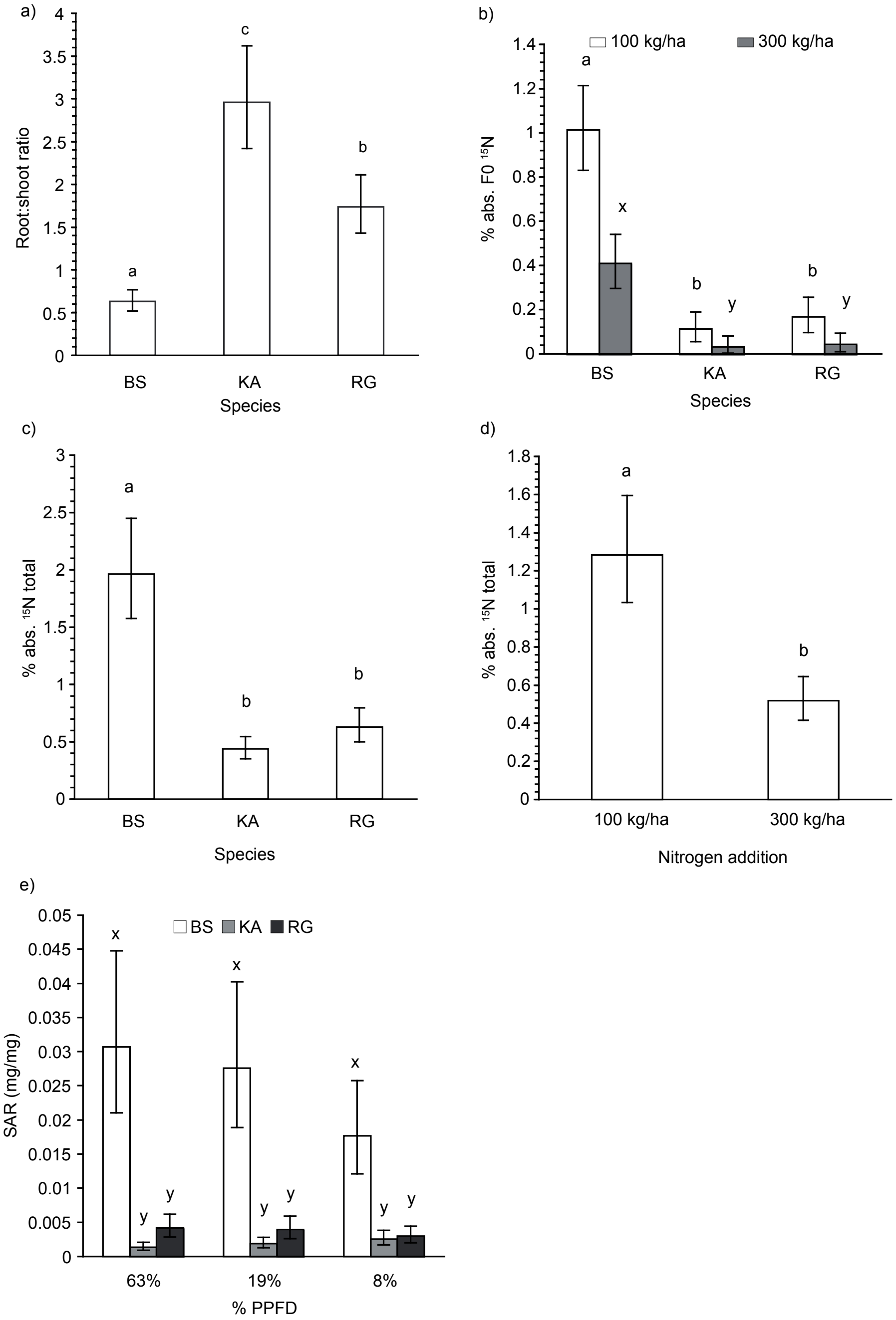

Figure 11: Species (a,c), species*nitrogen addition (b), nitrogen addition (d) and light*species (e) for root to shoot ratio, % of ^{15}N absorption and specific absorption rate. Letters represent Fisher protected-LSD results. % abs. ^{15}N F0 = % of ^{15}N absorbed by current year old foliage, % abs. ^{15}N total = % of ^{15}N absorbed by the entire plant, SAR = specific absorption rate. Analysis performed on ln-transformed data (% abs. ^{15}N total) or sqrt-transformed data (% abs. ^{15}N F0); back transformed means and 95 % confidence interval approximates are presented (Ung and Végiard, 1988).

