UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

EFFETS DE LA FERTILISATION, DE LA DIVERSITÉ CLONALE ET DE LA PLASTICITÉ PHÉNOTYPIQUE SUR LA PRODUCTIVITÉ DES PLANTATIONS DE PEUPLIER HYBRIDE SUR UN GRADIENT LATITUDINAL DE L'OUEST DU QUÉBEC

THÈSE

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Abréviation	Définition	Unité
A_b	Surface de la base du tronc à 10 cm du sol	m^2
AR	Précipitation annuelle	mm
BBD	Durée du débourrement	Jour
BBLS	Date du dernier stade du débourrement	Jour de l'année
BBS	Date du début l'aoutement	Jour de l'année
BD	Diamètre à la base du tronc (10 cm du sol)	mm
BSD	Durée de l'aoutement	Jour
BSS	date du début du débourrement	Jour de l'année
CEC	Capacité d'échange cationique	cmol kg^{-1}
CI	Indice de correction	
CV	Coefficient de variation	%
CV_{FK}	Coefficient de variation de Francis and Kannenberg	%
DM	Masse anhydre	g
DDA	Degrés jour de croissance du dernier mois d'aoutement (Octobre)	°C
DOY	Jour de l'année (jour julien à partir du 1er janvier)	
DRIS	Diagnosis and Recommendation Integrated System	%
FFA	Nombre de jours à température positive du mois du débourrement (Avril)	Jour
FFO	Nombre de jours à température positive du mois d'aoutement	Jour

GD	Durée de la saison de croissance	Jour
GDD	Degrés jour de croissance (T° de base = 5 °C)	°C
G_s	Conductance stomatique	mmol m^{-2} s^{-1}
H	Hauteur de l'arbre	m
J_{max}	Vitesse maximale de transport d'électron	µmol m^{-2} s^{-1}
MAT	Température annuelle moyenne	°C
MC	Teneur en humidité	%
MDI	Croissance moyenne journalière	cm^3 day^{-1}
N_a	Concentration de l'azote par unité de surface foliaire	g m^{-2}
N_m	Concentration de l'azote par unité de masse foliaire	mg g^{-1}
NBI	Indice d'équilibre nutritionnel	
PAR	Rayonnement photosynthétiquement actif	µmol m^{-2} s^{-1}
P_n	Photosynthèse nette (foliaire)	µmol m^{-2} s^{-1}
PNUE	Efficacité d'utilisation photosynthétique de l'azote	µmol CO2 g^{-1}N s^{-1}
R_d	Respiration à l'obscurité	µmol m^{-2} s^{-1}
RGR	Taux de croissance relative	m^3 m^{-3} $year^{-1}$
SPG	Période d'ensoleillement des mois de croissance (heures)	h
SLA	Surface foliaire spécifique	cm^2 g^{-1}
TNC	Carbohydrates non structurales totales	mg.g^{-1}
TP_i	Indice de plasticité phénotypique	
V	Volume du tronc	m^3
Vc_{max}	Vitesse maximale de carboxylation	µmol m^{-2} s^{-1}
VPD	Déficit de pression de vapeur de 1 'air	mba

RÉSUMÉ DE LA THÈSE

Cette thèse visait à acquérir une meilleure compréhension de l'effet des paramètres écophysiologiques (photosynthèse et nutrition minérale en particulier), en interaction avec les conditions du milieu, sur la productivité des plantations de peuplier hybride en milieu boréal. Plus spécifiquement, la thèse visait à : *i)* tester l'efficacité de la fertilisation basée sur la méthode DRIS (Diagnosis and Recommendation Integrated System). Cette approche est basée sur les ratios des nutriments, pour le diagnostic d'éventuelles carences nutritives en vue de déterminer plus précisément les besoins en fertilisant et optimiser le statut nutritif et la croissance du peuplier hybride, *ii)* déterminer l'effet de la diversité clonale sur le statut nutritif, la photosynthèse, le développement racinaire et la productivité des peupliers hybrides et *iii)* étudier la plasticité des clones de peuplier hybride suivant un gradient latitudinal et en réponse à l'espacement entre les arbres, et déterminer les traits physiologiques et morphologiques permettant de la caractériser.

Trois plantations expérimentales de quatre clones de peupliers hybrides ont été établies dans les régions de l'Abitibi-Témiscamingue et du Nord du Québec, Canada (747215, *Populus trichocarpa* Torrey & A.Gray × *P. balsamifera* L.; 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and 915319 *P. maximowiczii* × *P. balsamifera*). Nous avons comparé l'effet de différents traitements de fertilisation sur le statut nutritif et la croissance des peupliers hybrides en plantation. Des parcelles mixtes composées des quatre clones et des parcelles monoclonales ont été établies afin de comparer l'effet des deux types de déploiement sur la productivité du peuplier hybride. Finalement, des parcelles des quatre clones ont été établies dans trois sites le long d'un gradient latitudinal et à différents espacements (1×4 m, 2×4 m et 3×4 m), afin d'évaluer, respectivement, la plasticité des clones en réponse au gradient latitudinal et à la compétition intraclonale.

Nos résultats ont montré que la fertilisation basée sur la méthode DRIS permettait de bien corriger les carences en azote, alors que les carences en phosphore n'ont pas été corrigées. L'utilisation de ce type de fertilisation n'a cependant augmenté le taux de croissance moyen des arbres que de seulement 6.1% comparativement aux arbres non fertilisés. L'utilisation de la méthode DRIS a également donné des résultats légèrement supérieurs à la dose de fertilisants traditionnelle (40N, 20P, 20K). La fertilisation basée sur DRIS apparaît globalement avantageuse par rapport à la dose traditionnelle pour corriger la carence azotée, améliorer la productivité des clones et éviter une fertilisation excessive.

En ce qui a trait au type de déploiement, la productivité des arbres était souvent supérieure dans les parcelles polyclonales comparées aux parcelles monoclonales, après cinq années de croissance, en augmentant la croissance en volume des arbres des quatre clones de 21% en moyenne. Le développement des racines différait entre les deux types de déploiements, avec un ratio de biomasse racinaire / biomasse aérienne des arbres des parcelles monoclonales supérieur à celui des parcelles polyclonales. Nous avons également observé une différence dans la distribution latérale des racines grosses et fines; La fraction

des racines située à ≥ 60 cm était supérieure dans le déploiement monoclonal, ce qui suggère une compétition plus prononcée dans ce déploiement, poussant les racines à chercher les nutriments à distance. La photosynthèse nette avait tendance à augmenter dans les parcelles polyclonales chez la plupart des clones, ce qui est cohérent avec la teneur plus élevée en glucides totaux non-structuraux (TNC) des racines observées dans les parcelles polyclonales.

La date de débourrement du bourgeon terminal variait le long du gradient latitudinal et la saison de croissance raccourcissait à divers degrés selon les clones, en allant vers le nord. Le débourrement du clone 915319, le plus productif, a commencé plus tard mais duré moins longtemps que celui des autres clones, notamment le 747215, le moins productif. L'écart dans la date de débourrement entre le site du sud et celui du nord du premier clone était moins important ce qui lui a permis d'être plus productif sur tout le territoire et moins affecté par la latitude. La date de l'aoûtement a été peu influencée par le gradient latitudinal, mais différente entre les clones. Les clones ont démontré une plasticité de la capacité photosynthétique le long du gradient qui s'est traduite par une variation des vitesses maximales de carboxylation (Vc_{max}) et de transport photosynthétique des électrons (J_{max}) le long du gradient. Ces deux paramètres étaient souvent supérieurs dans le site méridional. L'acclimatation à la compétition par la réduction de l'espacement entre les arbres s'est manifestée essentiellement par des ajustements morphologiques, particulièrement pour la surface foliaire spécifique et la hauteur des arbres plantés à 1×4 m qui étaient supérieures à celles des arbres espacés de 2×4 m ou de 3×4 m. Ces réponses à la forte densité de plantation semblaient permettre une meilleure interception de la lumière par les feuilles et une allocation de l'azote foliaire aux protéines impliquées dans la photosynthèse. Ceci était en accord avec les résultats sur l'effet de l'espacement sur la photosynthèse montrant que le taux d'assimilation nette (P_n) des feuilles était généralement supérieur dans les parcelles à densité élevée, suggérant que la plasticité morphologique a permis de réduire l'effet de l'ombrage et de la compétition pour l'azote, et d'accroitre la photosynthèse des arbres.

Cette étude a permis d'approfondir les connaissances sur la nutrition minérale des peupliers hybrides en milieu boréal, leur acclimatation à la compétition intra et inter-clonale et sur la plasticité phénotypique le long d'un gradient sud-nord. Les résultats de ce travail pourront servir à établir des recommandations dans l'aménagement des zones à production ligneuse intensive au Québec.

Mots clés: Fertilisation, DRIS, peuplier hybride, mélange clonal, compétition, plasticité phénotypique.

Key words: Fertilization, DRIS, hybrid poplar, clones mixture, competition, phenotypic plasticity.

1. INTRODUCTION GÉNERALE

Avant-propos

Cette thèse est composée de cinq sections : la première partie est consacrée à introduire les thématiques de recherche à travers une revue de littérature et à définir les objectifs de travail. Dans la dernière section, nous avons discuté des principaux résultats et ouvert des perspectives de recherche dans la même thématique. Les chapitres 2 à 4 forment le corps de cette thèse et ont été dédiés à la vérification et la discussion des hypothèses relatives au travail. Ils ont été rédigés en langue anglaise sous forme d'articles scientifiques; le chapitre 2 a été publié dans "New Forests" (2012), le chapitre 3 dans Forest Ecology and Management (2014) et le chapitre 4 sera soumis prochainement à une revue avec comité de lecture.

1. 1 Problématique de recherche

La superficie des plantations forestières ne cesse de s'accroître un peu partout dans le monde (FAO 2010). Elles contribuent aux stratégies d'aménagement forestier durable car leur mise en place permet de réduire la pression d'exploitation des forêts naturelles tout en maintenant l'approvisionnement en bois. La sylviculture de courte rotation d'espèces à croissance rapide comme le peuplier hybride (*Populus spp.*), dite sylviculture intensive, représente un moyen efficace pour produire une importante quantité de fibre de bois en peu de temps, particulièrement dans les régions nordiques où la saison de croissance est courte (Larocque *et al.* 2013). Le peuplier compte plus de 35 espèces réparties en cinq sections botaniques et de nombreux hybrides naturels bien adaptés à diverses conditions climatiques et édaphiques, qui se caractérisent par un taux de croissance parmi les plus élevés des espèces forestières des régions tempérées et boréales (Dickmann *et al.* 2001). L'hybridation entre les espèces de la même section est facile et elle est possible entre certaines espèces de sections différentes. La sylviculture intensive du peuplier, ou populiculture, repose sur l'usage d'arbres issus de programmes d'amélioration génétique et de croisements dirigés inter-spécifiques (parents appartenant à des espèces de peuplier différentes). Le but de ces croisements est d'avoir des cultivars à forte vigueur hybride qui intègrent les traits d'intérêt

des deux parents tels que, entre autres, la résistance aux ravageurs, la tolérance au gel et l'architecture du houppier (Riemenschneider *et al.* 2001, Dillen *et al.* 2010). Le cultivar ainsi obtenu est par la suite multiplié végétativement. La populiculture avec des rendements escomptés au Québec jusqu'à 20 m^3 ha^{-1} an^{-1} et des courtes rotations (15-20 ans) exige en plus d'un matériel végétal hautement productif, un itinéraire cultural rigoureux qui comprend une préparation de terrain similaire à celle des cultures conventionnelles, l'élimination de la flore adventice et la fertilisation jusqu'à la fermeture de la canopée (Stanturf *et al.* 2001). De nombreuses connaissances ont été acquises sur la biologie du peuplier durant les dernières décennies, dont la plus remarquable est le séquençage complet du génome du peuplier de l'ouest (*Populus Trichocarpa* Torr. & Gray) en 2006 (Tuskan *et al.* 2006). Ceci a permis de mettre en place de nouvelles approches d'amélioration génétique du peuplier, basées sur l'identification de gènes contrôlant des caractères d'intérêt et la caractérisation de marqueurs génétiques (Stanton *et al.* 2010).

Par ailleurs, les programmes d'amélioration génétique du peuplier ne se contentent plus des traits directement liés à la productivité, mais aussi de ceux relatifs à l'adaptation et la plasticité. Ces derniers sont devenus importants à cause du rythme rapide des changements climatiques et de leur effet sur le réchauffement global. Les précipitations et la teneur atmosphérique en CO_2 représentent des éléments déterminants lors du déploiement et du calcul du rendement des plantations de peuplier hybride (Tissue *et al.* 1997, Zhu *et al.* 1999).

La nutrition minérale d'espèces à croissance rapide, comme le peuplier hybride, représente un élément clé de réussite surtout les premières années suivant leur plantation (Verwijst 1996). Ces espèces ont des besoins nutritionnels importants et exigent un apport équilibré en nutriments. La réduction des carences nutritionnelles qui nuisent au rendement, représente un défi de taille particulièrement lorsque les plantations sont installées sur des terres marginales, pauvres en nutriments (Heilman et Xie 1993). L'équilibre nutritionnel est indispensable et peut être assuré par un apport en nutriments (fertilisation), un entretien régulier ou la culture de plusieurs espèces ou clones dans le même site, qui permettrait de réduire la compétition pour les nutriments et favoriser la complémentarité entre les individus. Par ailleurs, la stabilité des rendements des cultivars sur un large spectre de conditions environnementales est un caractère recherché en sylviculture intensive. Cette stabilité est liée

à la plasticité phénotypique de certains traits relatifs à la productivité tels que l'activité photosynthétique, la morphologie foliaire ou le développement des racines.

1. 2 Nutrition minérale des plantations de peuplier hybride

La croissance rapide du peuplier (*Populus* ssp) est en lien avec leur haute teneur foliaire en nutriments (Heilman et Xie 1993). Les carences nutritionnelles représentent le facteur limitant pour la croissance des plantations de peuplier particulièrement en région boréale en Amérique du Nord (Weih 2004; Ollinger *et al.* 2008). La carence en azote est de loin la plus limitante dans cette région (Oren *et al.* 2001, van den Driessche 1999). On a ainsi souvent recours à la fertilisation azotée, surtout quand la densité élevée des plantations accroit la compétition entre les arbres (Sedjo 2001). En effet, les sols des régions boréales sont naturellement pauvres, notamment en azote, à cause du faible taux de minéralisation conséquent à l'acidité du sol et aux basses températures sur une longue période de l'année. Une carence en macroéléments, tels que le phosphore et le calcium, peut affecter le rendement surtout si les plantations se trouvent sur des sols forestiers acides (Dickmann *et al.* 2001, van den Driessche *et al.* 2005). Heilman et Xie (1993) ont montré qu'une fertilisation à l'urée de jeunes plantations de peuplier était efficace et avait accrût le rendement à l'hectare de 21 % après trois saisons de croissance. Brown et van den Driessche (2005) ont trouvé que le rendement de plantations de peuplier hybride fertilisées au DAP (Diammonium phosphate) était équivalent à trois fois celui des témoins non fertilisés. La fertilisation azotée peut toutefois augmenter la sensibilité du peuplier hybride au stress hydrique dans certaines conditions et ainsi compromettre sa croissance (Harvey et van den Driessche 1997). Une fertilisation plus équilibrée par l'ajout d'autres éléments, (notamment le phosphore) permet de réduire cet effet (Harvey et van den Driessche 1997; DesRochers *et al.* 2007). Un statut nutritif azoté adéquat doit être atteint en premier lieu et l'apport des autres éléments, le phosphore en particulier, devrait être établi par la suite afin d'atteindre un équilibre nutritionnel (Dickmann *et al.* 2001).

1. 3 Intérêt du diagnostique foliaire dans la fertilisation des plantations de peuplier hybride

Les plantations de peuplier hybride sont souvent établies sur des sites agricoles abandonnés, pauvres en nutriments (Rompré et Carrier 1997; Heilman et Norby 1998, van den Driessche *et al.* 2005, Weih 2004). La fertilisation dès les premiers mois suivant la plantation peut être utile dans de telles conditions pour favoriser une croissance initiale et un enracinement rapides et l'obtention de rendements satisfaisants à la récolte (Heilman *et al.* 1994). Les fertilisants azotés et phosphatés sont hydrosolubles et se trouvent souvent lixiviés par les précipitations polluant ainsi les nappes et les cours d'eau limitrophes. La détermination des besoins nutritifs des plantations d'une façon précise et fiable permet, outre une croissance optimale des arbres et un gain sur les coûts de production, de réduire la contamination des cours d'eau par le surplus d'engrais et par conséquent la durabilité des plantations forestières. Les analyses foliaires permettent de mieux évaluer le statut nutritif des arbres, comparées aux analyses de sol. Actuellement, la plupart des techniques utilisées pour déterminer les besoins nutritifs des essences forestières supposent que la croissance des arbres n'est pas affectée tant que la teneur foliaire demeure au-dessus d'un seuil (e.g. 2 % de N, Coleman *et al.* 2006). Chez le peuplier, il a été démontré que la croissance des arbres était fortement corrélée aux teneurs en éléments nutritifs dans les feuilles (N, en particulier), même au-delà des concentrations critiques (Coleman *et al.* 2006). Beaufils (1973) a montré que les teneurs foliaires en nutriments étaient fortement affectées par l'âge, la position ou l'ordre de la feuille ce qui pourrait être une source d'erreur lors de l'échantillonnage des feuilles. En revanche, les ratios des éléments minéraux dans les feuilles (e.g. N:P, Ca :Mg..etc.) varient peu et l'erreur due à l'échantillonnage s'en trouve fortement réduite (Fageria 2001).

Au niveau du sol, les nutriments interagissent et les concentrations des uns influent sur l'absorption des autres. La méthode DRIS (Diagnosis and Recommandation Integrated System, Beaufils 1973), consiste à développer des équations basées sur les ratios des nutriments et qui sont par la suite transformées en indices DRIS (Walworth et Sumner 1987). La méthode DRIS a donné de résultats satisfaisants avec de nombreuses espèces agricoles (Ruiz-Bello et Cajuste 2002; Junior *et al.* 2003; Hartz *et al.* 2007; Hundal *et al.* 2007) mais

son efficacité sur des arbres forestiers à croissance rapide, reste à confirmer (Ruiz-Bello et Cajuste 2002, Junior *et al.* 2003, Hartz *et al.* 2007, Hundal *et al.* 2007). Guillemette et DesRochers (2008) ont testé cette méthode avec des peupliers hybrides et ont montré sa fiabilité surtout pour la fertilisation phosphatée. Les besoins nutritifs varient entre les clones de peuplier hybride à cause des différences entre les espèces-parents et de leur provenance géographique (DesRochers *et al.* 2007). On ignore encore si les recommandations de fertilisation obtenues par la méthode DRIS peuvent être appliquées sur plusieurs clones plus ou moins apparentés. Aussi, les besoins peuvent varier en fonction de la fertilité du sol, sa texture ou la topographie du site, et ce même à une échelle régionale. Par conséquent, il reste à vérifier si les recommandations obtenues avec les indices DRIS peuvent être appliquées en forêt boréale.

1. 4 L'effet diversité-productivité dans la foresterie à courte rotation

La perte de biodiversité est susceptible d'affecter le fonctionnement des écosystèmes (Tilman *et al.* 1997, Hooper *et al.* 2012). Le terme diversité comprend aussi bien la diversité des espèces et des gènes que la diversité des populations et des écosystèmes. Dans le contexte de la sylviculture intensive, la diversité implique le déploiement sur un même site de différentes espèces ou clones. Cette diversité aurait un effet positif sur la résistance face aux épidémies d'insectes et sur le rendement biologique des plantations, en plus de consolider la diversité animale et microbiologique, comparativement à des plantations monospécifiques ou monoclonales (Brockerhoff *et al.* 2008, Potvin et Gotelli 2008, Paquette et Messier 2011). Les travaux réalisés dans des milieux naturels ont montré que la diversité spécifique avait un effet positif sur le fonctionnent et la productivité des écosystèmes (Naeem *et al.* 1994, Hooper et Vitousek 1997). Les plantations de peuplier hybride se caractérisent par leur haut potentiel productif, mais sont souvent peu résistantes aux attaques d'insectes ou de champignons pathogènes. Un mélange de plusieurs espèces ou clones crée une hétérogénéité qui agit comme une barrière à la propagation des pathogènes et à la sélection de pathogènes plus virulents (Miot *et al.* 1999). D'ailleurs, on dénombre plus de 3000 espèces d'insectes et 250 espèces de champignons en Amérique du nord, dont le peuplier est un hôte et il est recommandé de recourir aux plantations multi-espèces ou polyclonales comme mesure préventive à l'attaque de ces pathogènes (Mattson *et al.* 2001). Par ailleurs, l'effet des

plantations mixtes sur le rendement global était positif pour un bon nombre d'études (Tilman 1999, Balvanera et Aguirre 2006, Potvin et Gotelli 2008, Lei *et al.* 2009, Paquette et Messier 2011) et a été attribué essentiellement à une meilleure croissance en diamètre des arbres en mélange (Piotto 2008).

L'effet positif de la diversité sur la productivité est souvent plus manifeste sur des sites pauvres et des conditions peu propices à la croissance (Rothe et Binkley 2001, Oelmann *et al.* 2010). La pression sur les ressources pourrait être réduite dans un mélange d'espèces grâce à un partage mutuel des ressources du fait de la diversité morphologique et phénologique (Schmid 2002, Erskine *et al.* 2006). En effet, la relation positive entre diversité et productivité chez les plantes a été expliquée par trois mécanismes principaux ; (i) la complémentarité, qui se traduit principalement par l'occupation des génotypes de niches différentes réduisant ainsi la compétition pour les ressources et augmentant la croissance. La séparation des niches peut se manifester par une stratification des systèmes racinaires, par une architecture différentielle du houppier ou par des phénologies asynchrones entre les génotypes (Petchey 2003), (ii) la facilitation, qui a lieu lorsqu'une ou plusieurs espèces facilitent la survie et la croissance d'autres espèces en conditions de croissance contraignantes ou quand les ressources du milieu sont peu ou pas accessibles (Mulder *et al.* 2001; Bruno *et al.* 2003), et (iii) l'effet d'échantillonnage dans le cas où un ou plusieurs génotypes/espèces dominent les autres, et que la croissance des premiers augmente en faisant augmenter par le fait même la productivité globale du système (Loreau et Hector 2001).

L'activité photosynthétique des arbres dans les plantations mixtes est souvent supérieure à celle des monocultures (Forrester *et al.* 2006, Richards *et al.* 2010) et ceci serait lié à un statut nutritif optimal, notamment en azote. En effet, l'azote entre dans la composition des principales protéines et enzymes impliquées dans la photosynthèse telles que la Rubisco. Il est connu que la teneur foliaire en N est positivement corrélée au taux d'assimilation du CO_2 chez plusieurs espèces végétales (Evans 1989, Wright *et al.* 2004). Ainsi, dans la mesure où les plantations mixtes permettent d'améliorer le statut nutritif par un ou plusieurs des mécanismes cités, elles représenteraient un outil efficace à long terme pour accroitre la photosynthèse et par la suite la productivité en sylviculture intensive. La stratification des cimes dans les plantations mixtes permet une meilleure interception et diffusion de la lumière

et accroit, par conséquent, le taux d'assimilation du CO_2 (Pretzsch et Schütze 2009). La diversité de la morphologie du houppier agit ainsi d'une manière similaire à une baisse de la densité des arbres ou d'une éclaircie. Medhurst et Beadle (2005) ont montré que l'augmentation de la lumière disponible suite à une éclaircie avait diminué la surface foliaire spécifique, augmenté la concentration foliaire en azote et par la suite la capacité photosynthétique.

Le peuplier se caractérise par un système racinaire traçant relativement complexe (Dickmann *et al.* 2001). La diversité morphologique des systèmes racinaires chez le genre *Populus spp.* est importante et des différences ont été observées même entre clones issus des mêmes croisements pour le nombre, le volume, la profondeur et l'orientation des racines (Dickmann *et al.* 2001). Dans les plantations monoclonales, la densité des arbres est souvent élevée et la compétition est importante vu qu'ils exploitent le même volume de sol. Dans les plantations mixtes, on observe souvent une stratification des systèmes racinaires qui occupent des niveaux et des volumes de sol différents (Schmid et Kazda 2002, Richards *et al.* 2010) Ceci permet de réduire la compétition, d'accroitre la disponibilité et l'apport en nutriments et par conséquent la croissance (Richards *et al.* 2010). Aussi, la phénologie racinaire, comme celle du houppier, est souvent différente entre les génotypes (Steinaker et Wilson 2008). Le décalage des stades phénologiques entre les cultivars permet, par exemple, de décaler l'absorption des nutriments au début de la saison de croissance (Knops *et al.* 2002). Ceci est avantageux pour les essences à croissance rapide qui prélèvent d'importantes quantités de nutriments du sol, notamment l'azote (Heilman et Xie 1993). Outre son effet sur la photosynthèse, la disponibilité en nutriments du sol affecte l'allocation de la biomasse entre la partie aérienne et racinaire (Ericsson 1995). L'acquisition des nutriments par les racines est un processus qui requiert beaucoup d'énergie quand le sol est pauvre en ressources ou quand la compétition entre les individus est importante et ceci se fait souvent au détriment de la croissance de la partie aérienne (Coomes et Grubb 2000). Quand la teneur en nutriments est optimale, suite à l'ajout de fertilisants par exemple, les arbres tendraient à limiter le développement du système racinaire et à allouer plus de biomasse vers la partie aérienne (Ericsson 1995). Les plantations mixtes auraient donc un effet du même genre que celui de la fertilisation, en réduisant la compétition entre les arbres par complémentarité ou en

améliorant la disponibilité des nutriments (facilitation) avec, par exemple, des espèces fixatrices d'azote (Forrester *et al.* 2006). Le réchauffement climatique global pourrait entrainer un stress hydrique chez les espèces ligneuses comme le peuplier, jusqu'à des zones tempérées et boréales à cause de fluctuation des précipitations saisonnières et annuelles et de l'accroissement de l'évapotranspiration (Millar *et al.* 2007). Ceci diminuerait l'assimilation du carbone et la croissance des arbres et augmenterait la mortalité, surtout que la productivité des peupliers dépend considérablement de la disponibilité en eau (Monclus *et al.* 2006, Barber *et al.* 2000, Hogg *et al.* 2008). Les plantations mixtes permettraient donc ainsi de réduire la pression sur les ressources, la compétition entre les arbres et aussi accroitre l'efficience de l'utilisation de l'eau (Forrester *et al.* 2010).