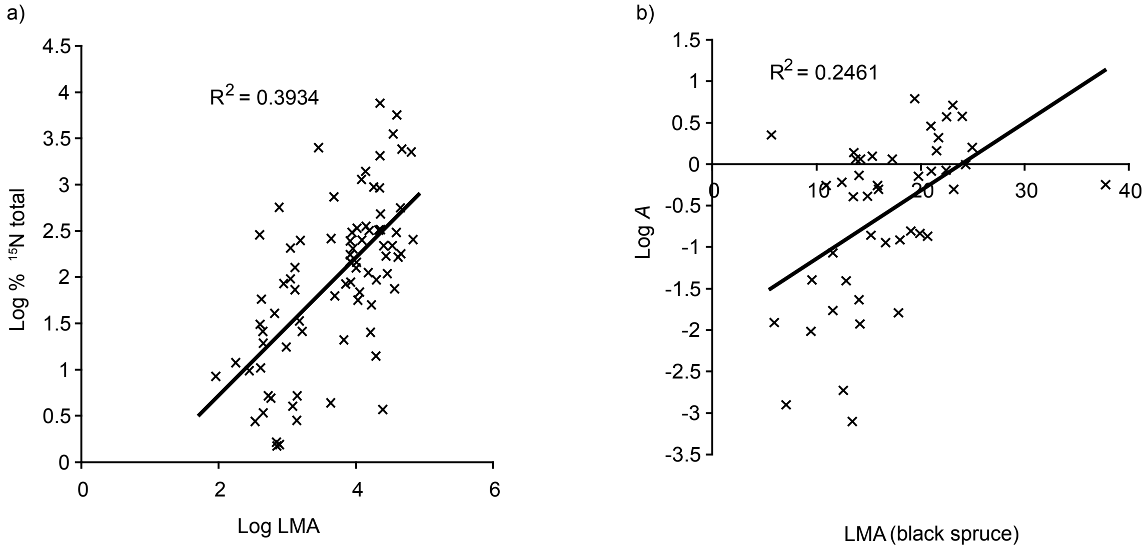

Figure 12: Relationship between selected physiological parameters. Refer to Table 15 for regression equations, *F* and *P* values.