1. 5 Plasticité phénotypique et productivité

Dans les régions froides, l'alternance entre une période de croissance et une période de dormance permet aux espèces feuillues de croitre tout en se protégeant du gel durant un hiver relativement long avec des températures très souvent négatives (Hanninen et Kramer 2007). A la fin de la saison de dormance, quand une somme de degrés-jours au-delà d'une température seuil est atteinte, les bourgeons éclatent. Ce stade phénologique est déclenché essentiellement par la température ambiante et secondairement par une photopériode croissante (Kozlowski et Pallardy 2002). Le débourrement est une phénophase critique et sa date est déterminante pour la croissance des arbres par la suite (Kozlowski et Pallardy 2002); Un débourrement précoce peut causer, suite à des gels printaniers tardifs, des dommages irréversibles sur les bourgeons, feuilles et branches et compromettre ainsi le démarrage de la saison de croissance et la productivité annuelle. Dans le cas contraire, les génotypes ayant un débourrement tardif ont une saison de croissance réduite et sont moins compétitifs que ceux qui débourrent plus tôt (Luquez *et al.* 2008). Par ailleurs, l'accroissement significatif des températures à l'échelle globale affecte d'ores et déjà le développement et la distribution des organismes vivants (IPCC 2007). Dans la région boréale, ce réchauffement ferait avancer la date de débourrement des arbres et allongerait, par conséquent, la saison de croissance car les espèces adaptées à ces régions sont capables d'ajuster leur phénologie mieux que les espèces des régions méridionales (Walther *et al.* 2002, Pellis *et al.* 2004, Menzel *et al.* 2006). Aussi, il permettrait d'étendre la zone de plantation vers le nord sans compromettre la croissance et

la survie des arbres (Shafer *et al.* 2001, Thomas 2010). La productivité des essences forestières de ces régions pourrait par conséquent, augmenter si les précipitations ne limitaient pas la croissance. En même temps, le réchauffement global engendre des fluctuations métrologiques qui deviennent de plus en plus fréquentes et aléatoires avec notamment des gels printaniers sporadiques ou des hivers plus longs (IPCC 2007). Dans ce contexte, la plasticité phénotypique devient un atout important en sylviculture intensive, et ce même à une échelle géographique restreinte, car elle permet aux arbres d'avoir une flexibilité vis-à-vis des conditions du milieu et de maintenir leur productivité. La plasticité phénotypique est définie comme étant la capacité d'un organisme à moduler certains de ses traits pour s'adapter à des changements de son environnement (Bradshaw 1965). Les végétaux manifestent une plasticité phénotypique assez remarquable à des facteurs biotiques ou abiotiques, qui se traduit par des changements plus ou moins importants de leur morphologie, physiologie, phénologie et de développement (Sultan 1987, Bradshaw et Hardwick 1989; Sultan 2000; Schlichting et Smith 2002). Dans les plantations forestières, la forte plasticité des cultivars est un atout car ils sont performants sur un plus large spectre de conditions environnementales. Outre les facteurs météorologiques, les arbres peuvent manifester une réponse plastique à d'autres facteurs tels que la disponibilité des ressources du milieu (Albaugh *et al.* 1998, King *et al.* 1999, Wu *et al.* 2004). En cas de carence en nutriments, la biomasse racinaire augmente afin d'explorer davantage de sol et d'accroitre la surface d'absorption (Gedroc *et al.* 1996). La plasticité en réponse à la disponibilité de la lumière est remarquable chez les essences forestières; Celles-ci adoptent des changements morphologiques et architecturaux leur permettant de réduire l'effet de l'ombrage et maximiser l'interception de la lumière (Benomar *et al.* 2013). Des traits relatifs à l'architecture de l'arbre tels que le nombre et la taille des branches ainsi que la surface spécifique des feuilles jouent un rôle important dans la plasticité du peuplier vis-à-vis de la variation de la lumière disponible (Wu et Stettler 1998). En revanche, la plasticité est un processus qui requiert de l'énergie pour l'expression, la synthèse et le métabolisme de plusieurs molécules et de leur transfert aux organes cibles (Callahan *et al.* 2008). Par conséquent, la productivité peut être plus ou moins affectée selon l'importance des ajustements à mettre en œuvre.

1. 6 Méthodologie et objectifs de recherche

L'objectif global de cette thèse était d'acquérir de nouvelles connaissances sur l'effet de la fertilisation, du mélange clonal et de et la plasticité phénotypique sur la croissance des plantations du peuplier hybride. Un dispositif expérimental composé de plantations de quatre clones de peuplier hybride établies sur trois sites le long d'un gradient nord-sud de l'ouest du Québec, Canada a été utilisé pour vérifier les différentes hypothèses. Ces clones ont été recommandés pour cette région par le ministère des Ressources Naturelles du Québec (MRNQ).

La 1ère partie de ce travail de recherche avait pour but d'évaluer l'efficience de la fertilisation basée sur la méthode DRIS sur le statut nutritif et la croissance du peuplier hybride. Deux traitements de fertilisation basés sur les équations DRIS développées par Guillemette et DesRochers (2008) et Leech et Kim (1981) sur des peupliers hybrides ont été appliqués sur quatre clones dans deux sites et comparés à des arbres témoins (non fertilisés) et des arbres fertilisés avec une recette standard (40N-20P-20K). Dans la 2ième partie, nous avons testé la relation diversité-productivité en comparant l'activité photosynthétique, le statut nutritif, le développement racinaire et la croissance des parcelles polyclonales (mélange de quatre clones) à des parcelles monoclonales. La 3ième partie a été consacrée à l'étude de la plasticité phénotypique des clones du peuplier hybride le long d'un gradient latitudinal et en réponse à différents espacements entre les arbres (3×4, 2×4 et 1×4 m). La phénologie du bourgeon terminal a été suivie au début et à la fin de la saison de croissance, et l'activité photosynthétique, la concentration foliaire en azote et de la surface foliaire spécifique ont été mesurées, afin d'évaluer la plasticité des clones et son effet sur la croissance des arbres.

Chapitre 2.

Elferjani R, DesRochers A. Tremblay F. 2012. DRIS-based fertilization efficiency of young hybrid poplar plantations in the boreal region of Canada. New Forests 44: 487–508.

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A. Desrochers a élaboré la démarche expérimentale, fait l'échantillonnage, révisé et corrigé le manuscrit. R. Elferjani a analysé les données, rédigé le manuscrit et réalisé une partie des mesures de croissance. F. Tremblay a contribué à l'élaboration des objectifs de recherche, révisé et corrigé le manuscrit.

Chapitre 3.

Elferjani R, DesRochers A Tremblay F. 2013. Comparison of root development and biomass production in monoclonal and polyclonal hybrid poplar plantations in Northeastern Canada.

R. Elferjani a contribué à l'élaboration des hypothèses et des méthodes. Il a effectué l'échantillonnage, fait les mesures sur le terrain et au laboratoire, analysé les données et rédigé le manuscrit. A. Desrochers et F. Tremblay ont contribué à l'élaboration de la problématique de recherche, ainsi qu'à la rédaction du manuscrit.

Chapitre 4.

Elferjani R, DesRochers A Tremblay F. 2013. Plasticity of bud phenology and leaf photosynthesis in hybrid poplar plantations along a latitudinal gradient of the Northeastern Canada.

R. Elferjani a contribué à l'élaboration des hypothèses et méthodes du travail, fait l'échantillonnage et les mesures sur le terrain et au laboratoire, analysé les données et rédigé le manuscrit. F. Tremblay et A. Desrochers ont contribué à l'élaboration des hypothèses et méthodes ainsi qu'à la rédaction du manuscrit.

2. CHAPITRE II

DRIS-BASED FERTLIZATION EFFICIENCY OF YOUNG HYBRID POPLAR PLANTATIONS IN THE BOREAL REGION OF CANADA*

Raed Elferjani, Annie DesRochers and Francine Tremblay

*Elferjani R, DesRochers A, Tremblay F. 2012. New Forests. 44: 487-508.

2. 1 Abstract

In order to maximize early growth and establishment of planted hybrid poplars in the boreal region of Eastern Canada, growth response of four clones to fertilization was tested in two plantations. The first two fertilization treatments were based on Diagnosis and Recommendation Integrated System (DRIS), a method based on nutrient ratios: DRIS I was based on previously established norms from a study that had been conducted in the same area, and DRIS II was based on DRIS norms developed from hybrid poplars in northern Ontario, Canada. Nutrient status and growth of trees under these 2 treatments were compared to unfertilized trees and to trees under standard (STD) fertilization treatment (40N-20P-20K). Leaf nutrient concentrations and DRIS indices showed that fertilization treatments, and especially DRIS I corrected N deficiencies but failed to correct P deficiencies. Fertilization increased volume relative growth rate by 7.51%, 4.76% and 13.25% on average at the agricultural site for DRIS I, DRIS II and STD treatments respectively, compared to no fertilizer application. At the forest site, fertilization treatments based on DRIS indices (DRIS I and DRIS II) increased growth rates (6.67%) slightly more than the standard treatment (5.80%). Overall, although DRIS-based fertilization treatments generally increased growth rates, they were often equal to or less efficient than the STD treatment, and may not be as practical as using a standard fertilization recipe.

Key words: Forest plantations, Fertilization, DRIS, *Populus spp*, growth, nutrient balance index

Résumé

Afin de maximiser la croissance de peupliers hybrides dès leur jeune âge dans la région boréale de l'Est du Canada, la réponse de quatre clones à la fertilisation a été testée dans deux plantations. Les deux premiers traitements de fertilisation ont .été déterminés à partir de la méthode DRIS (Diagnosis and Recommendation Integrated System), une méthode basée sur les ratios en nutriments contenus dans les feuilles: DRIS I a été établi sur des normes tirées d'une étude précédente menée dans la même région, alors que DRIS II reposait sur des normes DRIS développées à partir de peupliers hybrides plantés dans le nord de l'Ontario, Canada. Le statut nutritif et la croissance des arbres soumis à ces deux traitements ont été comparés à des arbres non fertilisés ainsi qu'à des arbres fertilisés avec une recette conventionnelle (STD = 40N -20P -20K). La concentration foliaire en éléments nutritifs et les indices DRIS ont montré que les traitements de fertilisation, et surtout DRIS I ont corrigé les carences en N, mais n'ont pas réussi à corriger les carence en P. La fertilisation a augmenté le taux de croissance en volume de 7.51%, 4.76% et 13.25 % en moyenne sur le site agricole pour DRIS I, II et STD, respectivement, comparativement aux arbres non fertilisés. Sur le site forestier, la fertilisation basée sur des indices DRIS (DRIS I et II) a augmenté le taux de croissance de 6.67 %, légèrement supérieure au traitement STD (5.80 %). Dans l'ensemble, bien que les traitements de fertilisation à base de DRIS aient généralement augmenté les taux de croissance, ils étaient souvent égaux ou moins efficaces que le traitement STD, et pourraient ne pas être aussi pratique que la recette de fertilisation conventionnelle.

Mots clés: Plantations forestières, fertilisation, DRIS, *Populus spp*, croissance, indice d'équilibre nutritionnel.

2. 2 Introduction

Nutritional deficiencies in plantations of fast-growing species have often been reported in boreal regions both on farmland and on forest sites (e.g., after a clearcut) (Tullus *et al.* 2007; Guillemette and DesRochers 2008). In boreal forest environments, soils are generally poor in many available nutrients because of slow decomposition of organic matter and low mineralization rate due to low temperatures and leaching (Piirainen *et al.* 2007; Allison *et al.* 2008, 2009). In conventional farming systems, the use of intensively-managed monocultures is common and may be a source of nutrient deficiencies (Varallyay 2007; Duggan *et al.* 2007; Toth *et al.* 2009). Nitrogen and phosphorus deficiencies can drastically affect yields of fast-growing plantations when they are established on farmland (Heilman and Xie 1993; Coleman *et al.* 2006). In addition to site history, tree growth in plantations may also be affected by inherent soil characteristics such as texture, depth, and pH which should be optimal to maximize growth of hybrid poplars (Stanturf *et al.* 2001). In an experiment conducted in Europe (Marron *et al.* 2010), tree growth of the same hybrid poplar clones (*P. deltoides* W.Bartram × *P. trichocarpa* Torrey & A.Gray and *P. alba* L. × *P. alba* L.) varied significantly among three sites.

Understanding nutritional requirements of tree species used in plantations is important to maximize yields (Gregoire and Fisher 2004; Oskarsson and Brynleyfsdottir 2009). On the one hand, nutritional deficiencies can lead to high mortality, slow early growth rates and low economic profitability (Pitre *et al.* 2007; Block *et al.* 2009; Pinno and Bélanger 2009; Rivest *et al.* 2009). On the other hand, excess fertilization can lead to tree nutrient imbalances and consequently to lower yields (Fageria 2001). It may also negatively affect environment quality (Adler *et al.* 2007; Van Miegroet and Jandl 2007; Flint *et al.* 2008) through the contamination of groundwater and surface waters by nutrient leaching or runoff (Löfgren *et al.* 2009). Nitrates and phosphates are the main constituents of the chemical pollution generated by fertilizer loss and wastage (Nikitishen and Lichko 2008). Therefore, accurate determination of the nutritional requirements of fast-growing trees should ensure high yields while mitigating effects on environmental quality and avoiding higher production costs (Jacobs and Timmer 2005).

Diagnosis methods that are based on foliar analysis have been developed to determine plant nutrient status because they are more reliable than those based on soil nutrient analyses (Beaufils 1973; Binkley 1986). Nutrient concentrations vary among the leaves of the same tree depending on their age and position (order and height) (Walworth and Sumner 1987) but these factors have much less impact on nutrient ratios than on their absolute concentrations (Beaufils 1973; Fageria 2001). Diagnosis and Recommendation Integrated System (DRIS) is based on the use of nutrient ratios that are standardized as DRIS formulas and then transformed into DRIS indices (Walworth and Sumner 1987). A nutrient index is a mean of the deviations of the nutrient ratios from their respective optimum or norm values (Sumner 1979). DRIS norms are obtained from highly-productive individuals of a population grown under field conditions, and assuming that their nutrient ratios are closest to tree optimal nutritional requirements, allows one to make fertilization recommendations.

DRIS has been successfully used as a fertilizer management tool for a number of agricultural crops (e.g., Walworth and Sumner 1987; Ruiz-Bello and Cajuste 2002; Junior *et al.* 2003; Hartz *et al.* 2007; Hundal *et al.* 2007), but this approach is less common for forest plantations and its effectiveness is still being debated (Drechsel and Zech 1994; Ouimet and Camiré 1994; Campion and Scholes 2008; Lteif *et al.* 2008). The aim of the current study was to evaluate the efficiency of the DRIS method to correct nutritional imbalances and increase productivity in hybrid poplar plantations that have been established under boreal conditions. We hypothesized that (i) DRIS would accurately diagnose nutrient status of trees and be a good predictor of tree growth and (ii) DRIS-based fertilization would be more efficient to increase growth rates and correct nutrient deficiencies rather than using a standard fertilization formulae.

2. 3 Materials and methods

2. 3. 1 Study sites and plant material

Four hybrid poplar clones were selected for planting on two sites in the Abitibi-Témiscamingue region of western Quebec (Canada). The first site was an abandoned farmland in the municipality of Duhamel (47°32' N, 79°59' W, Alt. 209m). The site, which was located in the sugar maple-yellow birch western bioclimatic sub-domain (Grondin 1996),

had been cultivated for hay in previous years (a perennial mixture of lucerne and timothy grass). Its soil type was a clayey (45% clay, Agriculture and Agri-food Canada 2012) luvisol and mean annual precipitations was 820 mm. Annual mean temperature was 2.8 ℃.

The second site was near the municipality of Duparquet, which was in the balsam fir-paper birch bioclimatic western sub-domain (Grondin, 1996; 48°29'N, 97°9'W, Alt. 295m), and had been previously forested until harvested in 2004. Mean annual precipitations and temperature were 918 mm and 0.7 ℃ respectively, and the soil of this site was classified as a heavy clay brunisol (70% clay; Agriculture and Agri-food Canada 2012).

Table 2.1 Soil chemical characteristics of the two study sites.

		Site			
		Duhamel		Duparquet	
Soil sample depth		0-20 (cm)	20-40 (cm)	0-20 (cm)	20-40 (cm)
pH		5.6	5.5	4.9	5.8
Available Cations (mg kg^{-1})	Ca	1853	2212	4392	4968
	K	116	130	266	265
	Mg	372	482	668	797
	Na	16	27	43	51
CEC (meq/100g)		12.7	15.5	28.3	32.3
MC		0.016	0.021	0.035	0.035
C (mg g^{-1})		15.60	10.64	7.98	7.17
N (mg g^{-1})		1.32	0.87	0.82	0.62
Ca (mg g^{-1})		6.18	6.48	7.05	9.23
K (mg g^{-1})		2.91	3.80	7.50	7.30
Mg (mg g^{-1})		10.41	12.26	17.59	17.59
P (mg g^{-1})		0.54	0.46	0.37	0.55

Note. CEC : cation exchange capacity, MC: moisture content.

Extensive site preparation and maintenance were performed both prior to planting and following the installation of the four clones. The agricultural site was ploughed using an agricultural cultivator in autumn 2004. Prior to plantation establishment at the forest site,

stumps and remaining logs were removed with a bulldozer. The site was then ploughed to a depth of 30 cm in autumn of 2004 with a forestry plough pulled by a skidder and disked in spring 2005 to level the soil before planting. Trees were planted at both sites as bare-root stock in June 2005 at 4×1 m spacing. Following planting, weeds were mechanically removed twice a year by cultivating between rows with a farm tractor and by tilling between trees with a Weed Badger (4020-SST, Marion, ND, USA).

The clones that were used in this study had been recommended for the region by the Québec Ministry of Natural Resources and Fauna (MRNF). They were as follows: 747215, *Populus trichocarpa* Torrey & A.Gray × *P. balsamifera* L.; 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and 915319 *P. maximowiczii* × *P. balsamifera*. At planting, the average height of the trees was 85.9 cm (714215), 89.4 cm (915004), 93.5 cm (915005), and 115 cm (915319), respectively. Stock type was one-year old, dormant bareroot stock, grown in Trecesson provincial nursery (Ministry of Natural Resources and Fauna, Québec). Trees were lifted in the fall and stored over the winter in a refrigerator at 2°C prior to planting. The experimental design was a split-plot where four fertilization treatments (sub-plot effect) were crossed within each of the four clones (main plot effect). Each fertilization treatment was applied to 15 trees (pseudo-replicates, three rows of five trees), and each clone-treatment combination was replicated in three blocks at each of the two sites (N=1440).

Height and basal diameter were measured at planting and at the end of 2005, 2006 and 2007 growing seasons. Stem volume was estimated with the formula:

$$V = A_b.H / 3$$

where V: stem volume (cm^3), A_b: basal area (cm) and H: height (cm) (Brown and van den Driessche 2002).

Relative growth rate (RGR, $cm^3\ cm^{-3}\ y^{-1}$) was used to take into account differences in tree volume among clones at planting ($p<0.01$):

$$RGR = [\ln (V_{n+1}) - \ln (V_n)] / T_{n+1}-T_n$$

where V_{n+1} and V_n are the tree volume in years (Tn and Tn+1) respectively and ln is the natural logarithm.

2. 3. 2 Leaf sampling and fertilizer application

About two months after trees were planted (end of July 2005), two leaves from each of the five trees that formed the middle row of each fertilization×clone treatment combination were collected in each block and pooled together to determine the nutrient status of trees prior to fertilization and thereafter quantities of fertilizers to apply for treatments "DRIS I" and "DRIS II". Leaves were oven-dried (72 h at 70 °C) and ground through a 60 µm sieve of a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). Nitrogen concentrations were obtained by dry combustion method with a LECO N-analyzer (Leco Corp., MI, USA) (Leco Corp. 1986). P, K, Ca and Mg concentrations were determined using inductively-coupled plasma spectrophotometry (ICP) following a nitrichydrochloric acid digestion (Masson and Esvan 1995).

The first fertilization treatment (DRIS I) was based on DRIS functions taken from Guillemette and DesRochers (2008) but using foliar nutrient concentrations that were obtained from our trees. These functions had been determined from a study by using 18 combinations of N-P-K fertilizers on three hybrid poplar clones grown in the same region (747210: *P. balsamifera* x *P. trichocarpa*, 915005: *P. balsamifera* x *P. maximowiczii* and 915319: *P. maximowiczii* x *P. balsamifera*). The DRIS I treatment was thus composed of 10 g tree^{-1} of ammonium nitrate (NH_4NO_3), 70 g tree^{-1} of potassium sulphate (K_2SO_4) and 40 g tree^{-1} of dolomite ($CaMg(CO_3)_2$). The DRIS II treatment was based on Leech and Kim's (1981) DRIS functions. The latter were obtained from an experiment in which growth response of hybrid poplars to various fertilization treatments was evaluated in northeastern Ontario. DRIS II consisted of 60 g tree^{-1} of NH_4NO_3, 20 g tree^{-1} of triple superphosphate ($Ca(H_2PO_4)_2)_3$), 30 g tree^{-1} of K_2SO_4, and 30 g tree^{-1} of calcium carbonate ($CaCO_3$). The third treatment (standard treatment, STD) had a 1:2:1 NPK ratio that is often used in agriculture (Wang *et al.*, 2008) and which consisted of 40 g tree^{-1} of NH_4NO_3, 20 g tree^{-1} of $Ca(H_2PO_4)_2)_3$ and 30 g tree^{-1} of K_2SO_4. A control treatment with no added fertilizer was also tested. In May 2006, fertilizers were placed in a 15 cm-deep hole 20 cm away from the base

of each tree (Guillemette and DesRochers, 2008). To avoid contamination between fertilization treatments, a buffer row of trees without fertilizers was retained between each treatment.

Leaves were sampled at the end of July 2006 (as described above in 2005) for nutrient analyses and to calculate DRIS indices.

2. 3. 3 Soil analyses

Five soil samples were collected in May 2007 at the farmland site and ten at the forest site (more heterogeneous) for chemical and physical characterization (Table 2.1). Soil samples were collected diagonally along plots. For each sample, two sub-samples from the 0-20 cm and 20-40 cm horizons were collected separately. Soil samples were subsequently dried in an oven at 50 °C, ground and sieved through a 60 µm mesh. The sub-samples at each level were then pooled for analysis. Soil pH was obtained after water-extraction of a saturated paste. Total carbon concentration in the soil was determined by high temperature combustion with a LECO N-analyzer (Leco Corp., MI, USA) and soil available cations concentrations and the cation exchange capacity (CEC, $cmol_c/kg$) were obtained by ICP after an ammonium acetate extraction at the Forest Resources and Soil Testing Laboratory, Lakehead University (Thunder Bay, Ontario).

2. 3. 4 DRIS norms and indices

The DRIS approach allows the determination of a nutrient index, which is the degree of deviation of that nutrient from its optimum value or norm. The nutrient norms are obtained from a high-yielding population (Partelli *et al.* 2007), and a nutrient is considered balanced when its index is around zero. The more positive an index, the greater the degree to which the nutrient is in excess; conversely, the more negative an index, the greater the degree to which the nutrient is limiting (Walworth and Sumner 1987).

At the end of June (2005), leaf samples were collected to calculate DRIS field norms and indices. The field norms were established as the nutrient ratios for the best growing trees of each clone at each site (Table 2.2).

Table 2.2 Calculated DRIS norms of nutrient ratios and their coefficients of variation (CV, %) for each of the four clones tested at a) farmland and b) forest site.