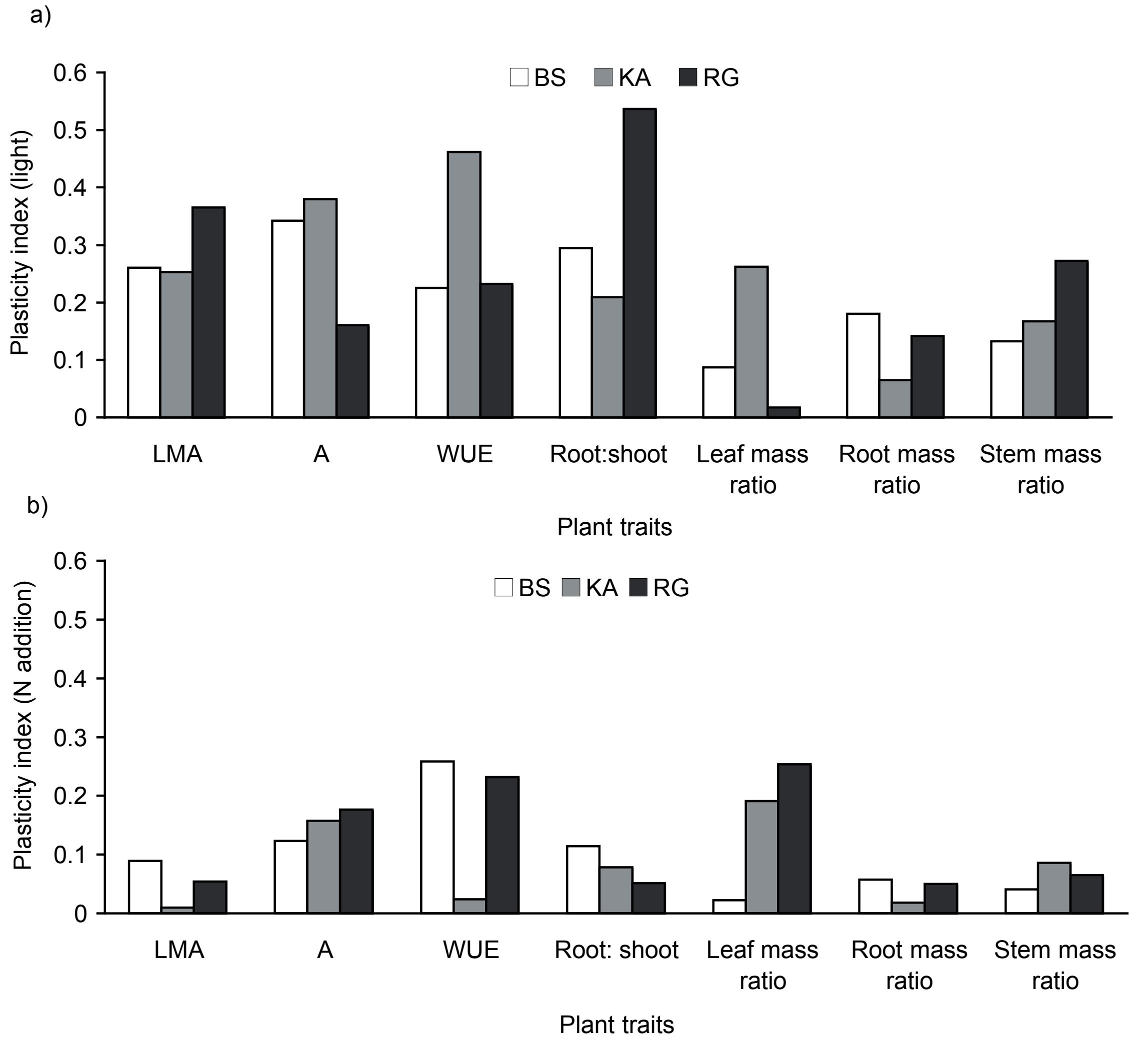

Figure 13: Plasticity index comparaison between light (a) and N addition (b) treatments for specific plant traits. LMA = Leaf mass per unit of area, A = photosynthetic capacity, WUE = water use efficiency.

4. Discussion

Kalmia and *Rhododendron* showed morphological plasticity to changes in light availability; however the variation in LMA did not translate into modification of photosynthetic or relative growth rates. As expected, LMA was higher in the HL treatment, possibly due to a greater fraction of palisade parenchyma with more tightly packed cells that contains higher concentrations of cell walls compounds, total non-structural carbohydrates and Rubisco:chl ratio, thus requiring more leaf nitrogen (Poorter et al. 2009). We expected the higher ^{15}N foliar absorption observed at HL and the significant relationship between total ^{15}N absorption and LMA to be concomitant with a positive link between photosynthesis and LMA, but it was not. This absence of relation may be due to an unplanned water stress induced by our fertilizer amendments, or by the higher soil temperature measured in the HL treatment, which was sometimes 10˚C higher than the shaded treatments (results not shown).

Greenhouse result of water use efficiency (WUE) for *Rhododendron* matches with measurments made under field conditions (see chapter 1). The higher WUE for *Rhododendron* could indicates a higher tolerance of this species to water stress, compared to black spruce, due to its rapid acclimation, which allows this species to adjust its physiological performance to changing growth conditions (Stratton and Goldstein 2001).

Black spruce showed no physiological or morphological acclimation at the leaf level and we measured relatively low values of LMA and *A*, which is typical of shade-adapted species (Givnish 1988, Kelly et al. 2009). Similar results for black and red spruce (*Picea rubens* Sarg.) were observed in the field; LMA remained constant regardless of the canopy opening following harvesting (Hébert et al. 2010, in press, Dumais and Prévost 2008). The inverse response of nutrient productivity (NP) to light availability could also indicates that black spruce foliage could have suffer from photoinhibition and, therefore, could have offset the acclimation response of this species.