Clone										
747215			915004			915005			915319		
	Mean	CV(%)		Mean	CV(%)		Mean	CV(%)		Mean	CV(%)
a)											
N/Ca	5.880	10.901	N/Ca	5.199	7.971	Ca/N	0.161	7.224	Ca/N	0.228	9.066
N/K	2.771	0.508	N/K	2.197	6.045	Ca/K	0.354	8.028	K/N	0.400	15.819
N/Mg	10.881	8.462	N/Mg	11.144	6.898	K/N	0.460	12.928	K/Ca	1.772	18.548
N/P	9.985	4.813	N/P	9.083	5.648	Mg/N	0.078	7.372	K/Mg	3.833	7.645
K/Ca	2.122	10.882	Ca/K	0.424	3.928	Mg/Ca	0.481	0.534	K/P	3.915	15.259
K/Mg	3.928	8.620	Ca/Mg	2.147	3.264	Mg/K	0.170	8.376	Mg/N	0.104	11.438
K/P	3.603	4.333	K/Mg	5.069	1.026	Mg/P	0.775	9.793	Mg/Ca	0.458	11.548
Mg/Ca	0.539	3.728	P/Ca	0.572	10.745	P/N	0.101	14.186	Mg/P	1.015	8.726
P/Ca	0.589	10.745	P/K	0.242	4.356	P/Ca	0.626	9.081	P/N	0.102	5.736
P/Mg	1.093	10.151	P/Mg	1.228	10.151	P/K	0.220	1.421	P/Ca	0.450	4.335
b)											
Ca/N	0.182	4.814	N/K	1.254	4.994	N/K	1.432	9.813	Ca/N	0.181	32.233
Ca/Mg	2.128	2.446	N/P	7.942	3.261	N/P	7.597	2.610	Ca/K	0.290	29.275
Ca/P	1.730	4.605	Ca/N	0.221	7.672	Ca/N	0.149	9.752	Ca/Mg	1.846	12.332
K/N	0.504	7.482	Ca/K	0.278	12.078	Ca/K	0.211	5.333	Ca/P	1.516	26.516
K/Ca	2.770	2.731	Ca/P	1.760	9.778	Ca/Mg	1.773	7.228	K/N	0.617	7.889
K/Mg	5.897	5.101	Mg/N	0.096	6.644	Ca/P	1.129	10.513	K/P	5.295	6.878
K/P	4.799	7.387	Mg/Ca	0.435	2.103	K/P	5.354	9.739	Mg/N	0.095	22.668
Mg/N	0.085	3.477	Mg/K	0.121	10.469	Mg/N	0.084	5.852	Mg/K	0.154	20.486
Mg/P	0.813	2.387	Mg/P	0.764	8.089	Mg/K	0.119	4.714	Mg/P	0.806	16.136
P/N	0.105	2.177	P/K	0.158	2.541	Mg/P	0.636	4.839	P/N	0.117	7.684

Trees selected as field standards had a volume yield ≥80% of the maximum yield (yield cutoff = 0.8). A DRIS function was developed for each clone at each site (Table 2.3) to take into account responses to fertilization due to genotype (clones) and environment (sites). For each pair of nutrients X and Y, there are three possible forms of nutrient expressions: X/Y, Y/X or X*Y. The selected expression was the one with the highest coefficient of variation (CV) between high-yielding and low-yielding groups. CV of X*Y were always the smallest in our experiment. The aim of this approach is to increase the diagnostic sensitivity and accuracy of nutrient imbalances (Walworth and Sumner, 1987).

$$f(X/Y) = [(X/Y)/(x/y)-1]*1000/CV, \text{ when } x/y \leq X/Y$$

or

$$f(X/Y) = [1-(x/y)/(X/Y)]*1000/CV, \text{ when } X/Y < x/y$$

where X/Y is the ratio of the two nutrients in the leaves diagnosed (after fertilization) and x/y is the optimum value (norm) of that ratio. CV is the coefficient of variation of the norm ratio (x/y).

Table 2.3 DRIS formulas used for nutrient indices for each of the four clones in the farmland and the forest sites.

	DRIS Formulae	
Clone	Farmland site	Forest site
747215	N_{ind} = [+ f(N/Ca) + f(N/K) + f(N/Mg) + f(N/P)]/4	N_{ind} = [- f(Ca/N) - f(K/N) - f(Mg/N) - f(P/N)]/4
	P_{ind} = [+ f(P/Ca) - f(K/P) + f(P/Mg) - f(N/P)]/4	P_{ind} = [- f(Ca/P) - f(K/P) - f(Mg/P) + f(P/N)]/4
	K_{ind} = [-f(N/K) + f(K/Ca) + f(K/Mg) + f(K/P)]/4	K_{ind} = [+f(K/N) + f(K/Ca) + f(K/Mg) + f(K/P)]/4
	Ca_{ind} = [- f(N/Ca) - f(Mg/Ca) - f(P/Ca) - f(K/Ca)]/4	Ca_{ind} = [+ f(Ca/N) + f(Ca/Mg) + f(Ca/P) - f(K/Ca)]/4
	Mg_{ind} = [+ f(Mg/Ca) - f(K/Mg) - f(N/Mg) - f(P/Mg)]/4	Mg_{ind} = [- f(Ca/Mg) - f(K/Mg) + f(Mg/N) + f(Mg/P)]/4
915004	N_{ind} = [+f(N/Ca) + f(N/K) + f(N/Mg) + f(N/P)]/4	N_{ind} = [- f(Ca/N) + f(N/K) - f(Mg/N) + f(N/P)]/4
	P_{ind} = [+f(N/Ca) + f(N/K) + f(N/Mg) + f(N/P)]/4	P_{ind} = [- f(Ca/P) + f(P/K) - f(Mg/P) - f(N/P)]/4
	K_{ind} = [- f(N/K) - f(Ca/K) + f(K/Mg) - f(P/K)]/4	K_{ind} = [-f(N/K) - f(Ca/K) - f(Mg/K) - f(P/K)]/4
	Ca_{ind} = [f(N/Ca) + f(Ca/Mg) + f(P/Ca) + f(Ca/K)]/4	Ca_{ind} = [+ f(Ca/N) - f(Mg/Ca) + f(Ca/P) + f(Ca/K)]/4
	Mg_{ind} = [- f(Ca/Mg) - f(K/Mg) - f(N/Mg) - f(P/Mg)]/4	Mg_{ind} = [+ f(Ca/N) - f(Mg/Ca) + f(Ca/P) + f(Ca/K)]/4
915005	N_{ind} = [- f(Ca/N) - f(K/N) - f(Mg/N) - f(P/N)]/4	N_{ind} = [- f(Ca/N) + f(N/K) - f(Mg/N) + f(N/P)]/4
	P_{ind} = [+ f(P/N) + f(P/Ca) + f(P/K) - f(Mg/P)]/4	P_{ind} = [- f(K/P) - f(Ca/P) - f(Mg/P) - f(N/P)]/4
	K_{ind} = [+ f(K/N) - f(Ca/K) - f(Mg/K) - f(P/K)]/4	K_{ind} = [- f(N/K) - f(Ca/K) - f(Mg/K) + f(K/P)]/4
	Ca_{ind} = [+ f(Ca/N) - f(Mg/Ca) - f(P/Ca) + f(Ca/K)]/4	Ca_{ind} = [+ f(Ca/N) + f(Ca/Mg) + f(Ca/P) + f(Ca/K)]/4
	Mg_{ind} = [+f(Mg/Ca) + f(Mg/K) + f(Mg/N) + f(Mg/P)]/4	Mg_{ind} = [- f(Ca/Mg) + f(Mg/K) + f(Mg/N) + f(Mg/P)]/4
915319	N_{ind} = [- f(Ca/N) - f(K/N) - f(Mg/N) - f(P/N)]/4	N_{ind} = [- f(Ca/N) - f(K/N) - f(Mg/N) - f(P/N)]/4
	P_{ind} = [+f(P/Ca) - f(K/P) - f(Mg/P) + f(P/N)]/4	P_{ind} = [- f(Ca/P) - f(K/P) - f(Mg/P) + f(P/N)]/4
	K_{ind} = [+f(K/N) + f(K/Ca) + f(K/Mg) + f(K/P)]/4	K_{ind} = [+f(K/N) - f(Ca/K) - f(Mg/K) + f(K/P)]/4
	Ca_{ind} = [+ f(Ca/N) - f(Mg/Ca) - f(P/Ca) - f(K/Ca)]/4	Ca_{ind} = [+ f(Ca/N) + f(Ca/Mg) + f(Ca/P) + f(Ca/K)]/4
	Mg_{ind} = [+ f(Mg/Ca) - f(K/Mg) + f(Mg/N) + f(Mg/P)]/4	Mg_{ind} = [- f(Ca/Mg) + f(Mg/K) + f(Mg/N) + f(Mg/P)]/4

2. 3. 5 Nutrient balance index (NBI) and correction index (CI)

The sum of the absolute values of the indices of different elements was divided by 5 (the number of nutrients considered) to obtain NBI (Nutrient Balance Index), where:

$$NBI = \Sigma \mid X_{ind} \mid / 5$$

This index gives quantitative information about the overall nutritional status before and after the application of fertilizers. To quantify the efficiency of each treatment in terms of correcting nutrient imbalances (deficiency or excess), a correction index (CI) was established. The CI is calculated for each nutrient and gives a value to the gap between the DRIS index of the nutrient and its optimum range. The closer to 0 the CI is, the more efficient is the fertilization treatment.

If DRIS index values of a nutrient X (e.g., N) are between -10 and 10 ($-10 \leq N_{ind} \leq 10$), the nutrient concentration is optimal and the correction index (CI) value is 0 (Mourão-Filho 2005):

$$If\ -10 \leq X_{ind} \leq 10 \Rightarrow CI=0$$

when nutrient index (X_{ind}) is out of [-10, 10] optimal interval

$$If\ X_{ind} < -10 \Rightarrow CI= (X_{ind}/10)+1$$

$$If\ X_{ind} > 10 \Rightarrow CI= (X_{ind}/10)-1$$

To simultaneously evaluate the effects of the different fertilization treatments on the nutrient status and the growth of trees at the same time, a grade was given to each combination of treatment/nutrient index:

F/0: unbalanced index (F) and RGR of treatment equal to control (0); **S/0**: balanced index (S) and RGR of treatment equal to control (0); **F/1**: unbalanced index and RGR of treatment higher than control (1); **S/1**: balanced index (S) and RGR of treatment higher than control (0); **f+/0** and **f-/0**: reduced imbalance (index >10 or <-10) and RGR of the treatment

equal to control (0); **f+/1** and **f-/1**: reduced imbalance (index >10 or <-10) and RGR of the treatment higher than control (1).

2. 3. 6 Statistical analyses

The data were subjected to split-plot ANOVA analysis with clone as the whole plot and fertilization treatment as the sub-plot. Blocks (replicates) were considered as random effects while fertilizers and clones were considered as fixed effects. Analysis of variance was used to test the effect of the different fertilization treatments on DRIS indices obtained after their application, and relative growth rates. Each site was analyzed separately and the significance level for all tests was set to α=0.05. Linear Mixed Models package of R software were used to perform statistical analyses (R. Foundation for Statistical Computing, Vienna, Austria) and least square means were compared using Tukey's honest significant differences (HSD) function.

2. 4. Results

2. 4. 1 Fertilizer-Growth

Average relative growth rate of the four clones was increased by fertilization at both sites but clones responded differently to fertilization treatments in 2006 (Table 2.4). At the forest site, trees fertilized with DRIS I, DRIS II and STD had greater growth rates (average of four clones) than unfertilized trees (3.75, 3.70, 3.70 and 3.49 $cm^3\ cm^{-3}\ y^{-1}$, respectively) (Fig. 2.1b). A significant Clone x Treatment interaction (P=0.02) was noticed as the "Treatment" effect depended on clones. Fertilization increased growth rates by 5.04% to 18.44% depending on treatments and clones. DRIS I generated the greatest growth increases for clones 915319 and 915004 (13.55% and 11.90%) and DRIS II for the other two clones (9.84% and 18.44%) (Fig. 2.1a).

Table 2.4 Analysis of variance showing the variables tested, degrees of freedom (d.f) and *P* and F values for volume relative growth rate (RGR) in 2006 and 2007 on the farmland and the forest sites.

Year	d.f	2006				2007			
		Farmland site		Forest site		Farmland site		Forest site	
		F value	*P*	F value	*P*	F value	*P*	F value	*P*
Clone	3	8.18	(< 0.01)	7.54	(< 0.01)	2.64	0.06	2.85	0.05
Treatment	3	0.86	0.45	2.88	0.03	0.88	0.46	1.71	0.18
Clone*Treatment	9	2.29	0.02	2.26	0.02	2.02	0.06	1.35	0.25

d.f: degrees of freedom

At the farmland site, relative growth rate was generally lower than at the forest site in 2006 and ranged between 2.73 cm^3 cm^{-3} y^{-1} (unfertilized) and 3.10 cm^3 cm^{-3} y^{-1} (STD), on average (Fig 2.1a). DRIS I increased relative growth rate of clone 915319 by 42.08%, but decreased it for two other clones by 11.95% and 12.82%, compared to unfertilized trees. DRIS II had an overall better effect over the 4 clones and increased growth rate of three of the four clones by 7.4% to 13.44%. However, STD treatment resulted in the greatest growth increases at the farmland site (13.25 % on average).

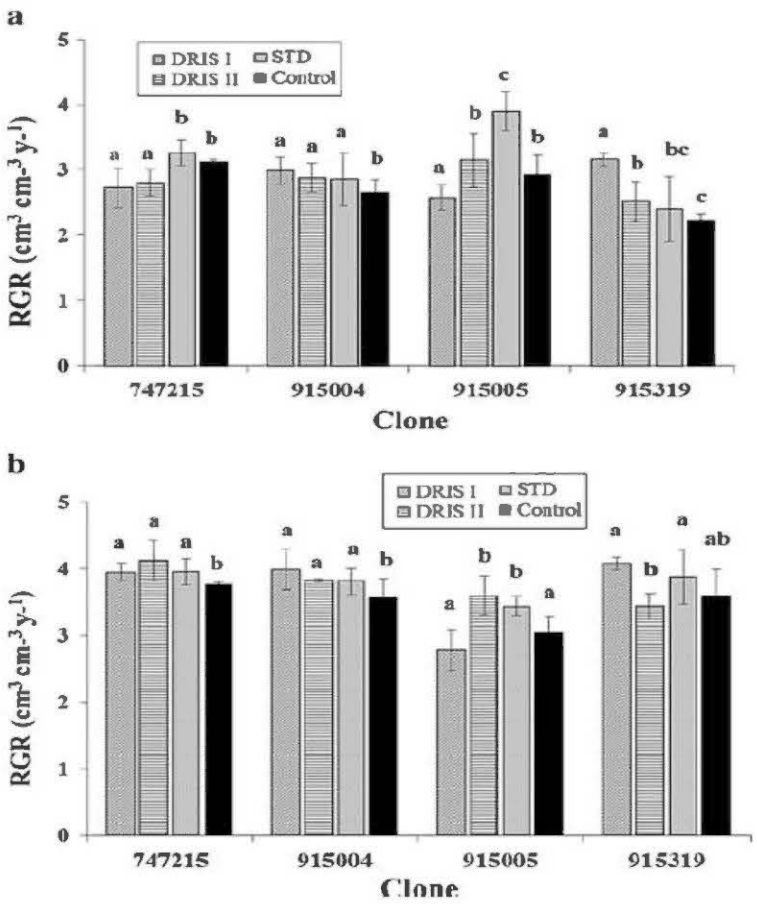

Figure 2.1 Relative growth rate (RGR) of each clone according to the fertilization treatment in the year it was applied (2006, two year old trees) at the a) farmland and b) forest site. Bars labelled with the same letter within the same clone are not significantly different at $P < 0.05$.

In 2007, variations in RGR were explained mainly by clones ($P = 0.05$) at the forest site (Table 2.4). Relative growth rate was increased by 6.94% to 20.47% with DRIS I and by 5.41% to 17.18% with DRIS II depending on clones. STD fertilizer treatment increased growth rate by 2.94% to 11.92% on average compared to unfertilized trees (Fig. 2.2a).

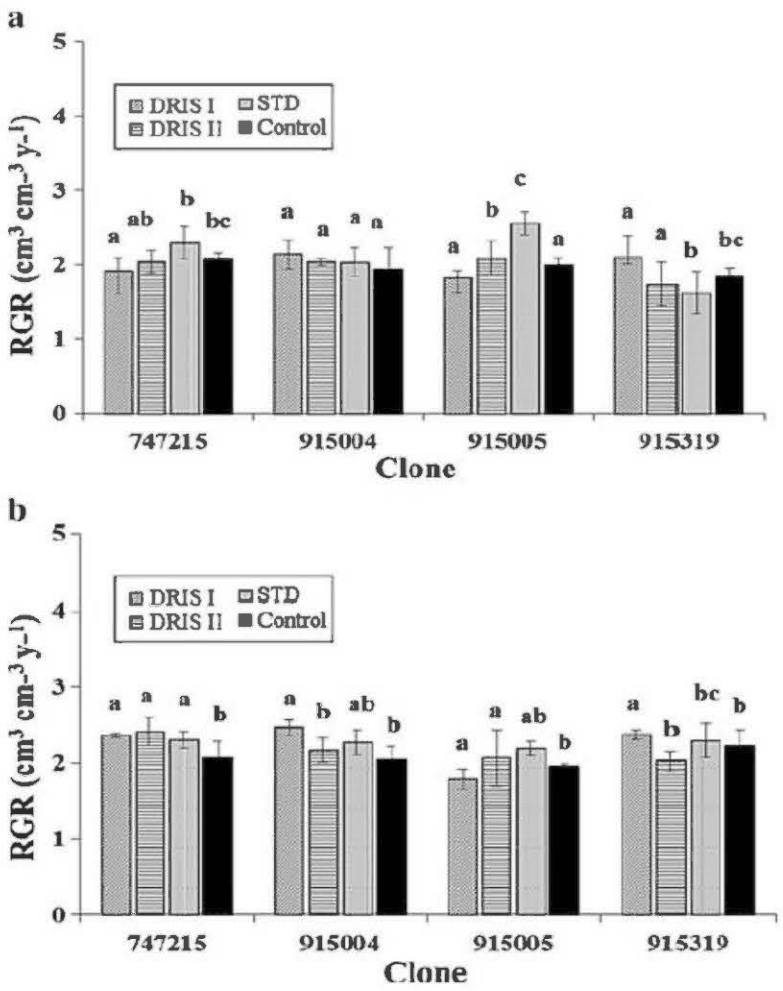

Figure 2.2 Relative growth rate (RGR) of each clone according to the fertilization treatment, a year after it was applied (2007, three year old trees) at a) farmland and b) forest site. Bars labelled with the same letter within the same clone are not significantly different at $P < 0.05$.

A marginal but not significant clone x treatment interaction (P=0.06) and clonal effect (P=0.06) were detected in the agricultural site in 2007 (two years following fertilizer application) (Table 2.4). STD fertilizer generated the greatest relative growth rate (2.12 cm^3 cm^{-3} y^{-1} on average) and increased it by 8.1% compared to unfertilized trees. DRIS I and DRIS II increased growth for two clones but decreased it for the others so that the average effect was almost nil (Fig 2.2b).

2. 4. 2 DRIS indices

At the agricultural site, the three fertilization treatments had no effect on N indices, which remained within optimum values in 2006 (between -10 and 10), except for clone 747215 (Table 2.5). Leaf N concentrations were higher or slightly lower in unfertilized trees, which implies that trees were not N-deficient (Table 2.6). Phosphorus (P) deficiency was apparent for non-fertilized trees, but fertilization failed to balance P DRIS indices, as their values ranged between -29 and -118 after fertilizer application (Table 2.5). Leaf P concentrations were consistent with DRIS indices, in that they did not increase with fertilization (Table 2.6). Significant potassium (K) deficiencies were noted for unfertilized trees of two clones (DRIS indices were -36.53 and -85.16 for clones 747215 and 915004 respectively); the deficiency was partially alleviated by DRIS I treatment but only for one clone (747215, Table 2.5). Unfertilized and fertilized trees had excess calcium (Ca), as reflected in the range of DRIS indices, i.e., from 37.8 to 286.5 (Table 2.5). With few exceptions, fertilization had no effect on leaf Ca concentration and the respective DRIS indices (Tables 2.5 and 2.6). Control trees of two clones (915004 and 915319) had magnesium (Mg) deficiencies, which were corrected with DRIS I and DRIS II treatments but only for clone 915319 (Table 2.5).

Table 2.5 DRIS indices of the four tested clones at the farmland and forest sites before fertilization (a, 2005) and after the application of the four fertilization treatments (DRIS I, DRIS II, STD and control, b)

Site	Farmland site					Forest site				
Clone	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}
(a)										
747215	−9.82	2.25	3.31	−0.84	2.35	−15.15	3.26	−10.13	8.03	−6.16
915004	−12.30	−4.90	4.08	−6.32	−12.19	−25.30	3.21	−13.04	−1.26	0.55
915005	−20.84	−6.64	14.42	20.21	−3.15	−25.40	2.37	−12.73	−2.36	4.23
915319	2.15	3.51	4.54	−2.54	−2.83	−33.04	7.71	−1.78	−10.78	−6.92

Site	Trt	Farmland site					Forest site				
Clone		N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}
(B)											
747215	DRIS I	−40.73	−56.91	17.59	99.76	−19.70	1.82	−17.38	11.10	65.63	−61.17
	DRIS II	−28.82	−51.83	−20.53	102.60	−1.40	−41.03	−25.48	9.59	72.36	−15.43
	STD	−15.18	−63.23	−29.58	106.86	1.13	−7.61	−10.62	−6.67	61.18	−36.27
	Control	−14.68	−58.71	−36.53	101.70	8.22	−121.45	−5.32	24.16	94.04	8.57
915004	DRIS I	5.35	−92.32	−80.02	177.57	−10.58	49.92	−58.70	−29.17	105.34	−67.38
	DRIS II	−0.56	−62.74	−31.64	168.89	−73.94	44.34	−50.26	−41.53	100.54	−53.09
	STD	6.90	−87.05	−125.62	189.24	16.52	44.71	−31.15	−41.70	94.09	−65.94
	Control	−0.84	−76.17	−85.16	177.59	−15.41	−6.93	−17.95	−36.49	100.81	−39.43
915005	DRIS I	−10.16	−115.80	51.21	336.55	−26.18	62.85	−115.80	−5.15	66.06	−7.96
	DRIS II	−5.85	−101.07	37.30	315.24	−24.56	33.79	−83.90	−15.82	79.92	−13.99
	STD	−14.05	−118.28	55.88	331.74	−25.53	54.75	−103.37	−19.85	74.63	−6.16
	Control	−12.78	−115.32	56.48	286.46	−21.48	−33.21	−105.62	−25.41	128.93	35.31

Table 5 continued

Site	Trt	Farmland site					Forest site				
Clone		N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}
915319	DRIS I	−8.28	−44.32	0.86	63.66	−11.91	11.78	−30.17	−2.94	49.39	−28.06
	DRIS II	2.75	−42.32	4.74	42.22	−7.39	17.88	−13.67	−14.63	46.34	−35.92
	STD	−1.38	−29.38	2.80	54.73	−26.77	4.61	−18.15	−12.88	52.77	−26.34
	Control	−4.00	−13.56	3.74	37.83	−24.01	−39.59	−16.36	7.85	56.03	−7.92

Trt fertilization treatments

At the forest site, all unfertilized trees showed nitrogen deficiencies, with DRIS values ranging between -121.5 and -6.9 (Table 2.5), and leaf N concentrations were low compared to the farmland site (Table 2.6). Trees N status was greatly improved by fertilization, particularly with the DRIS I treatment. Not all fertilization treatments improved K status. Except for one clone (915004), DRIS I was the most effective treatment for correcting K imbalances (Table 2.5). As for the agricultural site, P deficiencies were detected but were not corrected by fertilization; DRIS indices of fertilized trees ranged between -115.8 and -10.6 (Table 2.5). Similarly, fertilization did not increase leaf P concentration (Table 2.6). DRIS indices of fertilized and unfertilized trees also showed an excess of Ca for all clones at the forest site (56.03 to 128.9). The indices of fertilized trees were more balanced than unfertilized trees but still far from the optimum range (Table 2.5). Except for clone 915005, fertilization incurred magnesium deficiencies with DRIS indices ranging between -65.9 and -15.4 after fertilization (Table 2.5). Further, Mg leaf concentrations of clone 915319 were noticeably reduced by fertilization (Table 2.6).

Nutrient balance index (NBI) and correction indices (CI) showed that clones response to fertilization treatments was significantly different from one another (Table 2.7). Nevertheless, DRIS indices of fertilized trees were generally more balanced in forest than in the agricultural site. NBI values of DRIS I treatment, for example, were 46.94, 67.56, 155.11 and 25.8 at the farmland and 31.42, 62.11, 51.57 and 24.47 at the forest site for clones 747215, 915004, 915005 and 915319, respectively. Overall, the CI indicated that DRIS indices of clones 714215 and 915319 fertilized with DRIS I and DRIS II were closer to the optimum range (-10 and 10) than those of clones 915004 and 915005 at both sites (Table 2.7).

Table 2.6 Nutrient concentrations (%) for clones and treatments in 2006 at the farmland and the forest sites.

		Site									
		Farmland					Forest				
Clones	Trt	Nutrients (%)									
		N	P	K	Ca	Mg	N	P	K	Ca	Mg
747215	DRIS I	2.443	0.212	0.936	0.778	0.270	2.573	0.259	1.402	0.554	0.194
	DRIS II	2.432	0.222	0.891	0.817	0.299	2.518	0.263	1.300	0.546	0.206
	STD	2.407	0.206	0.862	0.812	0.296	2.248	0.246	1.380	0.558	0.211
	Control	2.341	0.205	0.841	0.786	0.299	1.956	0.263	1.534	0.616	0.232
915004	DRIS I	2.285	0.169	0.930	0.767	0.210	2.335	0.209	1.379	0.638	0.179
	DRIS II	2.450	0.210	1.062	0.810	0.202	2.360	0.230	1.364	0.623	0.180
	STD	2.293	0.170	0.878	0.781	0.218	2.311	0.214	1.331	0.650	0.190
	Control	2.329	0.184	0.958	0.796	0.216	2.051	0.241	1.412	0.666	0.199
915005	DRIS I	2.589	0.187	1.183	0.639	0.194	2.591	0.224	1.657	0.492	0.185
	DRIS II	2.648	0.190	1.145	0.627	0.194	2.565	0.221	1.561	0.503	0.187
	STD	2.534	0.188	1.203	0.640	0.196	2.493	0.238	1.651	0.532	0.188
	Control	2.498	0.186	1.185	0.612	0.197	1.923	0.214	1.669	0.634	0.221
915319	DRIS I	2.962	0.271	1.158	0.934	0.274	2.754	0.243	1.516	0.832	0.205
	DRIS II	3.131	0.274	1.235	0.891	0.296	2.678	0.264	1.432	0.883	0.214
	STD	3.193	0.300	1.247	0.982	0.274	3.164	0.296	1.539	0.854	0.202
	Control	3.228	0.325	1.307	0.937	0.289	1.876	0.266	1.594	0.960	0.268

Trt: fertilization treatments

Table 2.7 Correction index (CI) and nutrient balance index (NBI) for clones and treatments at the farmland and the forest sites.

Site		Farmland						Forest					
		Correction index					NBI=Σ|ind|/5	Correction index					NBI=Σ|ind|/5
Clone	Trt	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}		N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}	
747215	DRIS I	-3.07	-4.69	0.76	8.98	-0.97	46.94[a]	0	-0.74	0.11	5.56	-5.12	31.42[a]
	DRIS II	-1.88	-4.18	-1.05	9.26	0	41.05[b]	-3.10	-1.55	0	6.24	-0.54	32.78[a]
	STD	-0.52	-5.32	-1.96	9.69	0	43.20[b]	0	-0.06	0	5.12	-2.63	24.47[b]
	Control	-	-	-	-	-	43.97[b]	-	-	-	-	-	50.71[c]
915004	DRIS I	0	-8.23	-7.00	16.76	-0.06	67.56[a]	3.99	-4.87	-1.92	9.53	-5.74	62.11[a]
	DRIS II	0	-5.27	-2.16	15.89	-6.39	67.55[a]	3.43	-4.03	-3.15	9.05	-4.31	57.96[b]
	STD	0	-7.71	-11.56	17.92	2.65	85.07[b]	3.47	-2.12	-3.17	8.41	-5.59	55.52[b]
	Control	-	-	-	-	-	71.07[c]	-	-	-	-	-	40.33[c]
915005	DRIS I	-0.02	-10.58	4.12	32.66	-27.18	155.11[a]	5.29	-10.58	0	5.61	0	51.57[a]
	DRIS II	0	-9.11	2.73	30.52	-25.56	141.01[b]	2.38	-7.39	-0.58	6.99	-0.40	45.49[b]
	STD	-0.41	-10.83	4.59	32.17	-26.53	155.05[a]	4.48	-9.34	-0.99	6.46	0	51.76[a]
	Control	-	-	-	-	-	137.18[b]	-	-	-	-	-	65.70[c]
915319	DRIS I	0	-3.43	0	5.37	-0.19	25.80[a]	0.18	-2.02	0	3.94	-1.81	24.47[a]
	DRIS II	0	-3.23	0	3.22	0	19.88[b]	0.79	-0.37	-0.46	3.63	-2.59	25.69[a]
	STD	0	-1.94	0	4.47	-1.68	23.01[a]	0	-0.82	-0.29	4.28	-1.63	22.95[b]
	Control	-	-	-	-	-	16.63[c]	-	-	-	-	-	25.56[a]

Trt: fertilization treatments

Values with the same letter within the same clone and site are not significantly different at $P<0.05$.

2. 4. 3 DRIS indices vs. Growth

Overall, when DRIS indices were balanced ($-10<X_{ind}<10$), RGR of fertilized trees were, often, greater than for unfertilized trees (Table 2.8). In 2006, when the DRIS index for N was corrected, growth of fertilized trees was usually better than that of the control ((F/0, S/1 and f/1; Table 2.8a). It was the same for K and Ca indices at the forest site and Mg indices at the farmland site. However, in some cases, growth did not increase even though the DRIS indices were corrected (Table 2.8a).

Table 2.8 DRIS indices and relative growth rates (RGR) for clones and fertilization treatments at the farmland and the forest sites after the first (a, 2006) and the second growing season (b, 2007).

a)

Site		Farmland					Forest				
Clone	Trt	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}	N_{ind}	P_{ind}	K_{ind}	Ca_{ind}	Mg_{ind}
747215	DRIS I	F/0	f-/0	S/0	f+/0	F/0	S/1	F/1	S/1	f+/1	F/1
	DRIS II	F/0	f-/0	f-/0	f+/0	S/0	f-/1	F/1	S/1	f+/1	F/1
	STD	F/1	F/1	f-/1	f+/1	S/1	S/1	S/1	S/1	f+/1	F/1
915004	DRIS I	S/1	F/1	f-/1	F/1	S/1	f+/1	F/1	f-/1	F/1	F/1
	DRIS II	S/1	f-/1	f-/1	f+/1	f-/1	f+/0	F/0	F/0	F/0	F/0
	STD	S/1	F/1	F/1	f+/1	f+/1	f+/1	F/1	F/1	f+/1	F/1
915005	DRIS I	S/0	f-/0	f+/0	F/0	F/0	f+/1	F/1	S/1	f+/1	S/1
	DRIS II	S/0	f-/0	f+/0	F/0	F/0	f+/0	f-/0	f-/0	f+/0	f-/0
	STD	f-/1	F/1	f+/1	F/1	F/1	f+/1	f-/1	f-/1	f+/1	S/1
915319	DRIS I	S/1	F/1	S/1	F/1	S/1	S/1	F/1	S/1	f+/1	F/1
	DRIS II	S/1	F/1	S/1	F/1	S/1	F/0	f-/0	F/0	f+/0	F/0
	STD	S/0	F/0	S/0	F/0	F/0	S/0	F/0	F/0	f+/0	F/0

b)

747215	DRIS I	F/0	f-/0	S/0	f+/0	F/0	S/1	F/1	S/1	f+/1	F/1
	DRIS II	F/0	f-/0	f-/0	f+/0	S/0	f-/1	F/1	S/1	f+/1	F/1
	STD	F/0	F/0	f-/0	f+/0	S/0	S/1	S/1	S/1	f+/1	F/1
915004	DRIS I	S/0	F/0	f-/0	F/0	S/0	f+/1	F/1	f-/1	F/1	F/1
	DRIS II	S/0	f-/0	f-/0	f+/0	f-/0	f+/0	F/0	F/0	F/0	F/0
	STD	S/0	F/0	F/0	f+/0	f+/0	f+/1	F/1	F/1	f+/1	F/1
915005	DRIS I	S/0	f-/0	f+/0	F/0	F/0	f+/0	F/0	S/0	f+/0	S/0
	DRIS II	S/0	f-/0	f+/0	F/0	F/0	f+/1	f-/1	f-/1	f+/1	f-/1
	STD	f-/1	F/1	f+/1	F/1	F/1	f+/0	f-/0	f-/0	f+/0	S/0
915319	DRIS I	S/1	F/1	S/1	F/1	S/1	S/1	F/1	S/1	f+/1	F/1
	DRIS II	S/1	F/1	S/1	F/1	S/1	F/0	f-/0	F/0	f+/0	F/0
	STD	S/0	F/0	S/0	F/0	F/0	S/0	F/0	F/0	f+/0	F/0

F/0: unbalanced index (F) and RGR of treatment ≤ Control (0); S/0: balanced index (S) and RGR of treatment ≤ Control (0); F/1: unbalanced index and RGR of treatment > Control (1); S/1: balanced index (S) and RGR of treatment > Control (0); f+/0 and f-/0: reduced imbalance (index >10 or < -10) and RGR of the treatment ≤ Control (0); f+/1 and f-/1: reduced imbalance (index >10 or < -10) and RGR of the treatment > Control (1)

For the second growing season, DRIS indices were less accurate in predicting fertilizer effects on RGR, especially for N indices at the farmland site and for all nutrients at the forest site (Table 2.8b). At the farmland site, N DRIS indices of clones 915004, 915005 and 915319 were balanced for fertilized trees but without improving their relative growth rate (S/0). At the forest site, fertilization treatments were more efficient in enhancing growth rate for clones 747215 and 915004 than at the farmland site. However these growth increases did not correspond to predictions using DRIS indices which were rarely balanced. As for clones 915004 and 915005, relative growth rate of fertilized trees were not greater than those of unfertilized trees and DRIS indices were unbalanced in most cases (Table 2.8b).

Stem volume of all clones and treatments was negatively correlated with the Nutrient Balance Index (NBI) at the forest site. As NBI decreased, DRIS indices were more balanced (approached 0) and, consequently, stem volume of trees increased. When NBI values increased, DRIS indices deviated from 0 and stem volume decreased (Fig. 2.3). This relationship was evident for both growing seasons 2006 and 2007 with r^2 values of 0.59 (P<0.001) and 0.42, respectively. (P=0.02 respectively). No relationship between NBI and stem volume was found at the agricultural site (not shown).

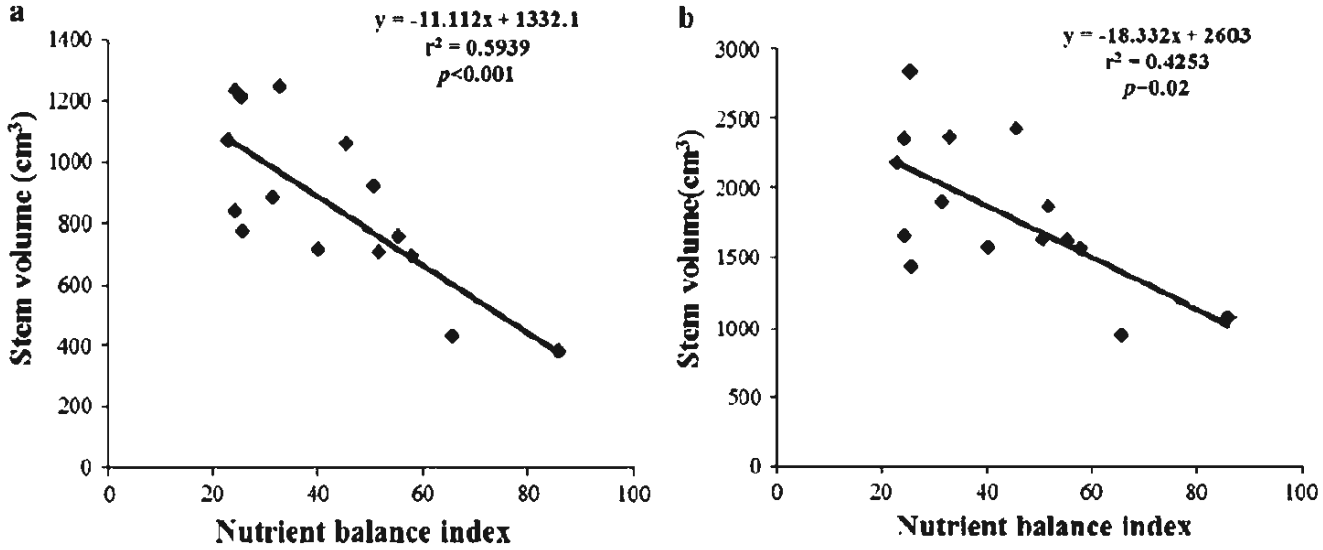

Figure 2.3 Relationship between stem volume and nutrient balance index (NBI) at the forest site in 2006 (a, two year old trees) and 2007 (b, three year old trees). Each point is the mean of tree volume for the different treatments and clones.

2. 5 Discussion

Hybrid poplar growth response to fertilization following DRIS norms have been shown to vary between sites and clones (Leech and Kim 1981; Guillemette and DesRochers 2008). In our study, effects of fertilization treatments on relative growth rates (RGR) also depended on the clone and site, which implies that quantities and types of fertilizers should be individually determined for each clone to optimize their respective growth rate. However, DRIS indices of the four clones were similar before fertilization (Table 2.5a) but application of the same fertilizer recipes resulted in different growth responses. Also, a significant Treatment*Clone interaction was obtained in both sites in 2006 which means that clones did not respond the same way to fertilization treatments. In fact, we noticed a more remarkable "Treatment" effect for clones 915005 and 915319. This might be explained by the genetic differences between clones in term of growth rate, biomass allocation and nutrient uptake and thus growth potential (Stanturf *et al.* 2001).

In the present study, nutritional imbalances were corrected more effectively at the forest site compared to the agricultural site. DRIS I was also the most effective fertilization treatment for correcting nutrient imbalances and increasing tree growth (Table 2.8). This was expected since DRIS I was based on DRIS formulae that had been developed in the same region with two of the four clones used in our study (Guillemette and DesRochers 2008). Although site conditions may not be differ that greatly between northwestern Québec and Ontario, experience has shown that requirements can vary greatly between hybrids (Coleman *et al.* 2006, van den Driessche *et al.* 2008; Rivest *et al.* 2009), and interaction of clones with specific environmental conditions (Marron *et al.* 2010) can also result in different DRIS norms such as we found in our study between DRIS I (Québec) and DRIS II (Ontario). DRIS indices after fertilization were often - but not always - good predictors of tree growth response to fertilization. Nutrient deficiencies are known to be a major factor limiting growth through the reduction of photosynthetic rate and biomass production. Also, nutrients in excess might be toxic or reduce the uptake of other nutrients (Hüner and Hopkins 2008). Indeed, the sum of DRIS indices (or NBI) was negatively correlated with tree volume of trees at the end of the first (2006) and second (2007) growing seasons at the forest site (Fig. 2.3). This negative correlation shows that tree growth was inversely proportional to NBI which is

an indicator of the deviation of DRIS indices from optimum values. Using NBI thus seems an easy way to predict fertilization treatment effects on growth, since it combines the overall imbalances into a single value (Nachtigall and Dechen 2007).

In the agricultural site, no significant relationship was detected between tree volume and NBI for the two growing seasons. Both foliar nutrient concentrations and DRIS indices of unfertilized trees in the agricultural site indicated that trees were slightly nutrient deficient and that fertilization did not increase growth rates to the same degree as it did at the forest site (Tables 2.5 and 2.6). The trees may have benefitted from residual fertilizer in this previously agricultural site. Actually, soil N and P concentrations at the agricultural site (0.13% and 0.05% respectively) were higher than the forest site (0.08% and 0.03%) (Table 2.1). N and P foliar concentrations of the four clones ranged between 23 to 32 mg N g^{-1} and from 2 to 3.2 mg P g^{-1} respectively. On the other hand, the better growth rates that we found at the forest compared to the agricultural site might be explained by differences in the physical and chemical characteristics and history of each site (Hüttl and Schaaf 1995; Table 2.1). Guillemette and DesRochers (2008) reached the same conclusion in their study of hybrid poplars fertilization on two sites of the same region (farm vs. forest lands). Concentrations of exchangeable cations (particularly K^+ and Mg^{++}) at the farmland site were significantly lower than those at the forest site. Cation exchange capacity (CEC) was also 2 times greater at the forest compared to the farmland site (30.3 and 14.1 $cmol_c/g$, respectively; Table 2.1). Tillage with agricultural machinery frequently leads to soil compaction and structural deterioration, which can affect the soil chemical properties such as CEC (Domzl *et al.* 1993; Simansky *et al.* 2008).

Other experiments using hybrid poplars in similar environmental conditions (north-eastern Canada) have found lower N leaf concentrations ranging between 17 to 22 $mg.g^{-1}$ and P concentrations between 1.4 and 2 $mg.g^{-1}$ (Guillemette and Desrochers 2008; Rivest *et al.* 2009). In general, for North American poplars and their hybrids, optimal leaf N and P concentrations should be between 28 and 40 mg N g^{-1}, and 2.5 and 5 mg P g^{-1} respectively (Heilman and Xie 1993; van den Driessche *et al.* 2008), which are greater than those measured in our study.

In many cases, even when imbalances were completely or partially corrected, growth did not increase (e.g., N indices for 915004 at the forest site in 2006). This result may be explained by a tendency of hybrid poplars for luxury consumption, i.e., the assimilation of specific nutrients in excess of immediate growth requirements (Chapin 1980). After fertilization, luxury consumption can be a strategy for the plant to stock nutrients and use them later when they might become unavailable (especially for mobile nutrients such as NO_3^-) when soil freezes under boreal conditions. It may also be a strategy for overcoming competition effects even though it is linked to a greater investment in root system biomass at the expense of shoot growth (Van Wijk *et al.* 2003, de Mazancourt and Schwartz 2010). This phenomenon has been observed in other tree saplings and seedlings, i.e., increased N contents in plant tissues after fertilization without concurrent growth increases (Boivin *et al.* 2004; Salifu *et al.* 2009).

For all clones, N and P were often the most deficient nutrients, especially at the forest site (Table 2.5), and correspondingly soil N and P concentrations were low, which is a common problem in soils of boreal regions (Weih 2004; Cooke *et al.* 2005). Fertilization treatments often successfully corrected N deficiencies, but they failed to correct for P imbalances. DRIS I fertilization treatment did not contain any P because DRIS indices of 2005 did not show a deficiency for this nutrient at that time (Table 2.5a). However, DRIS indices of control trees showed a clear deficiency for P, especially at the agricultural site. It is possible, then, that P concentrations were balanced by pre-fertilization through residual P from the nursery, which became exhausted after a full growing season (Table 2.5b). For DRIS II and STD treatments, 50 kg ha^{-1} of P were applied, but DRIS indices still remained under the optimum range. This might be explained either by insufficient input of P or by insufficient uptake of available P because of negative interactions with other nutrients such as N or Ca, the high inputs of which may reduce P availability (Fageria 2001; DesRochers *et al.* 2007). Phosphorus uptake by roots might also be limited by N deficiency (Güsewell 2004). Calcium was always in excess in unfertilized trees at the two sites, and DRIS I and DRIS II introduced more calcium as calcium carbonate ($CaCO_3$) and as calcium-magnesium carbonate ($CaMg(CO_3)_2$), which may explain the high leaf concentrations of this nutrient after fertilization. However, the standard treatment (STD) did not contain calcium and its

DRIS index remained in excess. This can be attributed either to a high concentration of this nutrient in the soil (Lteif *et al.* 2008) or to a low soil K^+ content which is known to significantly increase absorption of Ca^{++} and Mg^{++} (Fageria 2001). Indeed, the clay soils in our study (luvisol and brunisol) are usually rich in calcium (McKeague and Stonehouse 2008). In the present study, soil Ca^{++} content was high as concentrations were 0.81% and 0.63% at the forest and farmland sites respectively (0.29% or 14.5 $cmol_c/kg$ is considered as high content; Tisdale *et al.* 1985).

2. 6 Practical considerations

Overall, our study showed that even at an early age, fertilization increases hybrid poplar growth. At the farmland site, mean tree volumes of DRIS I, DRIS II and STD treatments exceeded those of unfertilized trees by 16.07%, 10.51% and 62.61%, respectively (Fig. 2.1), which represents volume gains of 0.17 $m^3ha^{-1}y^{-1}$, 0.11 $m^3ha^{-1}y^{-1}$ and 0.68 $m^3ha^{-1}y^{-1}$ (at 4x1m spacing). At the forest site, mean tree volumes of the three fertilization treatments were respectively 33.63%, 30.02% and 30.68% greater than those of unfertilized trees, which corresponds to volume gains of 0.68 $m^3ha^{-1}y^{-1}$, 0.6 $m^3ha^{-1}y^{-1}$ and 0.62 $m^3ha^{-1}y^{-1}$ (Fig. 2.1). The positive effect of fertilization on tree growth was carried through the year following fertilizer application (2007), especially at the forest site where the volume gains associated with DRIS I, DRIS II and STD for the four clones were 1.09 $m^3ha^{-1}y^{-1}$, 0.47 $m^3ha^{-1}y^{-1}$ and 0.87 $m^3ha^{-1}y^{-1}$, respectively (Fig. 2.2). Productivity gains following fertilization were in the range of previous experiments on hybrid poplar plantations in North America i.e., between 15% and 80% (Vance 2000; Brown and van den Driessche 2002; Coleman *et al.* 2006). The volume gains that were obtained in the first (2006) and the second growing season (2007) following fertilization are promising for successful plantation establishment in northwestern Québec. Fertilization also improves tree vigour and subsequent hybrid poplar resistance to pests (Weih 2004, Coleman *et al.* 2006), which may compensate for the costs of the fertilizer application.

However, although DRIS-based fertilization treatments (DRIS I and DRIS II) generally increased average growth, they were often equal or less efficient than the STD treatment in increasing volume growth rates. Moreover, they required expensive leaf analyses

and diagnosis calculations. In our study, DRIS indices prior to fertilization revealed a similar nutrient status among the four clones and, thus, only one fertilization treatment was applied. Perhaps these early analyses reflected equivalent nursery conditions rather than clone and site particular requirements. Physiological processes that are related to nutrient metabolism such as luxury consumption, dilution or nutrient antagonisms may also distort growth prediction based on nutrient status. For instance, a fertilized plant may have a balanced nutrient status but the same growth rate as those that are unfertilized (Inno and Timmer 1997).

On the other hand, DRIS-based fertilization allows planting operations to save considerable quantities - and costs - of fertilizers by avoiding over-fertilization. Over time, DRIS recommendations of fertilizer mixture should be refined for plantations on different sites, thereby maximizing growth rates. In agriculture, over-fertilization may cost 20%-50% more than what plants can actually use (Vance 2000; Jarecki and Lal 2003). For our study, the fertilizers costs of the three treatments were about \$95 ha^{-1}, \$106 ha^{-1} and \$158 ha^{-1} for DRIS I, STD and DRIS II respectively (prices were based on quotes provided in 2010). DRIS-based fertilization may also reduce nutrient losses through leaching and, thus, pollution of surface and groundwater (Stanturf *et al.* 2001). In our experiment, DRIS I reduced inputs of N by 75% (compared to STD), which is a major pollutant of water by leaching and runoff (Gundersen *et al.* 2006). Thus, in sites with high risk of water contamination, diagnosis methods would be highly recommended, together with careful planning of the timing and frequency of fertilizer application, which takes into account site and soil characteristics such as slope, texture and precipitation (Heilman 1992; Smethurst *et al.* 2004).

2. 7 Acknowledgements

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3. CHAPITRE III

EFFECTS OF MIXING CLONES ON HYBRID POPLAR PRODUCTIVITY, PHOTOSYNTHESIS AND ROOT DEVELOPMENT IN NORTHEASTERN CANADIAN PLANTATIONS*

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3.1 Abstract

Mixing tree cultivars or species in forest plantations can be efficient to reduce the risk of pest damages and could have a positive effect on yields if complementarity or facilitation between trees occurs. Four hybrid poplar clones (747215, *Populus trichocarpa* Torrey & A.Gray × *P. balsamifera* L.; 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and 915319 *P. maximowiczii* × *P. balsamifera*) were planted in monoclonal and polyclonal plantations in three sites located in Quebec, Canada, to assess effects of clonal diversity on (i) aboveground biomass productivity, (ii) net photosynthesis and nutrient status of trees, and (iii) root spatial distribution. Stem growth was measured over five growing seasons, while root development, foliar nutrient concentrations and photosynthesis were measured during the fifth growing season. Results showed frequent but not general overyielding of trees in the polyclonal plots compared to monoclonal plots, five years after plantation establishment. Overall, stem volumes were 21% higher in the polyclonal (7.4 m^3 ha^{-1}) versus monoclonal (6.1 m^3 ha^{-1}) plots. Effects of clone mixing on growth were greater in sites where soil nutrients were more limiting. However, foliar macronutrient concentrations (N, P, K, Ca and Mg) in trees growing in polyclonal plots were similar to those in monoclonal plots. Root development differed between the two plot layouts, with mean root:shoot ratio being greater in monoclonal (0.41:1) versus the polyclonal (0.35:1) plots. Mixing clones increased biomass allocation aboveground, which we attributed to reduced competition between individuals of different clones and could explain overyielding in the polyclonal plots. The root fraction most distant from the stem (≥ 60 cm) was greater in monoclonal (67% of total root biomass) compared to polyclonal (47% of total root biomass) plots, suggesting greater belowground competition in the former, which forced roots to extend further from the stems. Effects of plot layout on net assimilation rate (P_n) depended on site, with trees in polyclonal plots having greater P_n in two of the three sites. Root total non-structural carbohydrates were greater in the polyclonal (216 mg g^{-1}) compared to the monoclonal (159 mg g^{-1}) plots. Mixing hybrid poplar clones often resulted in greater aboveground growth, lower root:shoot ratios, and different spatial root distributions, when compared to clones planted in monocultures.

Key words: Clones mixture, hybrid poplar, root distribution, growth, photosynthesis.