We believe that the lack of plasticity of black spruce needle traits related to light had a more direct effect on seedling growth than traits related to nutrient acquisition. Evaluation of nutrient-related traits indicates that the low root:shoot ratio of black spruce, which favors light acquisition in shaded habitats, could be compensated by a higher nutrient assimilation efficiency compared to the ericaceous species. The percentage of ^{15}N absorbed by black spruce per unit of root biomass was higher than for the ericaceous species for all biomass compartments, and coupled with a higher specific absorption rate. These results confirm the high efficiency of the conifer roots to acquire soil nutrients, compared to the ericaceous species (Thiffault et al. 2004). Saldana-Acosta et al. (2009) found that shade-tolerant species can have either high or low root:shoot ratios, depending on species. It indicates that this trait may not be a good indicator of shade tolerance.

We found that the higher level of N addition did not increase growth for any of the species; % of ^{15}N absorption for all biomass compartments was higher under the lowest N addition treatments. In fact, the absolute amount of ^{15}N absorbed was similar between amendment treatments. This may be indicative of the resource-conservative strategy of all of these species; because they are well-adapted to low levels of soil nutrient availability typical of the black spruce-feathermoss soil conditions, they are not able to respond to nutrient levels that are much higher than normally available in their natural environment (Grime 1977).

Low root:shoot ratio can indicates that a species favors light acquisition in order to achieve higher growth when light increases (Givnish 1988). However, the low LMA of black spruce leaves did not permit such increased growth, when exposed to full sunlight. Therefore, it seems that black spruce LMA limited photosynthesis and growth more than nutrient acquisition because 1- LMA is linked with N content, which is higher in high LMA leaves and 2- higher foliar N content could lead to a higher photosynthesis rate that can ultimately be translated into a higher growth rate but it did not happen for this study.

We hypothesized that *Kalmia* shows a higher plasticity to light, followed by *Rhododendron* and black spruce. Photosynthesis rates and WUE partially confirmed this hypothesis, but LMA response did not. The PI of LMA was higher for *Rhododendron* than for *Kalmia*, which could indicate that *Rhododendron* could grow on a broader range of light environments. Furthermore, higher plasticity of WUE for *Kalmia* is in opposition with the results of Laberge-Pelletier (2007), who found that *Rhododendron* was found on a broader gradient of soil humidity, whereas *Kalmia* was particularly associated with drier soils. *Rhododendron* and black spruce have a tendency to be more plastic in relation to nutrient availability, which is in accordance with the late successional status of these two species, nutrients being more limited at the end of the succession.

Our results illustrate how LMA is an important indicator of plant ‘’strategies’’ that could explain the invasive nature of ericaceous species following disturbances in Canada’s northeastern boreal forest. Given their high level of plasticity for this trait, *Kalmia* and *Rhododendron* can respond positively to increased light levels following logging, with increased photosynthesis rate and growth (Feng et al. 2008). We thus conclude that the higher plasticity of these shrubs coupled with the absence of plasticity for black spruce is a potential explanation of ecosystem retrogression following major disturbances in Canada’s northeastern boreal forests.

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Conclusion générale

L'objectif de cette série d'études était d'expliquer, par des mesures physiologiques et morphologiques, le potentiel d'envahissement des éricacées et la stagnation de la croissance de la régénération naturelle d'épinette noire (*Picea mariana* Mill. [B.S.P.]) après CPRS dans le domaine de la pessière noire à mousses de l'est. Pour ce faire, j'ai mis en place deux expériences sur le terrain et une en serre. La première expérience terrain visait à comparer les traits fonctionnels du thé du Labrador (*Rhododendron groenlandicum* [Oeder] Kron & Judd) avec ceux de la régénération naturelle d'épinette noire soumis à différents niveaux de coupe en comparant la réponse avant et deux ans après coupe. Les coupes partielles utilisées dans ce dispositif visaient à préserver la structure irrégulière de ces peuplements, une approche proposée afin d'atteindre des objectifs d'aménagement écosystémique. Nous avions comme hypothèse que la réduction du couvert forestier augmenterait la disponibilité des ressources, et que le thé du Labrador montrerait une acclimatation physiologique et morphologique supérieure et une plus grande efficacité d'utilisation des ressources que l'épinette noire. La deuxième expérience visait plutôt à évaluer l'effet de la compétition par les éricacées sur les caractéristiques physiologiques et morphologiques des marcottes d'épinette noire selon un gradient de fertilité de sites dans des CPRS de 10 ans. Les hypothèses sous-jacentes à cette expérience étaient que la présence des éricacées affecterait les paramètres physiologiques de l'épinette noire (diminution des taux d'échanges gazeux, plus faible potentiel hydrique et contenu foliaire en nutriments) par les effets que les éricacées pourraient avoir sur les caractéristiques du sol (diminution de la disponibilité des nutriments), résultant en une plus grande efficacité d'utilisation des ressources des marcottes d'épinette noire. De plus, ces effets négatifs devraient être accentuées lorsque la fertilité intrinsèque du site était faible. Finalement, le dernier chapitre de la thèse visait à comparer les traits fonctionnels du kalmia à feuilles étroites (*Kalmia angustifolia* L.), du thé du Labrador et de l'épinette noire soumis, sous conditions contrôlées, à différents niveaux d'ombrage et de fertilité pendant une saison de croissance, l'hypothèse étant que les traits fonctionnels associés à l'acquisition de la lumière et des nutriments pourrait expliquer la dominance successionnelle de chaque espèce et une présence accrue des éricacées en début de succession.

Pour la première expérience, nous avons mesuré différentes variables morphologiques et physiologiques du thé du Labrador et de l'épinette noire avant et deux années après différentes intensités de coupe. Les résultats montrent que l'intensité de la coupe dans les pessières noires à éricacées n'a eu aucun impact sur la disponibilité des ressources du sol. Il semble que le thé du Labrador s'acclimate rapidement à l'augmentation de lumière causée par la coupe, plus spécifiquement dans les coupes les plus intenses (CPPTM et CPRS), par des modifications des traits physiologiques du feuillage tout en ayant des fonctions hydriques supérieures à l'épinette noire. Deux ans après coupe, le taux de photosynthèse a augmenté de 50 %. Quant aux marcottes d'épinette noire, la coupe, créant un déficit de pression de vapeur supérieur, a eu un effet sur les fonctions hydriques se traduisant par une plus faible conductance stomatique. Par contre, cette diminution de conductance n'a pas influencé le taux de photosynthèse, ni la masse foliaire par unité de surface de cette espèce. Il semble que la coupe a provoqué seulement un effet significatif sur les variables physiologiques des deux espèces à l'étude, possiblement parce que les mesures furent réalisées seulement deux ans après coupe. La réponse plus rapide de thé du Labrador semble être une indication que cette espèce pourrait avoir un avantage compétitif supérieur à l'épinette noire dans ces peuplements, deux ans après coupe. Par contre, il se pourrait que cette avantage disparaisse ou, du moins, diminue dans les futures années puisqu'il est reconnu que l'acclimatation des marcottes d'épinette noire à la coupe forestière peut prendre jusqu'à huit ans. Il serait donc pertinent de refaire cette expérience 10 ans après coupe, en prenant soin, cette fois, de mesurer la croissance de chaque espèce, ce qui permettrait de mesurer certains traits fonctionnels comme des ratios de biomasse. De plus, les mesures physiologiques devraient être réalisées sur les aiguilles d'épinette de l'année précédente puisque se sont celles qui obtiennent le plus grand taux de photosynthèse. Conséquemment, il serait donc possible de comparer le taux de photosynthèse plus tôt dans la saison et ainsi obtenir plus de périodes d'échantillonnage. Finalement, il serait nécessaire de mesurer la réponse de ces deux espèces dans différentes zones du parterre de coupe (sentier vs zone coupée, vs zone non perturbée) puisque la quantité d’arbre prélevées est différente et pourrait créer, à long terme, un patron spatial d’envahissement d’éricacées, notamment dans les traitements de coupes partielles.