Résumé

Quatre clones de peuplier hybride (747215, *Populus trichocarpa* Torrey & A.Gray × *P. balsamifera* L.; 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and 915319 *P. maximowiczii* × *P. balsamifera*) ont été déployés dans des plantations monoclonales et polyclonales sur trois sites de la région boréale de l'est du Canada afin d'évaluer les effets de la diversité clonale sur (i) la productivité de la biomasse aérienne (ii) la photosynthèse nette et le statut nutritif des arbres et (iii) la distribution des racines. La croissance du tronc a été évaluée pendant cinq saisons de croissance, alors que le développement racinaire, la concentration foliaire en nutriments et la photosynthèse nette ont été mesurés au cours de la cinquième saison de croissance. Les résultats ont montré un gain de croissance fréquent, mais non systématique, dans les parcelles polyclonales, comparativement aux parcelles monoclonales après cinq années de croissance. Le volume moyen du tronc des quatre clones sur les trois sites était de 6.1 *vs.* 7.4 m^3 ha^{-1} dans les parcelles monoclonales et polyclonales, respectivement, soit un accroissement de 21%. L'effet du mélange de clones sur la croissance a été plus important dans les sites où la concentration en nutriments du sol était plus faible. Cependant, les concentrations foliaires en nutriments (N, P, K, Ca et Mg) des arbres dans les parcelles polyclonales étaient souvent similaires à celles dans les parcelles monoclonales. Le développement racinaire différait entre les deux types de déploiement et le ratio *racines:tige* moyen des arbres dans le déploiement monoclonal (0.41) était supérieur à celui dans le déploiement polyclonal (0.35). L'augmentation de l'allocation de la biomasse à la partie aérienne semble attribuable à la baisse de la compétition entre les arbres de différents clones, et pourrait expliquer le gain de croissance dans les parcelles polyclonales. La fraction des racines situées loin du tronc (≥ 60 cm), était plus élevée dans le déploiement monoclonal (67% de la biomasse racinaire totale) par rapport au déploiement polyclonal (47%), ce qui laisse présager que la compétition souterraine était plus importante dans le premier déploiement, poussant les racines à s'étendre plus loin de la tige. L'effet du déploiement des clones sur le taux d'assimilation nette (P_n) dépendait du site et la P_n des arbres dans les parcelles polyclonales était plus élevée dans deux des trois sites. L'analyse des glucides totaux non structuraux (*TNC*) des racines a montré que la concentration moyenne en TNC était plus élevée dans les parcelles polyclonales (216 mg g^{-1}) comparativement aux parcelles monoclonales (159 mg g^{-1}). Le mélange de clones de peupliers hybrides a permis une

croissance aérienne souvent plus élevée, un ratio *racine:tige* plus faible et une distribution différente des racines, par rapport aux plantations monoclonales.

Mots clés : Mélange clonal, peuplier hybride, distribution des racines, croissance, photosynthèse.

3.2 Introduction

Much research has been conducted over the past twenty years to evaluate effects of diversity on ecosystem functioning, and has demonstrated that biomass production increases with increasing diversity (Loreau *et al.* 2001). The mechanisms underlying the positive effects of diversity on productivity have been classified into (i) complementarity and facilitation interactions between species, based on niche partitioning theory or the benefit that one species can receive from another, and (ii) sampling effects, which stipulate that within a group of species, one or more would dominate and increase overall ecosystem yield (Loreau *et al.* 2001). Most earlier trials tested this relationship on grass and shrub species, but many studies have now attempted to demonstrate the universality of this principle and are trying to elucidate the mechanisms that might explain diversity-productivity relationships (Menalled *et al.* 1998; Petit and Montagnini 2006; Horner-Devine *et al.* 2003). Results from forest ecosystems would appear to confirm previous findings and overall, a positive effect of tree diversity on biomass production in both natural stands and plantations has been found (Tilman 1999; Balvanera and Aguirre 2006; Potvin and Gotelli 2008; Lei *et al.* 2009; Paquette and Messier 2011).

Intensively managed forest plantations are used to produce large quantities of wood on limited land areas. In 2010, the total area of planted forests was only 7% of natural forest areas worldwide, while their contribution was about 40% of global fiber needs (FAO 2010). Plantations, however, are often managed as monocultures and have been described by some as "biodiversity deserts" (Evans and Turnbull 2004; Brockerhoff *et al.* 2008). Forest plantation monocultures are more common than mixtures of species or clones because they are easier to manage, nutrient requirements are easier to assess, harvesting operations can be uniform, and the timber that is logged has similar characteristics (Kelty 2006). In contrast, exhaustion of soil nutrients, the deterioration of soil physical and chemical properties, and increased vulnerability of crops to pest and pathogen attacks are often associated with monocultures (Bonduelle 1983; McCracken and Dawson 1997). When compared to natural forest stands, tree monocultures decrease biodiversity across the landscape and affect a wide spectrum of other plant and animal species, ranging from soil microorganisms to macrofauna (Stephan *et al.* 2000; Harvey *et al.* 2006; Eisenhauer *et al.* 2010). Mixtures of cultivars were

originally used in afforestation and intensively managed plantations as biocontrol strategies against the attacks of pests and pathogens that frequently target certain genotypes (Miot *et al.* 1999; Jactel and Brockerhoff 2007). Reducing pest damages was based on "Widespread Intimately Mixed Plantations" (WIMPs) approach where genotypes are randomly intermixed and in a lesser extent on "Mosaics of monoclonal stands (MOMS)" where stands of different genotypes are mixed (Libby 1987; Lindgren 1993). Current studies have shown that mixing cultivars may also positively affect biotic and abiotic environments through optimal use of nutrients according to niche differentiation theory (Diaz and Cabido 2001; Schmid 2002; Erskine *et al.* 2006) and, in this way, they can enhance specific and functional biodiversity relative to monospecific plantations. Other experiments that have been carried out in plantations have shown an effect on productivity that is sometimes positive (i.e., overyielding) and sometimes neutral (Benbrahim *et al.* 2000; Berthelot 2001; Joshi *et al.* 2001; Potvin and Gotelli 2008).

In 2006, plantations with more than one genotype represented less than 0.1% of the total area of industrial plantations worldwide (Nichols *et al.* 2006). It is expected that this area will increase in the future if benefits of mixing cultivars on productivity can be clearly demonstrated (Paquette and Messier 2011). Overyielding in mixtures of cultivars could be related to a facilitative interaction, for example, the facilitation of N uptake by interplanting N_2-fixing species (genera such as *Alnus* or *Acacia*). Complementarity, on the other hand, is related to the stratification of aboveground (for light) or belowground (for water and nutrients) niches (Hooper and Dukes 2004; Potvin and Dutilleul 2009). Complementarity can also occur if the timing of nutrient uptake or the phenology of two companion species is different (Garber and Maguire 2004; Oelmann *et al.* 2010) or if distinct nutrient species are used by trees (e.g., nitrate *vs.* ammonium nitrogen; Persson *et al.* 2006). Consequently, competition for resources is minimized between species or cultivars, overall photosynthetic activity is greater and more biomass can be allocated to aboveground structures (Montagnini 2000; Zeugin *et al.* 2010). When individuals share the same niche, resources become less available and root systems become denser and more extensive (Forrester *et al.* 2006). However, tree root systems are much less studied compared to aboveground structures, although they should provide important insights into belowground interactions between individuals in mixed stands (Fargione *et al.* 2007). Root development has a fundamental

influence on tree productivity and is closely linked to nutrient assimilation and photosynthetic activity (Kalliokoski *et al.* 2008; Ouimet *et al.* 2008). This study examined the diversity-productivity relationship of intensively managed tree plantations, to determine whether a mixture of hybrid poplar (*Populus* spp.) clones would increase the overall productivity of plantations relative to monocultures. The effects of clonal diversity on (i) aboveground biomass production in hybrid poplar plantations, (ii) net photosynthesis and nutrient status of trees, and (iii) spatial separation of niches at the root level were evaluated. We hypothesized that mixing clones would reduce biomass allocation to roots and change root distribution, increase nutrient uptake and net assimilation, and improve the overall growth of trees.

3.3 Materials and methods

3.3.1 Site description and plant material

The study sites were located in the Abitibi-Témiscamingue region of northwestern Québec, Canada, under a humid continental climate. Replicate plantations were established on three different sites. The first site was abandoned farmland located in the municipality of Duhamel (47°32'N, 79°59'W) in the sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britton) western bioclimatic sub-domain (Grondin 1996). The site had been previously cultivated for hay. The soil at Duhamel was a clayey Luvisol (45% clay; Agriculture and Agri-food Canada 2012) with mean annual precipitations and temperature of 820 mm and 2.8 °C, respectively (Environment Canada 2013).The second site was previously forested before being harvested in 2004 (48°29'N, 97°9'W). It was located near the municipality of Duparquet in the balsam fir (*Abies balsamea* L.)-paper birch (*Betula papyrifera* Marshall) bioclimatic western sub-domain (Grondin 1996) with mean annual precipitations and temperature of 918 mm and 1.2 °C, respectively. The soil at this site was classified as heavy clay Brunisol (70% clay; Agriculture and Agri-food Canada 2012). The third site was located in the municipality of Villebois and had been previously farmed organically for cereals and hay. This site (49°09'N, 79°10'W) was in the black spruce (*Picea mariana* (Mill.) BSP)-feather moss (*Pleurozium* spp.) domain (Grondin 1996) and the soil type was clay Grey Luvisol (50% clay). Mean annual precipitations and temperature at this site are 890 mm and 1.2 °C, respectively (Environment Canada 2013).

Four hybrid poplar clones that had been recommended for the region by the ministère des Ressources Naturelles du Québec (MRNQ) were selected for planting: clone 747215 (*Populus trichocarpa* Torrey & A. Gray × *balsamifera* L.*)*, clones 915004 and 915005 (*P. balsamifera* × *maximowiczii* Henry), and clone 915319 (*P. maximowiczii* × *balsamifera*). Prior to plantation establishment, stumps and woody debris at the Duparquet site were removed with a bulldozer. This site was then ploughed to a depth of 30 cm in autumn 2004 with a forestry plough pulled by a skidder and disked in spring 2005 to level the soil before planting. Duhamel and Villebois sites were ploughed using an agricultural cultivator in autumn 2004. Trees were planted in June 2005 at 4 × 3 m spacing, corresponding to a density of about 833 trees/ha. Stock type was bare-root dormant trees and the average tree height at planting was 96.3 cm. Following planting, weeds were mechanically removed twice a year by cultivating between rows with a farm tractor and by tilling between trees with a Weed Badger (model 4020-SST, Marion, ND, USA). The experimental design was comprised of three monoclonal and three polyclonal replicates (blocks) of the four hybrid poplar clones at each site. A monoclonal plot consisted of five rows of five trees of one clone, while a polyclonal plot consisted of a mixture of eight rows of eight trees where the position of the four clones was randomly assigned (N = 1476).

3.3.2 Growth

Height, basal diameter and diameter of all the trees were measured at planting (spring 2005) and at the end of each growing season until autumn 2009. Stem volume was estimated with the equation:

$$V = A_b.H / 3$$

where V: stem volume (m^3), A_b: basal area (mm) and H: height (cm) (Brown and van den Driessche 2002).

3.3.3 Specific leaf area (SLA) and chemical analyses

In May 2007, five soil samples were collected at Duhamel, and 10 at Duparquet and Villebois (more heterogeneous) for chemical and physical characterization (Table 3.1). Soil samples were collected diagonally along plots (periphery and centre of the two diagonals).

Two sub-samples from the 0-20 cm and 20-40 cm horizons were collected separately for each sample. Soils were subsequently dried in an oven at 50 °C, ground, sieved to pass a 60 µm mesh, and then pooled for analysis. Total carbon concentrations in the soil were determined by high temperature combustion with a LECO N-analyzer (Leco Corp., St. Joseph, MI, USA). Soil concentrations of available cations (Ca^{2+}, K^{+}, Mg^{2+} and Na^{+}) and cation exchange capacity (CEC, $cmol_c\ kg^{-1}$) were determined after ammonium acetate extraction. Soil samples pH were obtained from a water-saturated paste. Leaf and soil nitrogen concentrations were quantified with the LECO N-analyzer. KCl (2 M) extraction was first performed on the soil, according to application bulletin CHNP2-84 (Leco Corp. 1986).

Table 3.1. Soil chemical properties of the three sites measured in 2007.

		Site					
		Duhamel		Duparquet		Villebois	
Soil sample depth		0-20 (cm)	20-40 (cm)	0-20 (cm)	20-40 (cm)	0-20 (cm)	20-40 (cm)
pH		5.6	5.5	4.9	5.8	6.8	5.7
Exchangeable Cations ($mg\ kg^{-1}$)	Ca	1853	2212	4392	4968	4528	2056
	K	116	130	266	265	159	131
	Mg	372	482	668	797	342	347
	Na	16	27	43	51	24	28
CEC ($cmol_c\ kg^{-1}$)		12.7	15.5	28.3	32.3	51	13.6
Moisture content		0.016	0.021	0.035	0.035	0.015	0.017
Total C ($g\ kg^{-1}$)		15.60	10.64	7.98	7.17	15.25	16.65
Total N ($g\ kg^{-1}$)		1.32	0.87	0.82	0.62	0.90	1.05
Total Ca ($g\ kg^{-1}$)		6.18	6.48	7.05	9.23	11.28	6.28
Total K ($g\ kg^{-1}$)		2.91	3.80	7.50	7.30	4.35	3.84
Total Mg ($mg\ g^{-1}$)		10.41	12.26	17.59	17.59	12.60	11.28
Total P ($mg\ g^{-1}$)		0.54	0.46	0.37	0.55	0.61	0.54

Notes. CEC: cation exchange capacity, MC: moisture content.

In mid-July 2009, leaf samples were collected at the three sites for measurement of specific leaf area (SLA) and for analyses of N, P, K, Ca and Mg concentrations. Nine recently matured leaves from three randomly selected trees of each clone were collected from the monoclonal and polyclonal plots; three leaves were selected from the upper-third, middle-third and lower-third of the crown. Leaf samples were immediately packed in dry ice and their area was measured with a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE, USA) before oven-drying at 70 °C for 72 h and weighing. Specific leaf area (SLA) was calculated as the ratio of leaf area (cm^2) to leaf dry mass (g). Leaves were then ground in a Wiley mill to pass a 60 µm-mesh sieve and pooled to obtain a composite sample for the determination of nutrient concentrations. Soil and leaf concentrations of P, K, Ca and Mg were quantified by inductively-coupled plasma (ICP) spectroscopy following HNO_3-HCl digestion (Masson and Esvan 1995).

3.3.4 Photosynthesis

Net photosynthesis (P_n) was measured on two trees within each replicate, for each clone and for each layout type (monoclonal and polyclonal) at the three sites with a CIRAS-2 portable photosynthesis system using an infra-red analyzer (PP Systems, Amesbury, MA, USA) for the period 13-17 July 2009 (N = 144). Measurements were made on recently matured and well exposed leaves that did not show any apparent sign of senescence. The CIRAS-2 system was coupled with a broadleaf cuvette (PLC6-U, 25 mm diameter), which was equipped with a LED unit for automatic light control. Air flow and CO_2 concentrations in the cuvette were maintained at 300 mL min^{-1} and 360 µmol mol^{-1}, respectively. Photosynthetically active radiation (PAR) was set at 1600 µmol m^{-2} s^{-1} and measurements were taken between 8h30 and 12h00. During measurements, air temperature ranged between 18 °C and 25 °C, while relative humidity was between 50% and 70%. The order of tree measurements was randomized to reduce the time effect on photosynthesis parameters between 8h30 and 12h00. To avoid edge effect, trees of a buffer row around each plot were not sampled for photosynthesis, SLA and nutrients measurements.

3.3.5 Destructive sampling

The root and shoot systems of two randomly chosen trees per replicate for each clone and layout type (N = 24) were selected for destructive sampling at the Duparquet site. Roots were excavated, either using an AIR-SPADE (Arbortools, Hong Kong) or hydraulically with a high pressure water pump (Mark III, Wajax, Lachine, QC, Canada). Small roots were dug out manually using pickaxes, shovels and trowels. Roots were grouped into three classes according to their distance (d) from the stem: (i) $d \leq 30$ cm; (ii) 30 cm $< d \leq 60$ cm; (iii) $d >$ 60 cm. Maximum depth (D_{max}, cm) and maximum radial elongation (L_{max}, cm) of roots were also measured for each excavated tree. After roots were dried, the total length of coarse roots (diameter > 2 mm) and the mass of each root group were measured. Stems, branches and leaves of excavated trees were separated, dried (at 75°C) and weighed to calculate biomass allocation to roots and shoots. At the beginning of each tree excavation, a root sample of about 1 cm in diameter and 10 cm in length was collected for total non-structural carbohydrates (TNC) determination. Samples were located 50 to 70 cm from the stem to homogenize sampling.

Root samples were transported on ice from the field before being frozen (-20 °C) prior to TNC analyses. Root samples were then oven-dried at 75 °C, ground and sieved in a Wiley mill through a 40 µm mesh. Starch and sugar concentrations were measured colorimetrically according to Chow and Landhäusser (2004). Soluble sugars were extracted from 50 mg of root tissue with hot ethanol (5 mL). Sugar extracts were reacted with phenol-sulphuric acid (Dubois method), and their absorbances were measured by UV spectrophotometry (at 490 nm). Starch residue left after soluble sugar extraction was hydrolyzed to glucose with a mixture of α-amylase and amyloglucosidase. Glucose in the hydrolysate was measured colorimetrically (at 525 nm) using peroxidase-glucose oxidase-o-dianisidine colour reagent.

3.3.6 Statistical analyses

Linear mixed-effect models (nmle) analyzed the relationships between response variables and explanatory variables (Version 2.11.1, R Development Core Team, Vienna, Austria). Tree volume was subjected to repeated measures analysis of variance with year as the repeated measure. Clone, layout (monoclonal *vs.* polyclonal), year and site were considered as fixed effects, while block (replicate) was considered as a random effect in all models. Net photosynthesis, specific leaf area and nutrient concentrations were analyzed

using a model similar to that used for stem volume, without the repeated measures. To test the effects of clone, layout and site (fixed effects) on the root distribution variables and TNC concentrations, the data were subjected to three-way analysis of variance (ANOVA) after a tangent transformation (tan) to respect homoscedasticity assumption. Means were compared using Tukey's honest significant differences (HSD) for all possible comparisons and the significance level for all tests was set at $\alpha = 0.05$. Pearson product-moment correlations (r) were used to test relationships between root distribution traits and total non-structural carbohydrate concentrations, and stem volume.

3.4 Results

3.4.1 Stem volume

In 2009, differences in tree volume between the two layouts were significant but depended on clones and sites (Table 3.2). Five years after plantation establishment, stem volume of the four clones across the three sites ranged from 2.2 to 12.4 $m^3 ha^{-1}$ in the monoclonal plots and from 3.6 to 14.5 $m^3 ha^{-1}$ in the polyclonal plots (Fig. 3.1). Overyielding of stem volume in polyclonal plots compared to monoclonal plots ranged between 17% and 84% and was not significant for two of the four clones at Duhamel. At Duparquet and Villebois, stem volume of polyclonal plots were greater than monoclonal plots (especially for clone 747215), but not at Villebois for clone 915319 which was, the best performing clone (Fig. 3.1). Difference in stem volume between monoclonal and polyclonal plots showed the same trends in 2008 as in 2009, while no significant difference in tree volumes was recorded between plot layouts during the first three growing seasons (2005-2007; Index).

Table 3.2. ANOVA summaries for tree volume (V, repeated measures factor = year), net photosynthesis (P_n), specific leaf area (SLA), nutrients concentrations (N, P, K, Ca and Mg) of four hybrid poplar clones in the three sites showing sources of variation F and *P* values. Statistically significant values are indicated in bold.

Source of variation	V		Pn		SLA		N		P		K		Ca		Mg	
	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Site (S)	146.1	**<0.01**	55.3	**< 0.01**	5.9	0.05	10.8	**< 0.01**	33.7	**< 0.01**	15.3	**< 0.01**	14.2	**< 0.01**	2.6	0.08
Layout (L)	6.3	**0.01**	0.6	0.43	1.3	0.32	0.8	0.38	0.3	0.59	2.1	0.15	1.1	**< 0.01**	0.1	0.76
Clone (C)	64.6	**<0.01**	3.2	**0.02**	5.9	**< 0.01**	10.8	**< 0.01**	19	**< 0.01**	1.4	0.26	17.5	**< 0.01**	36.9	**< 0.01**
Year (Y)	1895.8	**<0.01**														
L*C	8.8	**<0.01**	1.1	0.38	0.9	0.42	0.3	0.84	0.7	0.56	1.3	0.27	4.1	0.01	3.4	**0.02**
L*S	16.6	**<0.01**	4.9	**0.01**	0.2	0.82	12.9	**< 0.01**	20.2	**< 0.01**	1.1	0.33	3.9	**0.02**	8.2	**< 0.01**
L*Y	8.8	**<0.01**														
L*C*Y	0.17	**0.99**														
L*C*S	3.19	**<0.01**	1.2	0.34	0.8	0.54	0.06	0.99	1.8	0.12	2.4	**0.03**	1.2	0.32	1.2	0.31
S*L*Y	1.54	0.15														
C*S	3.5	**<0.01**	0.4	0.87	0.8	0.58	2.3	**0.04**	1.6	0.17	2.5	**0.03**	1.4	0.25	1.6	0.17
C*Y	1.05	0.37														
S*Y	18.05	**<0.01**														
S*C*Y	0.32	0.99														
S*L*C*Y	0.26	0.99														

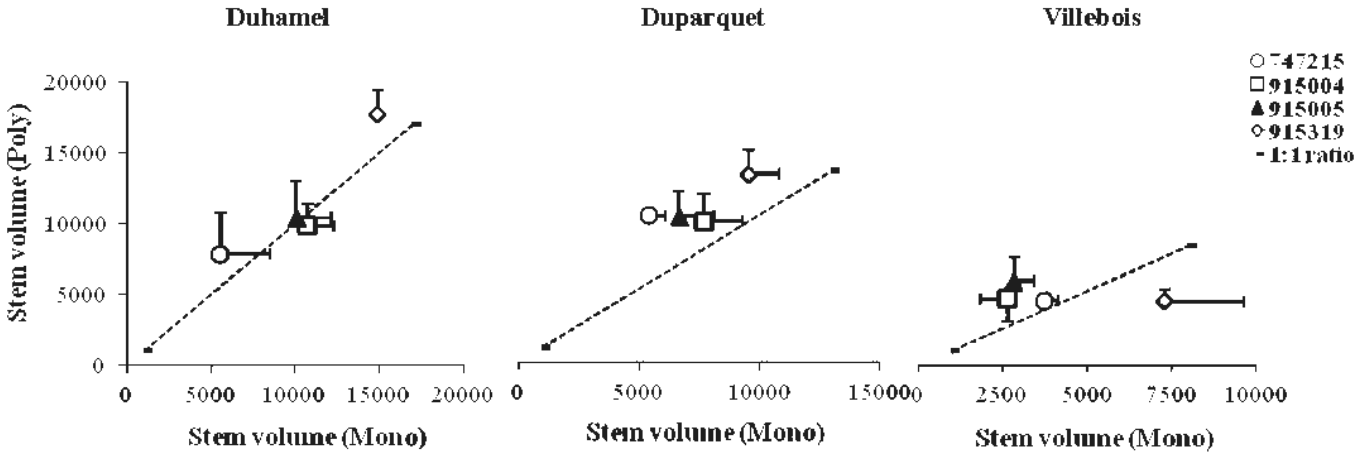

Figure 3.1 Mean stem volume (10^{-3} m^3 $tree^{-1}$) in the fifth growing season of four hybrid poplar clones in monoclonal (Mono) vs polyclonal (Poly) plots at Duhamel, Duparquet and Villebois. Dotted line indicates equal stem volume in polyclonal vs monoclonal plots (1:1 ratio). Horizontal and verticals bars are standard errors (SE) for monoclonal and polyclonal plots, respectively.

3.4.2 Nutrient concentrations

Nitrogen and P concentrations were significantly greater in the polyclonal plots at Duparquet compared to monoclonal plots, but were similar at Duhamel and Villebois (Table 3.2 and 3.3). For the other macronutrients (Ca, K and Mg), leaf concentrations between monoclonal and polyclonal plots varied, depending upon site (Layout x Site, $P < 0.01$), but were often greater in the polyclonal plots (Table 3.2). Leaf Ca concentration was on average 11.2 mg g^{-1} *vs.* 9.2 mg g^{-1} in polyclonal plots compared to monoclonal plots ($P < 0.01$) (Table 3.3).

Table 3.3. Leaf concentrations ranges (mg g^{-1}) of macronutrients (N, P, K, Ca and Mg) of the four hybrid poplar clones in the monoclonal and polyclonal plots at the three sites, measured in the fifth growing season.

Layout			Monoclonal	Polyclonal
	Duhamel	**N**	21.2 - 25.4	20.6 - 25.2
		P	1.9 - 2.5	1.7 - 2.4
		Ca	7.9 - 1.1	8.2 - 1.2
		K	9.3 - 11.1	9.7 - 11.1
		Mg	2.0 - 2.8	2.0 - 2.8
Site	**Duparquet**	**N**	15.7 - 18.2	18.7 - 21.0
		P	1.6 - 2.1	2.1 - 2.5
		Ca	8.7 - 12.5	10.6 - 14.9
		K	9.6 - 12.9	11.2 - 11.5
		Mg	1.6 - 2.7	2.2 - 2.7
	Villebois	**N**	18.8 - 23.5	20.7 - 25.6
		P	1.9 - 2.6	2.1 - 3.0
		Ca	7.8 - 11.7	8.5 - 13.5
		K	11.8 - 13.3	11.6 - 12.6
		Mg	2.1 - 2.5	2.1 - 3.0

3.4.3 Specific leaf area and net photosynthesis

Specific leaf area (SLA) was similar between the monoclonal and polyclonal plots although it was different between clones and marginally different between sites (P=0.05, Table 3.2). At Duhamel, average SLA of the monoclonal and polyclonal plots ranged between 79.4 cm^2 g^{-1} (clone 747215) and 89.4 cm^2 g^{-1} (clone 915004). At Duparquet and Villebois, average SLA ranged between 67.5 and 89.1 cm^2 g^{-1} and between 74.7 and 90.8 cm^2 g^{-1}, respectively (Table 3.4A).

P_n was greater in the polyclonal plots for two clones (747215 and 915005) at Duhamel and was usually similar between monoclonal and polyclonal plots at Duparquet and Villebois

(Table 4B). P_n ranged from 17.9 to 22.1 µmol CO_2 m^{-2} s^{-1} at Duhamel and from 15.1 to 17.1 µmol CO_2 m^{-2} s^{-1} at Duparquet (clone 915319 excluded, Table 3.4B).

Table 3.4. A) Mean specific leaf area (SLA, cm^2 g^{-1}) and B) mean net photosynthesis (µmol CO_2 m^{-2} s^{-1}) of the four hybrid poplar clones in the monoclonal and polyclonal plots at the three sites measured in the fifth growing season.

	Site					
	Duhamel		**Duparquet**		**Villebois**	
Clone	Monoclonal	Polyclonal	Monoclonal	Polyclonal	Monoclonal	Polyclonal
A)						
747215	61.98±0.4 [a]	67.43±10.94 [a]	81.52±5.41[a]	74.58±2.55[b]	89.23±5.63 [a]	84.76±5.2 [b]
915004	79.01±7.85 [b]	65.78±7.9 [a]	82.05±2.56 [a]	56.34±21.42 [c]	83.28±4.29 [b]	78.28±5 [c]
915005	77.67±5.64 [c]	72.17±5.32 [c]	79.3±1.25 [c]	71.29±4.08 [b]	83.4±5.1 [b]	80.96±2.29 [c]
915319	85.49±1.78 [d]	99.06±19.37 [d]	89.22±3.02 [d]	98.54±22.45 [d]	93.6±4.74 [d]	87.05±9.67 [b]
B)						
747215	19.43±1.16 [a]	22.07±1.06 [b]	16.2±0.42 [a]	17.15±1.2 [a]	15.7±0.6 [a]	16.67±1.77 [a]
915004	20.2±1.47 [a]	20.53±1.37 [a]	15.15±0.91 [b]	17.1±0.98 [c]	17.8±2.1 [a]	15.97±1.03 [a]
915005	17.9±2.49 [c]	21.67±0.96 [b]	15.7±0.56 [b]	16.6±0.98 [b]	16.67±1.04 [a]	15.73±1.1 [a]
915319	21.03±2.5 [b]	21.6±1.87 [b]	18.4±0.84 [d]	16.35±0.21b [c]	18±1.25 [b]	17.43±1.19 [b]

Note. Within the same site, values followed by same letters do not differ at $P < 0.05$.

3.4.4 Biomass allocation

Biomass measurements that were made at Duparquet in 2009 showed that the root:shoot ratios of trees in the monoclonal plots were significantly greater than that of the polyclonal plots (P = 0.03, Fig. 3.2). Average shoot biomass of the four clones in the polyclonal plots was 4.55 kg DM $tree^{-1}$ while root biomass was 1.61 kg DM $tree^{-1}$, giving an average root:shoot ratio of 0.35 (Fig. 3.2). In the monoclonal plots, this ratio was 0.41 as root and shoot biomasses were respectively 1.57 and 3.85 kg DM $tree^{-1}$. Depending on clones, total aboveground biomass represented 69 to 72% and 72 to 76 % of the total tree biomass in the monoclonal and polyclonal plots, respectively. The same pattern was observed for the stem biomass, with mean values of 2.39 kg DM $tree^{-1}$ in polyclonal plots and 1.88 kg DM $tree^{-1}$ in monoclonal plots which represented 39% and 35% of the total biomass (Fig. 3.2). The plot

layout did not affect the proportion of leaves and branches and average percentages of the total tree biomass were 17% for leaves and 18% for branches (data not shown).

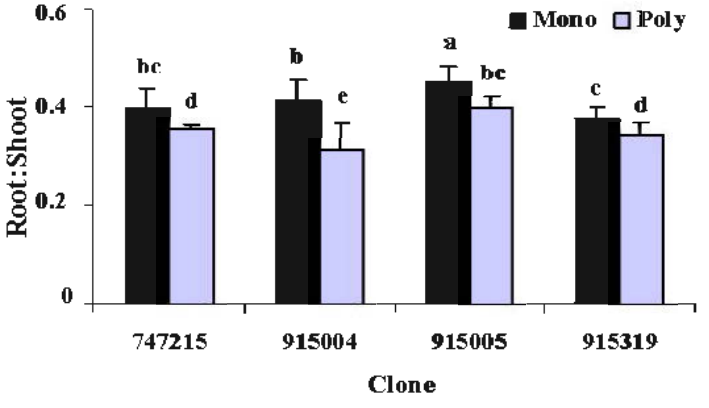

Figure 3.2 Mean root:shoot ratios of four hybrid poplar clones in monoclonal (Mono) vs polyclonal plots (Poly) at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

3.4.5 Radial distribution of roots

Mean total coarse root length within the first 30 cm from the stem was similar in the monoclonal *vs.* polyclonal plots for all clones at Duparquet (Table 3.5). The root fraction relative to the total length of coarse roots contained in the 0-30 cm distanced class averaged 18% (range: 10-27%; Fig. 3.3A). The relative coarse root fraction within 30-60 cm from the stem was greater in the polyclonal compared to monoclonal plots (Fig. 3.3B, Table 3.5). In contrast, the fraction of roots that was located > 60 cm from the stem was significantly greater ($P = 0.02$) in the monoclonal plots compared to the polyclonal plots (67 *vs.* 47%, respectively) (Fig. 3C). Mean fine root fraction within 30 cm from the stem, relative to total fine root dry matter, was greater in the polyclonal plots compared to monoclonal plots ($P < 0.01$); this proportion ranged between 10% and 60% respectively (Fig. 3.4A). Fine root fractions within 30 to 60 cm from the stem were similar in the two types of plot layout (Table 3.5), averaging 20% of the total.

Table 3.5. ANOVA summary showing sources of variation and *P*-values for fine and coarse root distribution of four hybrid poplar clones at Duparquet in the fifth growing season: proportion of total roots at 0-30 cm, 30-60 cm and > 60 cm from the stem, maximum horizontal extension of roots from the stem (L_{max}), maximum vertical depth of roots from the soil surface (D_{max}), total non-structural carbohydrates (TNC), starch and soluble sugars concentrations of roots (mg g^{-1} DM).

Source of variation	***P*-value**										
	Coarse roots (%)			**Fine roots (%)**			**L_{max}**	**D_{max}**	**TNC**	**Starch**	**Soluble sugars**
	0-30	**30-60**	**> 60**	**0-30**	**30-60**	**> 60**					
Layout	0.49	0.01	0.02	<0.01	0.33	<0.01	0.19	0.95	0.02	<0.01	0.80
Clone	0.40	0.56	0.35	0.01	0.06	0.02	0.16	0.86	0.19	0.02	0.40
Layout x Clone	0.76	0.68	0.62	<0.01	0.27	<0.01	0.02	0.89	0.29	0.92	0.66

The > 60 cm fraction of fine roots for clones 915004, 915005 and 915319 was significantly greater in monoclonal plots and, for clone 747215, was not affected by layout (Table 3.5). Relative fine root fraction at this distance ranged between 61% and 763% in the monoclonal plots, and between 55% and 64% in the polyclonal plots, respectively (Fig. 3.4C). Maximum radial root elongation (L_{max}) was greater in the monoclonal plots compared to the polyclonal plots, except for clone 915005 (clone x layout interaction, $P = 0.02$; Table 3.5). L_{max} values ranged respectively between 294 –and 394 cm in the monoclonal plots *vs.* 251 to 324 cm in the polyclonal plots (Fig. 3.5). Maximum root depth (D_{max}) was not affected by clone or plot layout (Table 3.5), averaging 76 cm (data not shown). Tree volume and the coarse root fraction within the 30-60 cm distance class were positively correlated ($r = 0.52$, $P = 0.02$; Fig. 3.6A), while the proportion of roots at distances > 60 cm was negatively correlated with tree volume ($r = -0.47$, $P = 0.05$; Fig. 3.6B).

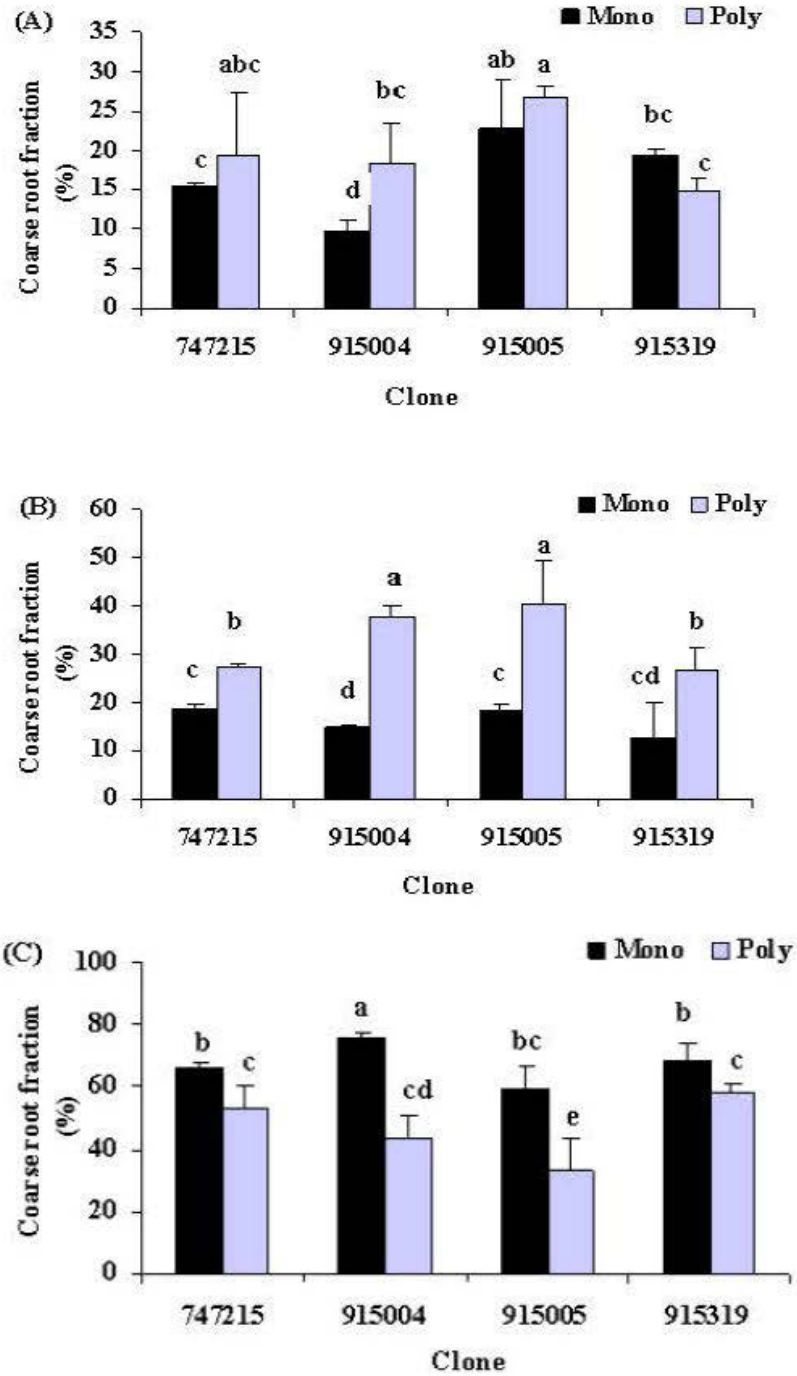

Figure 3.3 Coarse root fraction relative to the total root length (%) of four hybrid poplar clones in monoclonal (Mono) vs polyclonal (Poly) plots at 0-30 cm (A), 30-60 cm (B) and > 60 cm (C) distances from the stem at Duparquet in the fifth growing season. For the same trait, values followed by the same letters, do not differ at $P < 0.05$.

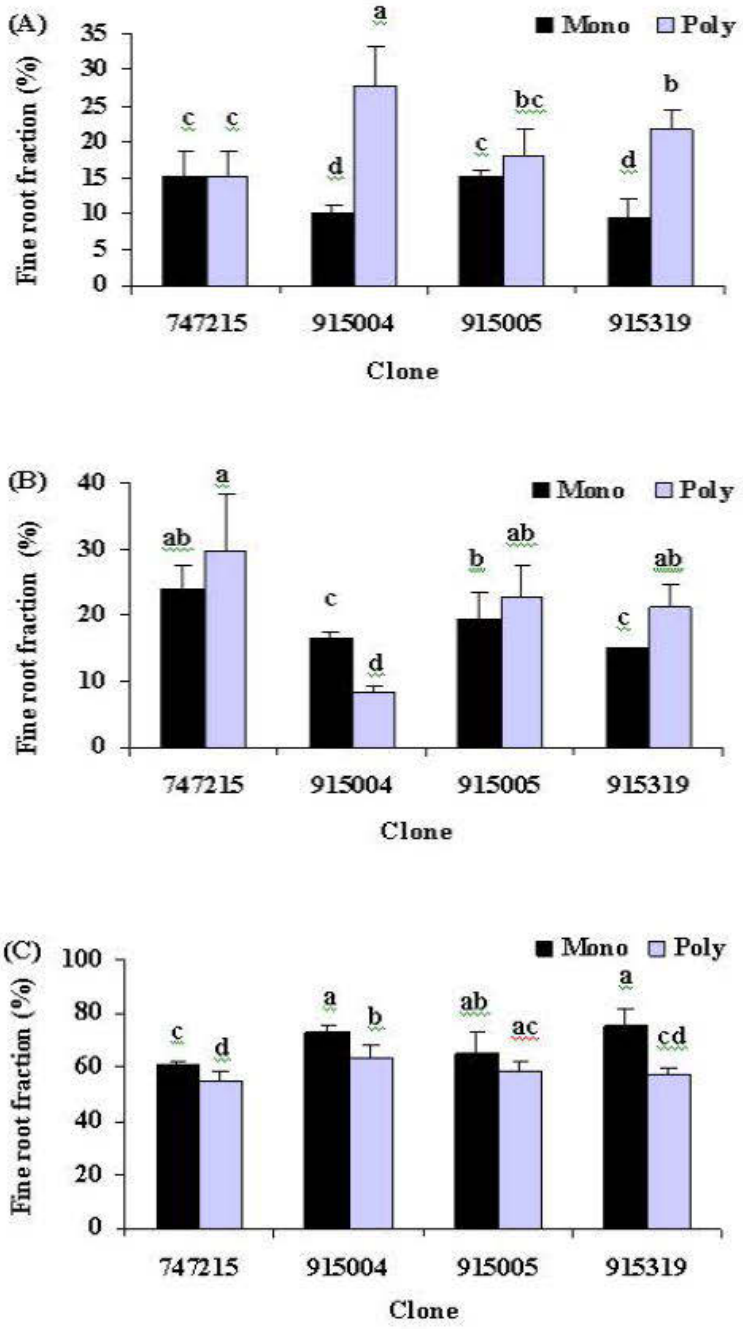

Figure 3.4 Fine root fraction relative to the total fine root dry matter (%) of four hybrid poplar clones in the monoclonal (Mono) and polyclonal (Poly) plots at 0-30 cm (A), 30-60 cm (B) and > 60 cm (C) distances from the stem at Duparquet in the fifth growing season. For the same trait, values followed by the same letters, do not differ at $P < 0.05$.

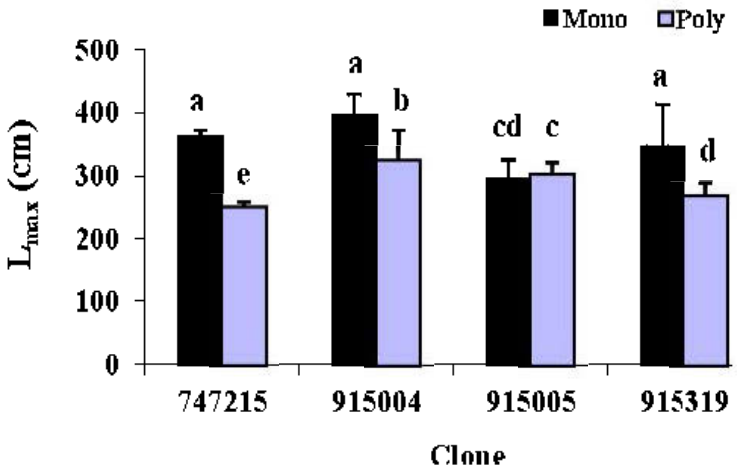

Figure 3.5 Maximum root length (L_{max}, A) of four hybrid poplar clones in the monoclonal (Mono) vs polyclonal (Poly) plots at Duparquet in the fifth growing season. For the same trait, values followed by the same letters, do not differ at $P < 0.05$.

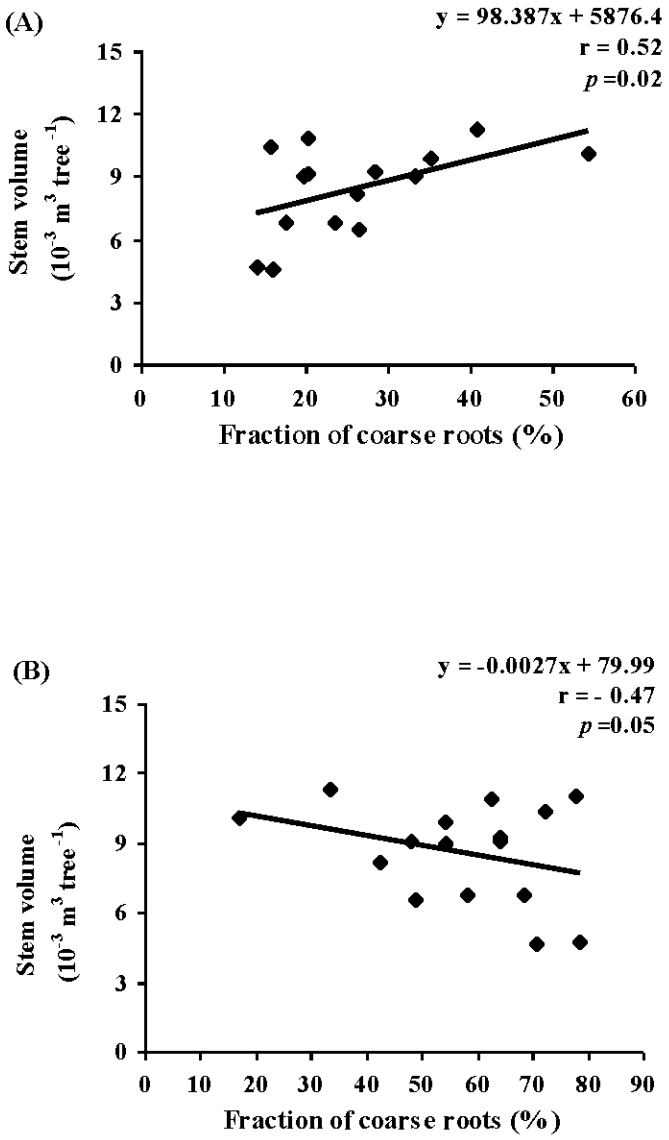

Figure 3.6 Relationship between coarse root fraction (%) and stem volume of four hybrid poplar clones at 30-60 cm (A) and >60 cm (B) distances from the stem at Duparquet in the fifth growing season.

3.4.6 TNC content of roots

Coarse root analysis showed that TNC concentrations were greater in polyclonal plots than in monoclonal plots (P = 0.02) and averaged 216.2 and159.2 mg g^{-1} DM, respectively (Fig. 3.7A, Table 3.5). Soluble sugar concentrations did not differ between the different layouts or clones (Table 3.5). Mean soluble sugar concentrations of the monoclonal and polyclonal plots, when averaged for the four clones, was 103 mg g^{-1} (data not shown). Root starch concentrations, however, were significantly (P < 0.01, Fig. 3.7B) greater for trees in the polyclonal plots (84-111 mg g^{-1}) compared to monoclonal plots (26-82 mg g^{-1}). Starch concentrations of roots also differed between clones (P = 0.02) and ranged from 58 mg g^{-1} (mean of polyclonal and monoclonal plots of clone 915319) to 108 mg g^{-1} (clone 915004, Fig. 3.7B). There was a positive correlation between root starch concentrations and stem volume (P = 0.04, Fig. 3.8), and between starch concentrations and N and P concentrations (P = 0.01 and P = 0.05, respectively; data not shown).

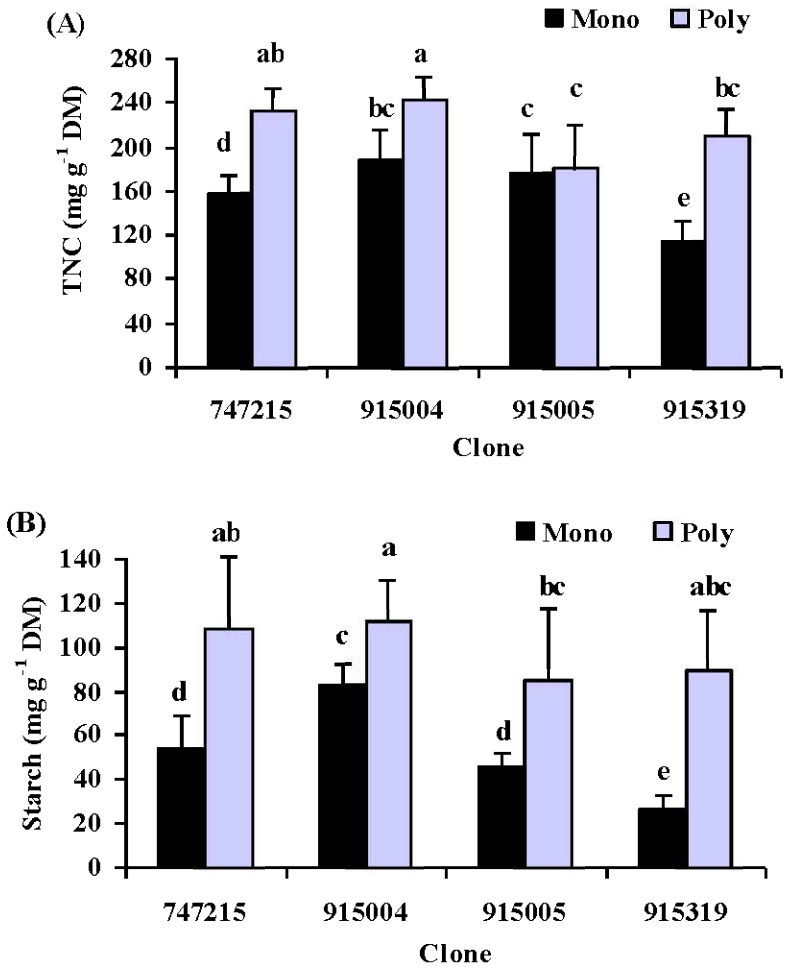

Figure 3.7 Mean total non-structural carbohydrates (TNC) (A) and starch (B) concentrations (mg g^{-1} DM) of coarse roots of four hybrid poplar clones in the monoclonal (Mono) vs polyclonal (Poly) plots at Duparquet in the fifth growing season. For the same trait, values followed by the same letters do not differ at $P < 0.05$.

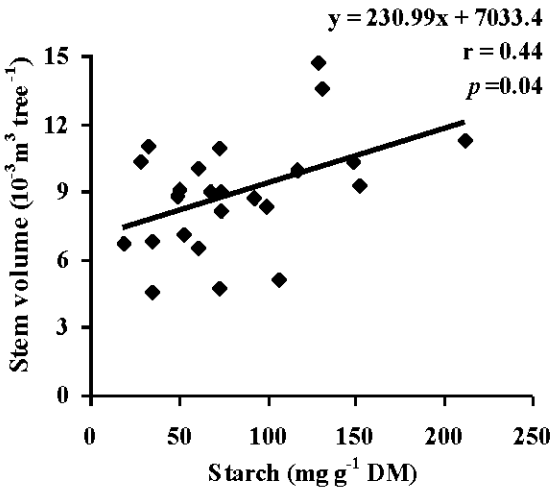

Figure 3.8 Relationship between coarse root concentrations (mg g^{-1} DM) starch and tree volume (V) of all four hybrid poplar clones at Duparquet in the fifth growing season.

3.5 Discussion

Yield differences between pure and mixed forest stands depend on environmental conditions, and overyielding is often more noticeable in nutrient-poor sites compared to fertile sites (Pretzsch *et al.* 2010). In our study, growth was not always greater in the polyclonal plots, as the effects of mixing clones depended upon both clones and sites. Our sites were located in the boreal region of Quebec and are known to be poor in nutrients, especially N. This has been confirmed by nutrient deficiencies in hybrid poplar that was planted in the same areas (Guillemette and DesRochers 2008; Elferjani *et al.* 2013). Soil N concentrations in our soils were below 1.1 g kg^{-1}, while they can typically reach 2 g kg^{-1} to 5 g kg^{-1} in other forest ecosystems, and up to 25 g kg^{-1} in cultivated lands (Martinelli *et al.* 1999). High nutrient availability in fertile soils, reduces competition between species or genotypes and could reduce segregation of niches by root stratification (Oelmann *et al.* 2010). P deficiencies and low Ca availability that is due to high acidity (low pH) have also been reported in boreal conditions and could contribute to the presence of overyielding in the polyclonal plots (Ericsson 1995; Lindahl *et al.* 2002). Soil pH of our sites ranged between 4 and 6, which favours immobilization of P by aluminium, reducing availability to plants (Marschner 1996). In a fertilizer experiment that was conducted on the same sites (Duparquet and Duhamel), hybrid poplar clones showed substantial differences in macronutrient requirements (Elferjani *et al.* 2013). In our current study, differences in leaf macronutrient concentrations were often noticeable between monoclonal and polyclonal plots at the clone level suggesting an effect of clone mixing on nutrient uptake.