La régénération naturelle d’épinette noire a servi de phytomètre au cours de la deuxième expérience terrain et nous avons mesuré la physiologie de l’épinette noire et la disponibilité des nutriments du sol durant deux saisons de croissance selon un gradient de fertilité de sites en accord avec la classification écologique du ministère des ressources naturelles et de la faune du Québec. Nous avons sélectionné trois types écologiques de différents niveaux de fertilité où il y avait un risque d’envahissement des éricacées. Ces trois types écologiques étaient (du moins fertile au plus fertile): RE21, RS20 et RS22 que nous avons reclassés comme site de faible, moyenne et haute fertilité. L’éradication complète de la végétation de compétition a augmenté la disponibilité en NH_4-N et K du sol, avec des augmentations de 67 % et 28 % comparativement aux parcelles témoin. Ces augmentations pourraient être un effet combiné de la compétition des éricacées pour l’azote du sol et de l’augmentation de la disponibilité de l’azote du sol libérée par la décomposition du système racinaire des éricacées éradiquées. Le taux de photosynthèse (A) et le contenu foliaire en K étaient plus élevés dans les parcelles sans compétition, peu importe la qualité de la station. La photosynthèse n’a pas semblé être limitée par la disponibilité de l’azote ou de l’eau, mais possiblement par un déficit en K foliaire, résultant possiblement d’une diminution provoquée par la séquestration du système racinaire des éricacées. Tout comme dans l’expérience terrain du premier chapitre, il serait nécessaire de reconduire cette expérience 10 ans après traitement afin que l’on puisse constater, s’il y lieu, un effet du retrait de la végétation de compétition sur la croissance de l’épinette noire étant donné que cette espèce réagit lentement aux changements de conditions de croissance. L’absence d’interaction entre la fertilité de la station et l’éradication des éricacées suggère que le contrôle de la végétation éricacée doit être planifiée indépendamment de la qualité de la station. Par contre, il est possible que les types écologiques choisis dans cette expérience ne reflètent pas véritablement un gradient suffisamment grand de fertilité afin que l’on puisse détecter des différences sur la physiologie de l’épinette noire. Il aurait possiblement été plus efficace d’effectuer une recherche de site sans recourir aux types écologiques, mais plutôt en établissant des catégories de fertilité de site (avec présence d'éricacées) à partir d'analyses de sols faites *a priori*.

Afin de tester les hypothèses du troisième chapitre, une expérience en serre a été réalisée en comparant deux espèces d'éricacées de début et de fin de succession (*Kalmia* et *Rhododendron*) et l'épinette noire soumis à trois niveaux de lumière (63, 19 et 8 %) et deux niveau d'addition d'azote ^{15}N (100 kg/ha/an et 300 kg/ha/an) pendant une saison de croissance simulée. Nous avons mesuré différents traits fonctionnels associés à l'acquisition de lumière (LMA, concentration d'azote foliaire, photosynthèse) et à l'acquisition des nutriments (productivité d'azote, ratio d'absorption spécifique, absorption de ^{15}N). En ce qui a trait à la réponse à la lumière, seul le LMA des deux espèces éricacées a diminué avec l'ombrage; le LMA du *Rhododendron* et du *Kalmia* étant 54 % et 31 % plus élevé dans le traitement ayant la plus grande disponibilité lumineuse. La morphologie du feuillage des éricacées s'acclimate donc plus rapidement afin de maximiser la capacité photosynthétique en présence d'une plus grande quantité de lumière disponible. Quant à l'épinette noire, les traits morphologiques et physiologiques relies à la l'acquisition de lumière mesurés lors de cette expérience reflètent le comportement de cette espèce en conditions naturelles. Ceci nous laisse croire que les plants provenant de pépinière se comportent de la même façon que les semis naturels. Malgré tout, il serait peut-être bénéfique de recommencer l'expérience en comparant cette fois-ci des plants d'éricacées avec des semis naturels d'épinette noire. De son côté, l'addition d'azote a eu le même effet pour toutes les espèces à l'étude mais le ratio d'absorption spécifique et l'absorption d'azote furent supérieurs pour l'épinette noire. Cette absence d'effet pourrait être la résultante d'un taux de fertilisation d'azote (100 kg/ha/an) supérieur à la demande des trois espèces à l'étude. Un troisième traitement avec une plus faible quantité d'azote appliquée (ex. 20 kg/ha/an) aurait peut-être donné des résultats différents quant à la réponse des traits à l'addition d'azote. La plasticité en réponse à la lumière fut supérieure pour le *Kalmia* à l'exception du LMA et la plasticité en réponse à l'addition d'azote a été supérieure pour le *Rhododendron* et pour l'épinette noire, ce qui est en accord avec le statut successionnel des deux espèces. Les résultats suggèrent que la plasticité pour le LMA semble être le trait fonctionnel qui explique le plus l'avantage compétitif des éricacées (spécialement le

Rhododendron) et un potentiel d'envahissement des peuplements après perturbation. Cependant, comme il fut impossible de tester statistiquement les différences de ces indices de plasticité, nous devons être très prudents quant aux conclusions que nous pouvons en tirer.

Les résultats de cette thèse confirment que les traits reliés à l'acquisition de la lumière permettent de mesurer de la dynamique de compétition entre les espèces éricacées et l'épinette noire lorsque les conditions de lumière sont modifiées, du moins à court terme; les traits fonctionnels, comme le taux de photosynthèse et la masse foliaire par unité de surface, étant reconnus comme ayant un effet sur les traits liés à la prise de nutriments et sur la croissance (Figure 14). Tout comme dans d'autres études concernant l'acclimatation de l'épinette noire, les résultats de cette thèse semble démontrer que cette espèce réagit lentement aux changements de conditions de lumière, et ce, indépendamment de la présence ou non de végétation de compétition. Cette période de latence pourrait être néfaste à court terme et mener à un envahissement graduel des éricacées qui, contrairement à l'épinette noire, profitent de l'ouverture du couvert en modulant leurs traits afin de profiter d'une augmentation de lumière disponible. Par contre, en éliminant la compétition éricacée à l'intérieur du peuplement, il est possible de mesurer une réponse physiologique des marcottes d'épinette noire qui pourrait permettre d'assister à une reprise de croissance à moyen terme, et ce, peu importe la qualité de la station. Ceci nous laisse croire que l'épinette noire profite plus rapidement d'une augmentation de la quantité disponible de nutriments du sol que d'une augmentation de lumière disponible.