Differences between the two types of planting layouts were greater at Duparquet and Villebois than at Duhamel. In these first two sites, soil N was less available and overyielding was more frequently observed relative to Duhamel. These results are consistent with previous work, which has shown that mixing species in poor sites result in increased macronutrient concentrations in aboveground tissues of some species compared to monocultures; in turn, this response suggests a greater complementarity in nutrient uptake compared to richer sites (Rothe and Binkley 2001; Oelmann *et al.* 2010; Richards *et al.* 2010). Clones that were used in our study also showed differences in phenological traits such as bud -break and bud-set dates (unpublished data), which might differentiate growth cycle niches between clones and,

consequently, reduce competition for nutrients (Kelty 2006). We also noted that clone mixtures enhanced growth more strongly for lower yielding clones (747215 and 915004) than they did for higher yielding clones (915319 and 915005). Further, clone mixing favoured growth of less productive clones, suggesting that these were subjected to greater intra-clonal competition in monoclonal plots, when compared to the most productive clones.

Nitrogen leaf concentration strongly affect net photosynthetic rate (P_n) of woody species (Marenco *et al.* 2001). At Duparquet, net photosynthesis and leaf N concentrations were correlated, and both were greater in the polyclonal compared to the monoclonal plots. Nitrogen is a major component of Rubisco and other enzymes that are involved in photosynthetic processes. Many studies have reported a strong relationship between leaf N concentration and net photosynthesis (Evans 1989; Ripullone *et al.* 2003), but we were unable to demonstrate a relationship between these two variables at the Duhamel and Villebois sites. This discrepancy might be explained by greater N soil concentrations at Duhamel compared to Duparquet, but not at Villebois.

For the other macronutrients, plot layout did not affect leaf concentrations at Duhamel, even though yields were different. Greater nutrient uptake in polyclonal plots was probably masked by a dilution effect due to greater growth rates at Duhamel compared to the other sites, which resulted in similar nutrient concentrations in polyclonal *vs.* monoclonal plots. Numerous studies have reported a nutrient dilution effect for fast-growing species when tree growth is more rapid than nutrient accumulation (Lteif *et al.* 2008; Rivest *et al.* 2009).

When light is reduced by shade, leaves of trees acclimate by adjusting their specific leaf area (SLA) to increase light interception (Benomar *et al.* 2012). Our study showed that SLA was unaffected by the layout, which suggested that aboveground competition for light was not important with our 4×3 m spacing, five years after plantation establishment.

Root development was noticeably different between monoclonal and polyclonal plots for coarse and fine roots at Duparquet. Overall, the density of fine roots that were located next to the stem (0- 30 cm class) was greater in the polyclonal plots for clones 915004 and 915319, and similar for the other clones, while the density of roots (coarse and fine) that were located beyond the 60 cm distance was greater in the monoclonal plots. Maximum horizontal rooting

(L_{max}) was also greater in the monoclonal plots (except for clone 915005). Belowground competition could force trees to extend their roots further in monoclonal plots to acquire nutrients because trees of the same clone had similar rooting patterns and, thus, exploited the same soil volumes, making resources less available. As a consequence, trees acclimated by expanding their root systems further from the stem to overcome competition. Previous work has shown that roots can explore a greater soil volume and forage to a greater distance when nutrients, especially N, are limiting (Bhatti *et al.* 1998). Hodge *et al.* (1999) reported that grass species competition induced root proliferation and elongation, and that this elongation depended upon soil nutrient richness and heterogeneity. Kobe *et al.* (2010) found similar results with roots of black oak (*Quercus velutina* Lambert), sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrhart) and black cherry (*Prunus serotina* Ehrhart) growing at high *vs.* low N soil concentrations. Different clones often have different rooting patterns and occupy different soil layers, which could lower competition for nutrients (Kelty 2006). It was similarly shown that when trees were subject to lower competition in mixed stands, fine roots were more concentrated next to the tree boles (Wang 2002). Other factors such as nutrient distribution within a volume of soil can modulate root elongation to increase uptake (Hutchings and John 2004).

Competition for nutrients between plants is often greater in monocultures and can lead to greater allocation of resources to establishing, maintaining and developing the belowground system (Ericsson 1995; Gersani *et al.* 2001). Consequently, root:shoot ratio increases and fewer resources are allocated to aboveground structures. This acclimation to nutrient limitation might explain the lower stem volumes that were recorded in our monoclonal plots. The horizontal distribution of roots in the polyclonal *vs.* monoclonal plots was an indirect indicator of resource allocation to shoots since growth was -moderately- correlated with the horizontal distribution of roots. Growth was positively correlated ($r = 0.52$) with the root fraction near the stem (30-60 cm) and negatively correlated with the root fraction farthest from the stem ($r = 0.47$). This finding indicated that when the trees invested in longer roots (further from the stem), less biomass was allocated to shoots and aboveground volumes decreased. This result agrees with previous studies, which have shown that root elongation was triggered or inhibited by nutrient availability via signal transduction pathways that

measure nutrient concentrations external and internal to the roots (Takei *et al.* 2002; Malamy 2005).

The root system not only supplies nutrients but also acts as a major storage organ during the growing season for starch, which is mobilized as soluble sugars during the dormancy period for maintenance respiration and tree survival (Kobe *et al.* 2010). Non-structural carbohydrates are also essential for bud flush and early growth until foliar production of photosynthates meets tree needs. A lack of starch reserves might decelerate startup growth of trees and reduce plantation yields (Canham *et al.* 1999). Starch and soluble sugar concentrations in roots are subject to seasonal changes and are also affected by environmental factors such as soil nutrient availability (Von Fircks and Sennerby-Forsse 1998). Soluble sugars also tend to accumulate in roots in response to disturbance and might be an indicator of stress in forest ecosystems (McLaughlin *et al.* 1996; Landhäusser and Lieffers 2002; Kasuga *et al.* 2007). Greater amounts of non-structural carbohydrates (TNC) are frequently stored in the roots of hybrid poplars and other pioneer species compared to later serial species (Bollmark *et al.* 1999). We found greater concentrations of starch in coarse roots of trees within the polyclonal plots, which could have indicated lower competition for nutrients between trees of different clones. The negative correlation between root elongation and biomass production supports the hypothesis that genotype mixtures reduced competition for nutrients, resulting in better growth and greater carbohydrate reserves. We argue that greater competition for nutrients between trees in monoclonal plots reduced the availability of N (and other nutrients) and its uptake, which then decreased photosynthesis rate and accumulation of carbohydrate reserves in the roots. Wargo *et al.* (2002) demonstrated that correcting nutrient imbalance of a maple plantation with fertilizer inputs decreased stress-indicating poly-amines and increased root starch concentrations. Application of a water stress to two black poplar (*Populus nigra* L.) clones substantially mobilized stored starch and decreased allocation of carbohydrates to roots (Régier *et al.* 2010). Therefore, TNC concentrations could be a good indicator of tree vigour or of stressful growing conditions.

In conclusion, mixing clones did not always increase yield and its effect differed among clones and sites. On the whole, the effect of clone mixing was positive, but it occasionally yielded null or negative responses. When growth was greater in the polyclonal plots,

overyielding was more frequent and greater at Duparquet and Villebois compared to Duhamel. This response could be explained by a greater complementarity effect among clones in poor sites where soil nutrients limited growth. Horizontal root distribution was noticeably different between the two types of layouts and also differed among clones, suggesting a belowground niche partitioning among clones. We also noted greater investment in root systems in the monoclonal plots compared to polyclonal plots, which resulted in greater root:shoot ratios in the former compared to the latter. This response suggests that competition for soil nutrients was lower among trees in the polyclonal plots, which might explain their frequently greater aboveground growth. Greater TNC concentrations in roots of polyclonal plots was consistent with the positive effects of mixing on the status of most of the nutrients (e.g., N and P) and supported the hypothesis that mixing clones might decrease competition among trees and enhance carbon assimilation and growth. Net photosynthesis was generally greater in the polyclonal plots at Duhamel and Duparquet, while specific leaf area was unaffected by the type of layout, which suggested limited aboveground competition in the monoclonal plots. Assessing clonal interactions within the polyclonal plots in the future would be interesting since aboveground competition should increase in the next years, together with belowground interactions.

Appendix

Stem volume (10^{-3} m^3 $tree^{-1}$) of the four hybrid poplar clones from 2005 (planting year) to 2009 in the monoclonal (Mono) and polyclonal (Poly) plots at Duhamel (Dhl), Duparquet (Dpq) and Villebois (Vlb). Values for 2005, 2006 and 2007 have been averaged between monoclonal and polyclonal plots since they were not statistically different.

Year		2005			2006			2007			2008			2009		
Clone	Layout	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb	Dhl	Dpq	Vlb
747215	Mono	48.4	80.7	43.7	345.2	1077.2	339.1	1176.1	2706.8	941.2	2272.8 [a]	4007.6 [a]	1676.8 [a]	5531.2 [a]	5375.4 [a]	3717.8 [a]
	Poly										3177.6 [b]	5072.0 [b]	2357.9 [b]	7851.2 [b]	9916.4 [b]	4363.3 [b]
915004	Mono	45.8	82.9	43.5	310.3	1022.8	339.8	1195.3	2760.7	767.1	4286.3 [c]	5096.6 [b]	1487.0 [c]	10721.6 [c]	7672.1 [c]	2644.8 [c]
	Poly										3894.6 [c]	5166.8 [b]	2804.6 [d]	9830.8 [c]	9537.2 [b]	4458.9 [b]
915005	Mono	51.6	73.5	44.7	435.6	963.4	397	1421.2	2655.6	963.6	4094.7 [c]	4703.6 [c]	1518.6 [a]	10060.7 [c]	6646.8 [d]	2834.8 [c]
	Poly										4101.6 [c]	5346.5 [d]	2763.7 [d]	10398.3 [c]	9868.9 [b]	5649.6 [e]
915319	Mono	55.9	90.1	62.1	729.2	878.1	464.7	2661.1	38.17	1303.8	6128.1 [d]	6956.5 [e]	3955.1 [e]	14883.0 [d]	9531.9 [b]	7295.2 [d]
	Poly										7709.9 [d]	7380.7 [f]	2360.1 [b]	17719.3 [e]	12743.2 [e]	4283.3 [b]

N.B. Values followed by same letters, within the same site, are not statistically different at $p<0.05$.

4. CHAPITRE IV

PLASTICITY OF BUD PHENOLOGY AND PHOTOSYNTHETIC CAPACITY IN HYBRID POPLAR PLANTATIONS ALONG A LATITUDINAL GRADIENT AND IN RESPONSE TO SPACING IN NORTH EASTERN CANADA.

Raed Elferjani, Annie DesRochers and Francine Tremblay

4.1 Abstract

Intensively managed plantations are being established in a wide range of environmental conditions and densities for operational and yield-related considerations. In this study, we investigated the plasticity of four hybrid poplar (*Populus spp.*) clones established in 2005 along a latitudinal gradient and at different spacings (3×4, 2×4 and 1×4 m) in northwestern Quebec, Canada. The effect of latitudinal gradient on maximum rates of electron transfer (J_{max}) and carboxylation (Vc_{max}), dark respiration (R_d), spring and fall bud phenology, net photosynthesis (P_n), specific leaf area (SLA), per area nitrogen leaf concentration (N_a) were assessed in order to evaluate if clonal plasticity would result in increased overall productivity. Growing season duration (GD) ranged 132-153 days at the southernmost site and 111-126 days at the northernmost site, which corresponded to a volume growth increment of 184% and 100% between the clones with the shortest and longest GD at the two sites, respectively. GD of the least plastic clone (747215) increased by 21 days from north to south, corresponding to a stem volume increase of 17%, while GD and stem volume of the most plastic clone (915005) increased by 31 days and 59%, respectively. Stem volume was positively correlated to GD and negatively to bud burst and bud set duration. Maximum rates of carboxylation and photosynthesis electron transfer (Vc_{max} and J_{max}) decreased northwards for three of the four clones, suggesting that photosynthesis of trees did not acclimate to lower temperatures from south to north. Specific leaf area (SLA) and tree height increased in response to the reduced spacing, while nitrogen concentration per area (N_a) decreased and net photosynthesis (P_n) changed little. Consequently, photosynthesis nitrogen use efficiency (PNUE) was greater under the narrowest spacing suggesting that leaf and crown morphology were the main adjustments regarding increased competition. Degree of adjustment to spacing of SLA and P_n, as revealed by trait plasticity index (TP_i), were greater for the slowest growing clone, showing a leaf morphology adjustment to competition, while the best performing clones had lower leaf traits plasticity but the greatest height variability, which indicated a crown morphology adjustment.

Key words: Phenotypic plasticity, bud phenology, photosynthetic capacity, latitude, spacing, hybrid poplar, growth.

Résumé

Les plantations à croissance rapide intensivement aménagées sont établies sur un large spectre de conditions environnementales et de densités pour des raisons opérationnelles et de productivité. Dans ce travail, nous avons étudié la plasticité de quatre clones peuplier hybride (*Populus spp.)* sur des plantations établies en 2005 à différents espacements (3×4, 2×4 et 1×4 m) le long d'un gradient latitudinal dans le nord-ouest du Québec, Canada. Des mesures des taux maximum de transfert d'électrons (J_{max}) et de carboxylation (V_{cmax}), la respiration à la noirceur (R_d)), de la photosynthèse nette (P_n), de la concentration en azote par unité de surface (N_a), de l'efficience photosynthétique de l'utilisation de l'azote (PNUE) et un suivi phénologique ont été effectués pour les quatre clones. La durée de la saison de croissance (GD) a varié de 132 à 153 jours sur le site méridional et de 111 à 126 jours sur le site septentrional, ce qui correspond à des accroissements en volume entre les clones avec la plus courte et la plus longue saison de croissance de 184 % et 100 %, respectivement pour le sites méridional et septentrional. La GD a augmenté de 21 à 31 jours du nord au sud, respectivement pour le clone le moins plastique (747215) et le plus plastique (915005), alors que la croissance en volume augmentait de 17 % et 59 %. Le volume du tronc était positivement corrélé à la GD et négativement à la durée de la période d'aoûtement et de débourrement des bourgeons. La Vc_{max} et J_{max} ont diminué du sud vers le nord pour trois des quatre clones ce qui suggère qu'ils n'ont pas manifesté une acclimatation de la photosynthèse à la baisse de la température le long du gradient latitudinal. La surface foliaire spécifique (SLA) et la hauteur des arbres ont augmenté avec la densité de plantation, alors que la concentration d'azote par unité de surface (N_a) a diminué et la photosynthèse nette (P_n) n'a que peu varié. Par conséquent, l'efficience photosynthétique de l'utilisation de l'azote (PNUE) était plus élevée à forte densité de plantation ce qui montre que la morphologie de la feuille et du houppier ont été les principaux ajustements en réponse à l'accroissement de la compétition entre les arbres. Les indices de plasticité (TP_i) de la SLA et de P_n étaient plus élevés pour le clone le moins productif, ce qui suggère un ajustement axé sur la morphologie de la feuille. Le clones le plus productif avait par contre une faible plasticité des attributs foliaires (SLA et P_n) mais une forte variabilité de la croissance en hauteur en réponse à l'espacement suggérant un ajustement plutôt axé sur de la morphologie du houppier.

Mots clés: Plasticité phénotypique, phénologie, capacité photosynthétique, latitude, espacement, peuplier hybride, croissance.

4.2 Introduction

Forests of north eastern Canada represent a major source of wood for the timber industry, especially *Populus spp.* which account for about half of the total timber volume in Canada (Zasada *et al.* 2001). The decrease of harvestable natural forests near wood mills and increasing conservation pressures have prompted managers to develop intensively managed plantations scenarios to maintain or even increase wood allocation (Messier *et al.* 2009). Fast-growing plantations can produce greater volumes of timber on a limited land area through intensive silvicultural management such as heavy site preparation, weeding and fertilization. Plasticity of structural and functional traits of woody species can also be important to increase tree productivity in a silvicultural context (Gornall and Guy 2007, Soolanayakanahally *et al.* 2010). Phenotypic plasticity expresses the capacity of a genotype to exhibit different phenotypes in response to distinct environmental conditions (Bradshaw, 1965). Recent studies on plants acclimation, demonstrated the importance of phenotypic plasticity in overcoming effects of short-term environmental conditions changes and maintaining physiological integrity and productivity (Schlichting 1986, van Kleunen and Fischer 2005, Visser 2008). Studying phenotypic variation is thus important to anticipate the increasing occurrence of extreme climatic events such as drought and flooding with climate change (IPCC, 2007). Species with a large geographical distribution such as *Populus* constitute good models for studying plasticity (Hansen *et al.* 2012).

Changes in environmental conditions also include co-existence with neighbours and the subsequent sharing of resources (Muth and Bazzaz 2003). Stand density in natural or managed forest ecosystems considerably affect interactions and competition for resources between trees that adapt by adjusting morphological and physiological traits to survive or maintain growth rates (Archibald and Bond 2003, Delagrange *et al.* 2006, Zhang *et al.* 2008). Trees can show varying degrees of phenotypic plasticity to abiotic and biotic environmental variables, with marked differences between species or provenances (Chmielewski and Rötzer 2001). The link between phenotypic plasticity to stressful or heterogeneous environments and growth has yet to be established, but some previous works on horticultural and forest trees found that plasticity in some physiological traits such as stem water potential and photosynthetic capacity were correlated with productivity (Sadras *et al.* 2011, Paquette *et al.*

2012). However, phenotypic plasticity can sometimes cause structural and developmental shifts that could affect normal plant development and slow growth (DeWitt *et al.* 1998).

Bud burst and bud set are prominent events in the annual cycle of tree species and are related to growth rate since they determine the length of the growing season (Rathcke and Lacey 1985, Chuine and Beaubien 2001). In temperate and boreal climates, bud burst timing is crucial since spring frost could irreversibly damage tissues, very vulnerable at this stage. On the other hand, early onset of dormancy decreases aboveground growth since growth ceases while nutrients and photosynthates are redirected to storage (Keskitalo *et al.* 2005). Bud phenology was reported to be a plastic attribute for many forest tree species (Vitasse *et al.* 2009, Hall *et al.* 2007; Fabbrini *et al.* 2012).

The shorter growing season at northern latitudes might be compensated by more efficient photosynthetic activity. Plasticity of photosynthesis was reported for many species in response to variation in temperature, photoperiod and leaf nitrogen (Benowicz *et al.* 2000, Reich and Oleksyn 2004). Recent works on forest tree species showed that populations from northern latitudes exhibited greater photosynthetic efficiency than populations from lower latitudes (Gornall and Guy 2007, Soolanayakanahally *et al.* 2009), while leaf nitrogen was inversely proportional to mean annual temperature (Reich and Oleksyn 2004); This suggest compensatory photosynthetic response to cooler temperatures and shorter growing seasons. Numerous studies have also shown that slower growth rates of trees at higher latitudes were not due to lower photosynthetic efficiency but to the shorter length of the growing season (Benowicz *et al.* 2000, Ellis *et al.* 2000). Under boreal conditions, maximum growth rates of conifers were also related to longer days rather than warmer temperatures (Rossi *et al.* 2006). The plasticity of specific leaf area (SLA) and crown geometry play a major role in maintaining light interception, as well as allocation of nitrogen to the photosynthetic apparatus to reduce the effects of nitrogen limitations in response to increasing competition (Evans 1989). These adjustments overall aim at enhancing uptake and use of resources, particularly light and nitrogen, and maintain photosynthesis rate (Ellsworth *et al.* 2004).

In this study, bud phenology of four hybrid poplar clones was monitored at the beginning and at the end of the growing season along a latitudinal gradient in the boreal region of eastern Canada. This region (Abitibi-Témiscamingue) is widespread and has lots of

abandoned farmlands available for the establishment of fast growing plantations. With a climatic gradient encompassing five plant hardiness zones (Agriculture and Agri-Food Canada 2013), highly productive but plastic cultivars are more desirable than specific cultivars that do very well only under specific conditions (Marron *et al.* 2006); Plasticity may enhance economical profitability in heterogeneous environments and cultivation conditions (Marron *et al.* 2006). Photosynthesis and leaf specific area were measured to assess how phenology and physiology influenced observed growth rates along a large latitudinal gradient. The effect of spacing between trees was also monitored to evaluate tree plasticity to increasing competition. We tested the following hypotheses: (i) bud phenology and timing of bud set and bud burst would vary along the latitudinal gradient, (ii) photosynthetic activity would increase northwards to compensate for the shorter growing season, (iii) trees will acclimate to high-density planting by adjusting their resources uptake and light and nitrogen use efficiency, and (iv) higher plasticity will reduce fluctuations in productivity at the different sites or competition levels (spacing).

4.3 Materials and methods

4.3.1 Study sites and plant material

The three study sites were located in the Abitibi-Témiscamingue region in north-western Québec, Canada. The northernmost site was located next to Villebois, in the James Bay municipality (49°09' N, 79°10' W), and was an organic farm of cereals and hay. This site was in the spruce-moss domain and the soil was a clay-grey luvisol (50% clay), with mean annual precipitations and temperature of 890 mm and 1.2 °C, respectively. The second site was in the Lake Duparquet Research and Teaching Forest (FERLD; 48°29'N, 97°9'W, Alt. 295 m) and in the balsam fir-paper birch bioclimatic western sub-domain (Grondin, 1996). It had been previously forested until harvested in 2004. Mean annual precipitations and temperature were 918 mm and 1.2 °C respectively, and the soil of this site was classified as a heavy clay brunisol (70% clay; Agriculture and Agri-food Canada 2013). The southernmost site was an abandoned farmland next to the town of Duhamel (47°32' N, 79°59' W, Alt. 209 m). The site is located in the sugar maple-yellow birch western bioclimatic sub-domain (Grondin 1996), and had been cultivated for hay in previous years (a perennial mixture of lucernes and timothy grass). Soil type was a clayey luvisol (45% clay; Agriculture and Agri-

food Canada). Mean annual precipitations and temperature were respectively 820 mm and 2.8 °C (Environment Canada 2013). Extensive site preparation and maintenance were performed both prior to planting and following plantation establishment. Duhamel and Villebois sites were ploughed using an agricultural cultivator in autumn 2004. Prior to plantation establishment at Duparquet, stumps and remaining logs were removed with a bulldozer. The site was then ploughed to a depth of 30 cm in autumn of 2004 with a forestry plough pulled by a skidder and disked in spring 2005 to level the soil before planting. Trees were planted at the three sites in June 2005 at 1×4 m, 2×4 m and 3×4 m spacings. Following planting, weeds were mechanically removed twice a year by cultivating between rows with a farm tractor and discs and by tilling between trees with a Weed Badger™ (4020-SST, Marion, ND, USA).

The clones used in this study had been recommended for the region by the ministère des Ressources Naturelles du Québec (MRNQ): Clone 747215, *Populus trichocarpa* Torrey & A. Gray × *P. balsamifera* L.; Clones 915004 and 915005, *P. balsamifera* × *P. maximowiczii* Henry; and clone 915319 *P. maximowiczii* × *P. balsamifera*. At planting, average height of the trees was 85.9 cm (714215), 89.4 cm (915004), 93.5 cm (915005), and 115 cm (915319), respectively. Stock type was one year-old dormant bareroot hybrid poplars, grown at Trecesson provincial nursery (MRNQ) and stored in a refrigerator at 2 °C prior to planting. The experimental design consisted of three blocks (replicates), randomly distributed in each of the three sites. A block contained four plots of each clone (sub-plots) and each plot contained three randomly laid out sub-plots of each spacing.

4.3.2 Phenology

Bud burst was assessed in April-May 2009 and divided into six phenophases based on a visual observation of terminal bud development as followed: Stage 0: all buds are completely closed; Stage 1: bud is split and tiny leaves are appearing and are barely coming out of bud scales; Stage 2: fusiform and wrapped leaves double bud length; Stage 3: leaves are still wrapped and fusiform but become bifurcated; Stage 4: leaves are half unfolded but remain in bunch; Stage 5: leaves unfurl and are completely separated. Bud set was assessed in September-November 2009 and divided into five phenophases based on the visual observation of bud and foliage presence: Stage 5: the foliage is completely present and the bud is active (green); Stage 4: 33% of foliage has fallen; Stage 3: 66 % of foliage has fallen;

Stage 2: 100% of foliage has fallen and buds are barely active (green); Stage 1: all buds are closed and brown in color (dormant). The growing season length was defined as the number of days between the last stage of bud burst (BBLS) date (stage 5) and the stage 4 of bud set, marking the beginning of growth cessation. All the trees on the middle row of each Site×Block×Clone×Spacing combination were visually inspected (N=540) and phenology stage (S_x) was assigned for each block when 60% of trees reached S_x.

4.3.3 Meteorological data

Meteorological data of the three sites were obtained from nearby station of the National Climate Data and Information database (Environment Canada, 2013). Frost free days of bud burst month (April, FFA), mean annual temperature (MAT), degree days (5 ºC base, Cannell and Smith 1983) of the bud burst month (April, DDA), degree days of the growth months (May-October, GDD) and annual rainfall (AR) were used to calculate their correlation with photosynthesis traits: dark respiration (R_d) and maximum rates of carboxylation and electron transfer (Vc_{max}, J_{max}), bud burst last stage (BBLS), bud burst duration (BBD), growing season duration (GD) and leaf nutrient concentration (%) of N, P, K, Ca and Mg (Table 4.1).