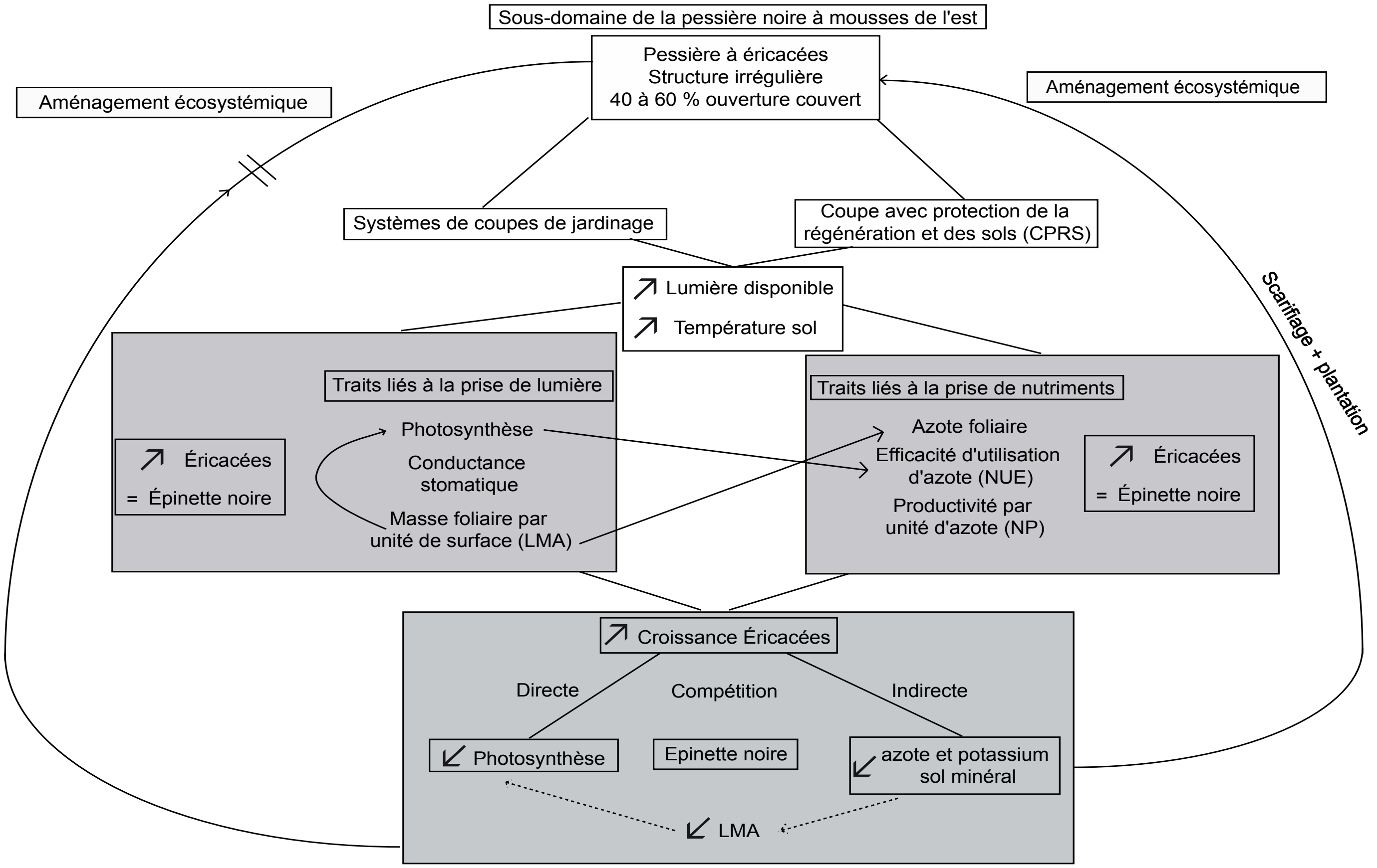

Figure 14: Schéma conceptuel de la dynamique entre la vegetation de compétition et l'épinette noire dans la pessière noire à mousses de l'est soumise à des perturbations anthropiques

Implications pour l'aménagement de la pessière noire à mousses de l'est du Québec

En regard des résultats obtenus, je conclus que les traitements de coupe partielle dans les peuplements irréguliers et inéquiens d'épinette noire avec une forte présente d'éricacées ne constituent pas une stratégie sylvicole appropriée et ne feraient que retarder la perte de production ligneuse du peuplement, qui pourrait n'être que ponctuelle étant donnée le peu de données disponibles actuellement. Cette approche avait été choisie et testée afin de respecter le concept d'aménagement écosystémique qui consiste à assurer le maintien de la biodiversité et la viabilité des écosystèmes en diminuant les écarts entre la forêt aménagée et la forêt naturelle. Il semble que l'application de coupes partielles dans ce genre de peuplements, dans la pessière noire à mousses de l'est, ne permettrait pas l'atteinte de cet objectif étant donné qu'il existe toujours un risque de conversion en une lande improductive ou, du moins, à une perte de productivité ligneuse. De plus, la structure diamétrale des peuplements étudiés laisse croire que les coupes partielles, telles que proposées, sont peut-être mal adaptés et causent un changement dans la structure laissant sur pied une quantité importante de tiges ayant un diamètre à hauteur de poitrine en 9 et 14 cm. Par contre, d'autres traitements sylvicoles pourraient être effectués dans ce genre de peuplement tout en respectant le principe d'aménagement écosystémique (Figure 15).

Il est impératif de choisir des traitements sylvicoles qui permettront de détruire temporairement le système souterrain de cette famille de plantes afin d'empêcher la régénération végétative privilégiée par les éricacées. Parmi les solutions envisageables, il semble que le scarifiage après coupe soit un des seuls traitements efficaces pour enrayer la compétition afin de permettre à l'épinette noire de refermer le couvert, étant donné que l'application des phytocides est interdite au Québec et que le brûlage dirigé ne permet pas de détruire la partie souterraine des éricacées. Par contre, il faudra procéder par plantation après scarifiage, afin de permettre le retour de la strate arborescente.

À l'échelle du paysage, le scarifiage après coupe proposé pour les pessières à éricacées peut s'intégrer dans un principe d'aménagement écosystémique puisque ces peuplements ne représentent qu'une faible proportion du territoire de la pessière noire à mousses de l'est. En appliquant les coupes partielles dans des peuplements irréguliers et inéquiens sans présence d'éricacées, il sera quand même possible de conserver ces structures. On pourrait donc affecter les pessières à éricacées, et ce, peu importe la qualité de la station, à un zonage de sylviculture intensive qui pourrait être compensé par des zones de conservation intégrales.