Table 4.1 Climatic normals (1971-2000)[1] of the three sites.

	Duhamel	Duparquet	Villebois
FFA (frost free days in bud burst month, April)	7.9	6.8	5.1
FFO (frost free days of the bud set month, October)	16.6	14	10.1
MAT (mean annual temperature, C)	2.8	1.2	0.7
SPG (sunshine period of growth months, hours)	1209.4	1128.3	N/A
GDD (growth degree days, 5C)	1600.6	1400.2	1340
DDA (Degree days of the bud burst month)	36.8	25.3	31.5
AR (annual rainfall, mm)	624	671	583
Total day length of growth months (hours)	2211	2225	2235

[1] Source: Environment Canada 2013

4.3.4 Growth

Height (H) and basal diameter (BD) were measured at planting and at the end of each growing season between 2005 and 2009. Stem volume (V) was estimated from:

$$V = A_b.H / 3$$

where V: stem volume (cm3), A_b: basal area (cm) and H: height (cm) (Brown and van den Driessche 2002).

To better described growth rates in relation to the growing season duration (in days), mean daily increment (MDI) for tree volume of each clone was calculated using the following formula:

$$MDI= V_{2009}-V_{2008}/\triangle t$$

where V2009 and V2008 are, respectively, tree volume per hectare (cm^3 $tree^{-1}$) at the end of 2009 and 2008 growing seasons; $\triangle t$ is the 2009 growing season duration in days as defined on the basis of phenological observations. MDI was expressed in cm3 $tree^{-1}$ day^{-1}.

4.3.5 Leaf nitrogen concentration and specific leaf area (SLA)

Leaf samples were collected in mid-July 2009 for per mass nitrogen concentration (N_m) analyses and specific leaf area (SLA) measurements at the three sites. A total of nine recently matured leaves were collected on three randomly selected trees of each clone as followed; three leaves from the upper, middle and lower third of the crown. Leaf samples were immediately packed in dry ice and their surface area was measured with a leaf area meter (LI-3100C; LI-COR Biosciences, Lincoln, NE, USA) before oven-drying at 70 °C (for 72 h) and weighing. Specific leaf area (SLA) was calculated as the ratio of leaf area (cm^2) to dry mass (g). Leaves were ground using a 60 µm sieve of a Wiley mill grinder (Thomas Scientific, Swedesboro, NJ, USA) and pooled together to determine nutrients concentrations. Nitrogen concentration per mass (N_m) was obtained after dry combustion using a LECO N-analyzer (Leco Corp., MI, USA) (Leco Corp. 1986) and nitrogen concentration per area (N_a) was calculated as the ratio between N_m and SLA.

4.3.6 Photosynthesis

To better understand the effect of latitudinal gradient on CO_2 assimilation components between the four clones and the possible difference in physiological acclimation, net photosynthesis (P_n), maximum rate of photosynthesis electron transport (J_{max}), dark respiration (R_d) and maximum rate of carboxylation limited by Rubisco (Vc_{max}) of the four clones were estimated using CO_2 assimilation rate *vs* internal leaf CO_2 concentration (A-C_i) curves at the three sites. *A-Ci* curves were built for three randomly selected trees of each clone growing under the 1×4 m spacing at the three sites. Net photosynthesis (P_n), a productivity-related trait, was measured for each spacing × clone × site combination, in mid-July 2009 to evaluate the effect of competition on yields. Measurements were made on recently matured leaves that did not show any apparent sign of senescence, between 9 am and 12 am. Clones and spacings were randomized to minimize the effect of time on photosynthesis variables. Photosynthesis was measured with a CIRAS-2 portable photosynthesis system using an infra-red analyzer (PP systems, MA, USA) and a broadleaf cuvette of 25 mm in diameter equipped with a LED unit for automatic control of light (PLC6-U, PP Systems). Leaf chamber temperature, vapour pressure deficit and photosynthetically active radiation were set to 25 °C, 10 mbar and 1500 µmol m^{-2}, respectively. During measurements, air temperature ranged 18-25°C and humidity 50-70%. To obtain *A-Ci* curves, CO_2 partial pressure was set to 360 µmol mol^{-1} and kept at a steady state during 10 minutes before measurement was recorded, and then changed in the following sequence: 360, 250, 100, 60, 40, 360, 500, 600, 700, 800, 1000, 1200 and 1400 µmol mol^{-1} during measurement. J_{max} R_d and V_{cmax} were obtained using *Photosyn Assistant* software based on models proposed by Farquhar *et al.* (1980) and modified by von Caemmerer and Farquhar (1981), Sharkey (1985), Harley and Sharkey (1991) and Harley *et al.* (1992). Net photosynthesis was obtained with the same parameters except for CO_2 partial pressure which was set to 360 µmol mol^{-1} and not changed. Photosynthetic nitrogen use efficiency (PNUE) was calculated as the ratio of P_n by N_a.

4.3.7 Plasticity

Phenotypic plasticity of traits related to leaf phenology and photosynthesis was measured using the trait plasticity index (TP_i) elaborated by Valladeras *et al.* (2000) to

quantify the variability and possible acclimation of traits across environments. TP_i formula included the mean of the trait value and the difference of the trait values between each couple of sites or spacings:

$$\mathbf{TPi} = \frac{\sum_{i}^{n} |\mathbf{xi} - \mathbf{xj}|}{\bar{x}}$$

Where x_i and x_j are the trait value of a clone in sites i and j (sites = i, j,.....,n) or spacings i and j, and x is the trait mean of a clone in "i,j,.....,n" environments or "i,j,.....,n" spacings. Plasticity for latitudinal gradient and spacing were evaluated separately. TP_i for latitudinal gradient were calculated for the four clones planted at 1×4 m, while TPi for spacing was the mean TP_i of the three sites.

Growth stability of clone "i" along the latitudinal gradient and different spacings was measured with the coefficient of variability (CV_i) of Francis and Kannenberg (1978) in order to evaluate the effect of changing environments and less favourable conditions on productivity variation of each of the four clones, using the formula:

$$CV_i = \sqrt{S_i^2} / m_i \cdot 100$$

Where S_i^2 and m_i are, respectively, the stem volume, height and basal diameter variance and mean of clone "i" across sites or spacings. The lower the value of CV, the greater is the clone stability among environments. S_i^2 is calculated using the following formula.

$$S_i^2 = \sum_{j=1}^{q} (X_{ij} - m_i)^2 / (q-1)$$

Where X_{ij} is the mean stem volume, height and basal diameter of 2009 ($m^3\,ha^{-1}$) of clone i, at the j^{th} site or spacing and q is the number of sites or spacing.

4.3.8 Statistical analysis

R software was used for statistical analyses (Version 2.11.1, R. Foundation for Statistical Computing, Vienna, Austria). To evaluate clone plasticity along the latitudinal gradient,

ANOVA within linear mixed model package (nlme) was used to test the effects of site and clone (fixed) and their interaction on response variables with blocks as replicates (random). The same procedure was used to evaluate plasticity in response to density by testing the effect of clone and spacing on the dependant variables. Tree height, basal diameter and volume were subjected to a repeated measures analysis of variance with year as the repeated measure. Spacings were nested within clones and the significance level for all tests was set to $\alpha = 0.05$. Bud phenology was assessed during the 2009 growing season to compare sites, clones and spacings. Pearson's coefficient of correlation (r) was used to describe relationships between photosynthesis and phenology traits, and climatic normals. Least square means were compared using Tukey's honest significant differences (HSD) function.

4.4 Results

4.4.1 Clonal growth patterns

Stem volume (V, m^3 $tree^{-1}$) was the greatest at the southernmost site ranging between 3.44 and 21.6 10^{-3} m^3 $tree^{-1}$ from north to south after five growing seasons (Tables 4.2 and 4.3). Average V was 13.32 10^{-3} m^3 $tree^{-1}$ in 2009 for the most productive clone (915319) and 6.42 10^{-3} m^3 $tree^{-1}$ for the least productive clone (747215). Average V decreased respectively by 32% and 31% for these two clones from the southernmost to the northernmost sites (Table 4.3). Growth of the other two clones was similar and V ranged between 6.34 to 12 10^{-3} m^3 $tree^{-1}$ decreasing by 41% on average from south to north. Mean daily increment (MDI) followed the same pattern than V for all clones and decreased northwards (Table 4.3). The best performing clone (915319) had the greatest MDI at the southernmost site (66.9 cm^3 $tree^{-1}$ day^{-1}) and it decreased by 53% northwards. The least performing clone (747215) had a MDI of 35.5 cm^3 $tree^{-1}$ day^{-1} on average at the southernmost site and it decreased by 35% at the northern site (Villebois). After five growing seasons, mean height at the 1× 4 m spacing was 4.1 m for clone 747215 and 6.4 m for clone 915319 compared to 4.5 m and 5.1 at the 3 × 4 m spacing (Table 4.3). When the distance between trees within rows increased from 1 to 3 m, H decreased by 2.3 to 21% while BD increased by 0.8 to 29%, and V by 7 to 76%, depending on clones (Table 4.3).

Table 4.2 Analysis of variance of stem growth traits of hybrid poplar clones. Degree of freedom (d.f) and *P* value are reported

		P-value			
Source of variation		**V**	**H**	**BD**	**MDI**
	d.f.				
Site	2	**	**	**	**
Clone	3	**	**	**	**
Spacing	2	**	*	**	**
Year	5	**	**	**	
Site × Clone	6	ns	Ns	ns	Ns
Site × Spacing	4	**	**	**	**
Clone × Spacing	6	**	**	**	**
Site × Clone × Spacing	12	**	Ns	**	**
Site × Year	10	**	**	**	
Clone ×Year	15	**	**	**	
Spacing × Year	10	**	**	*	
Site × Clone ×Year	30	ns	**	ns	
Site × Spacing × Year	20	**	**	**	
Clone × Spacing ×Year	30	**	**	ns	
Site × Clone × Spacing ×Year	60	ns	Ns	ns	

V: stem volume (10^{-3} m^3 $tree^{-1}$), H: height (cm), BD: basal diameter (mm), MDI: mean daily increment (cm^3 $tree^{-1}$ day^{-1}).

** $P<0.01$; * $0.05<P<0.01$; ns: non significant ($P> 0.05$).

Table 4.3 Means of growth traits and physiological parameters of hybrid poplar clones at the three sites and three spacings measured in 2009. Values of the same variable within the same clone labeled with different letters are statistically different at $P < 0.05$.

Clone	Site	Spacing	V	H	BD	MDI	SLA	N_m	N_a	P_n	PNUE
747215	Dhl	1m	5.87 ^{d}	4.66 ^{b}	68 ^{cd}	25.7 ^{d}	77.9 ^{d}	23.6 ^{bc}	3 ^{b}	21.4 ^{a}	7.1 ^{c}
		2m	6.71 ^{c}	4.4 ^{b}	75.3 ^{b}	28.6 ^{c}	72.1 ^{e}	22.6 ^{cd}	3.1 ^{b}	19.9 ^{b}	6.3 ^{d}
		3m	11.26 ^{a}	4.96 ^{a}	85.6 ^{a}	52.3 ^{a}	69.8 ^{f}	24.1 ^{ab}	3.5 ^{a}	19.4 ^{b}	5.6 ^{e}
	Dpq	1m	3.77 ^{f}	3.84 ^{c}	61 ^{e}	15.1 ^{g}	89.8 ^{b}	21.2 ^{de}	2.4 ^{e}	20.9 ^{ab}	8.9 ^{a}
		2m	5.46 ^{de}	3.93 ^{c}	71.6 ^{c}	18.3 ^{f}	80.7 ^{d}	20.7 ^{e}	2.6 ^{de}	20.5 ^{ab}	8 ^{b}
		3m	8.59 ^{b}	5.16 ^{a}	81.8 ^{ab}	31.6 ^{b}	81.1 ^{d}	22.9 ^{c}	2.8 ^{bc}	20.2 ^{ab}	7.2 ^{c}
	Vlb	1m	5.00 ^{e}	3.84 ^{c}	62.7 ^{e}	23.8 ^{de}	95.2 ^{a}	20.6 ^{e}	2.2 ^{f}	17.8 ^{c}	8.2 ^{b}
		2m	5.30 ^{e}	3.96 ^{c}	69.2 ^{cd}	22.9 ^{de}	85 ^{c}	21.4 ^{de}	2.5 ^{de}	19.6 ^{b}	7.8 ^{b}
		3m	5.85 ^{d}	3.30 ^{d}	66.5 ^{d}	22.1 ^{d}	92.7 ^{ab}	25.3 ^{a}	2.7 ^{cd}	17.9 ^{c}	6.6 ^{d}
915004	Dhl	1m	10.36 ^{b}	6.61 ^{a}	76.3 ^{cd}	44.6 ^{b}	89.6 ^{a}	25.2 ^{b}	2.8 ^{c}	18.7 ^{b}	6.6 ^{d}
		2m	12.58 ^{a}	6.26 ^{a}	84.6 ^{b}	54.5 ^{a}	86.7 ^{ab}	25.4 ^{b}	2.9 ^{c}	21.3 ^{a}	7.3 ^{bc}
		3m	13.05 ^{a}	5.05 ^{cd}	92.5 ^{a}	56.7 ^{a}	86.7 ^{ab}	31.9 ^{a}	3.7 ^{a}	21 ^{a}	5.7 ^{ef}
	Dpq	1m	6.99 ^{e}	5.49 ^{b}	72.6 ^{d}	26.9 ^{d}	83.4 ^{c}	21 ^{d}	2.5 ^{de}	17.7 ^{bc}	7 ^{cd}
		2m	8.05 ^{d}	4.78 ^{e}	79.1 ^{c}	26.2 ^{d}	76.9 ^{d}	18.2 ^{e}	2.4 ^{e}	16.3 ^{c}	6.9 ^{cd}
		3m	8.77 ^{c}	5.10 ^{c}	82.6 ^{b}	32.3 ^{c}	76.9 ^{d}	25.2 ^{b}	3.3 ^{b}	17.5 ^{bc}	5.3 ^{f}
	Vlb	1m	5.76 ^{f}	4.70 ^{e}	66.9 ^{e}	21.2 ^{e}	87.5 ^{ab}	15.7 ^{f}	1.8 ^{f}	16.7 ^{c}	9.3 ^{a}
		2m	8.12 ^{d}	5.05 ^{cd}	75.8 ^{d}	31.5 ^{c}	86.1 ^{b}	18.7 ^{e}	2.2 ^{e}	16.8 ^{c}	7.7 ^{b}
		3m	5.15 ^{g}	3.28 ^{f}	66.9 ^{e}	21.2 ^{e}	88.8 ^{ab}	23.6 ^{c}	2.7 ^{cd}	15.7 ^{d}	5.9 ^{e}
915005	Dhl	1m	9.72 ^{c}	5.86 ^{a}	77.4 ^{d}	36.6 ^{c}	83.2 ^{c}	20.1 ^{c}	2.4 ^{bc}	16.1 ^{d}	6.8 ^{e}
		2m	10.65 ^{b}	5.54 ^{b}	83.4 ^{c}	43 ^{b}	77.1 ^{d}	25.7 ^{a}	3.3 ^{a}	16.2 ^{d}	4.9 ^{g}
		3m	15.57 ^{a}	5.36 ^{b}	97.1 ^{a}	62.3 ^{a}	90.8 ^{ab}	15.9 ^{d}	1.8 ^{d}	16.5 ^{cd}	9.4 ^{b}
	Dpq	1m	3.44 ^{f}	3.86 ^{e}	56.9 ^{g}	11.5 ^{g}	94.3 ^{a}	16 ^{d}	1.7 ^{d}	20.1 ^{a}	11.9 ^{a}
		2m	7.16 ^{d}	4.60 ^{d}	75.8 ^{de}	20.2 ^{f}	89.5 ^{b}	26.8 ^{a}	3 ^{a}	17.6 ^{bc}	5.9 ^{f}
		3m	10.05 ^{bc}	5.05 ^{c}	84.2 ^{c}	23.3 ^{e}	83.2 ^{c}	20.5 ^{c}	2.5 ^{b}	18 ^{b}	7.3 ^{d}
	Vlb	1m	6.12 ^{e}	4.40 ^{d}	64 ^{f}	23.3 ^{e}	88.7 ^{b}	23.5 ^{b}	2.6 ^{b}	16.2 ^{d}	6.2 ^{ef}
		2m	10.35 ^{b}	5.3 ^{b}	85.3 ^{b}	42.5 ^{b}	92.3 ^{ab}	19.6 ^{c}	2.1 ^{c}	17.3 ^{bc}	8.1 ^{c}
		3m	6.89 ^{d}	3.36 ^{e}	73.6 ^{e}	27.3 ^{d}	77.8 ^{d}	25.6 ^{a}	3.3 ^{a}	15.7 ^{bc}	4.8 ^{h}

Table 4.3 Continued

915319	Dhl	1m	16.68 ^{b}	7.37 ^{b}	88.8 ^{b}	59.7 ^{b}	112.3 ^{a}	18.8 ^{d}	1.7 ^{d}	16.6 ^{d}	9.9 ^{a}
		2m	21.60 ^{a}	7.54 ^{a}	102.4 ^{a}	82.5 ^{a}	86.6 ^{d}	20.5 ^{bc}	2.4 ^{ab}	17.1 ^{bc}	7.2 ^{ef}
		3m	15.04 ^{c}	5.81 ^{c}	97.6 ^{a}	58.6 ^{b}	89.8 ^{c}	20.7 ^{bc}	2.3 ^{bc}	17.8 ^{bc}	7.7 ^{cd}
	Dpq	1m	11.66 ^{e}	5.98 ^{c}	85.3 ^{b}	29.9 ^{e}	88.8 ^{c}	19.2 ^{cd}	2.2 ^{bc}	15.1 ^{e}	7 ^{f}
		2m	6.62 ^{g}	5.47 ^{d}	67.2 ^{d}	21.3 ^{f}	92 ^{bc}	19.7 ^{cd}	2.1 ^{c}	14.7 ^{f}	6.9 ^{f}
		3m	11.52 ^{e}	5.41 ^{d}	88.9 ^{b}	29.7 ^{e}	95.2 ^{b}	21.6 ^{ab}	2.3 ^{bc}	16.7 ^{cd}	7.4 ^{de}
	Vlb	1m	10.01 ^{f}	5.98 ^{c}	74.8 ^{c}	36.4 ^{d}	91.5 ^{bc}	18.8 ^{d}	2.1 ^{c}	17.2 ^{bc}	8.4 ^{b}
		2m	12.14 ^{d}	5.81 ^{c}	85.4 ^{b}	44.1 ^{c}	93.7 ^{bc}	21.4 ^{ab}	2.3 ^{bc}	19.3 ^{a}	8.5 ^{b}
		3m	14.68 ^{c}	4.07 ^{e}	64.3 ^{d}	17.1 ^{g}	86.7 ^{d}	22.6 ^{a}	2.6 ^{a}	18 ^{b}	6.9 ^{f}

V: stem volume (10^{-3} m^3 $tree^{-1}$), H: height (m), BD: basal diameter (mm), MDI: mean daily increment (cm^3 $tree^{-1}$ day^{-1}), SLA : Specific leaf area (cm^2 g^{-1}), N_a: per area nitrogen concentration (g m^{-2}), N_m: per mass nitrogen concentration (mg g^{-1}), Pn: net assimilation rate (µmol s^{-1} m^{-2}), PNUE : photosynthetic nutrient use efficiency (µmol CO_2 g N^{-1} s^{-1}), Dhl: Duhamel, Dpq: Duparquet, Vlb: Villebois.

4.4.2 Growth stability

The stability index (CV_{FK}, Francis and Kannenberg 1978) of tree volume (V) was the most stable across sites for clone 747215 (CV_{FK} = 87.34), while it was the most variable for 915319 (CV_{FK} = 721.01) and intermediate for clones 915004 and 915005 (Table 4.4). Variance of MDI of clones across sites followed the same trends as V, and CV_{FK} ranged between 0.46 (747215) to 2.95 (915319) (Table 4.4). In response to increasing density, two clones (747215 and 915005) showed greater H stability (CV_{FK} =106 and 178 respectively), compared to 915004 and 915319 (CV_{FK} = 681 and 904). The stability of BD was noticeably lower (CV_{FK} = 130), for clone 915005 compared to the others (CV_{FK} ranged between 30 to 70, Table 4.5).

Table 4.4 Plasticity index (TP_i) and stability index (CV_{FK}) of traits measured in hybrid poplar clones in three sites along a latitudinal gradient .Values are means of three replicates for each site and those labeled with different letters within the same variable are statistically different at $P < 0.05$.

	Trait plasticity index (TP_i)												Stability index (CV_{FK})	
	Leaf			Photosynthesis			Phenology					Mean TP_i		
	SLA	N_m	R_d	J_{max}	Vc_{max}	J_{max}/Vc_{max}	BBLS	BSS	BBD	BSD	GD		V	MDI
Clone														
747215	4.9 ^{b}	22.4 ^{b}	77.4 ^{a}	53.4 ^{c}	18.1 ^{d}	52.1 ^{b}	22.3 ^{a}	3.8 ^{c}	98.7 ^{a}	12.2 ^{d}	35.2 ^{c}	36.4 ^{c}	87.3 ^{d}	0.5 ^{d}
915004	6.8 ^{a}	21.2 ^{b}	68.1 ^{b}	74.7 ^{a}	56.4 ^{c}	73.9 ^{a}	22.1 ^{a}	3 ^{d}	80.5 ^{b}	37.5 ^{c}	32.6 ^{d}	43.3 ^{b}	241.9 ^{c}	1.7 ^{c}
915005	1.3 ^{c}	9.4 ^{c}	71.6 ^{b}	69.7 ^{b}	100.9 ^{a}	32.5 ^{c}	22.1 ^{a}	10.7 ^{b}	98.9 ^{a}	101.2 ^{a}	45.5 ^{a}	51.2 ^{a}	549.6 ^{b}	2 ^{b}
915319	1.1 ^{c}	42.4 ^{a}	21.8 ^{c}	59.8 ^{c}	83.4 ^{b}	31.1 ^{c}	13.6 ^{b}	11.9 ^{a}	64 ^{c}	81.1 ^{b}	39.1 ^{b}	40.8 ^{b}	721 ^{a}	2.9 ^{a}

SLA : Specific leaf area ($cm^2\ g^{-1}$), N_m: per mass nitrogen concentration ($mg\ g^{-1}$), J_{max}: maximum rate of photosynthesis electron transport ($\mu mol\ s^{-1}\ m^{-2}$), Vc_{max}: maximum rate of carboxylation limited by Rubisco ($\mu mol\ s^{-1}\ m^{-2}$), R_d: dark respiration ($\mu mol\ s^{-1}\ m^{-2}$), BBLS: bud burst last stage (DOY), BSS: bud set start (DOY), BBD: duration of bud burst (days), BSD: duration of bud set (days), GD: duration of the growing season (days), V: stem volume ($10^{-3}\ m^3\ tree^{-1}$), MDI: mean daily increment ($cm^3\ tree^{-1}\ day^{-1}$).

Table 4.5 Mean trait plasticity index of N_a, P_n, SLA and PNUE, stability of tree height (H) and stem basal diameter (BD) of the hybrid poplar clones with spacing. Values of the same variable labeled with different letters within a column are statistically different at $P < 0.05$.

	Trait plasticity index (TP_i)				CV_{FK} stability index	
	N_a	P_n	SLA	PNUE	H	BD
Clone						
747215	4.2 ^{c}	14 ^{a}	12.9 ^{b}	0.4 ^{b}	105.9 ^{d}	69.9 ^{b}
915004	32.6 ^{b}	2.2 ^{c}	17.9 ^{a}	0.5 ^{a}	681.1 ^{b}	30 ^{d}
915005	42.5 ^{a}	5.1 ^{c}	8.8^{c}	0.5 ^{ab}	178.4 ^{c}	130.3 ^{a}
915319	25.5 ^{b}	7.8 ^{b}	14.1 ^{b}	0.1 ^{c}	904.4 ^{a}	59.3 ^{c}

N_a: per area nitrogen concentration, P_n: net assimilation rate, SLA: Specific leaf area, PNUE: photosynthetic nutrient use efficiency, H: height (m), BD: basal diameter.

4.4.3 Bud phenology

Growing season duration (GD) was 132 to 153 days at the southernmost site (Dhl), 115 to 135 at Dpq and 111 to 126 at the northernmost site (Vlb) (Table 4.6). The difference in GD between Dhl and Vlb ranged from 20 (915004) to 31 days (915005). The difference in growth duration between Dhl and Dpq *vs* Dpq and Vlb was 17 *vs* 4 days (747215), 20 *vs* 0 days (915004), 16 *vs* 15 days (915005) and 18 *vs* 11 days (915319). Spacing between trees had no effect on phenology variables (Table 4.7).

4.4.4 Kinetics of bud burst (BB) and bud set (BS)

At the southernmost site (Dhl), the last stage of BB was synchronous for clones 747215, 915004 and 915005 (134 DOY) while it occurred later for clone 915319 (140 DOY) (Fig. 4.1). At Dpq, the last stage of BB occurred 10 to 12 days later than at Dhl depending on clones (DOY 146 to 150) and again the clone 915319 was the latest to reach the last stage of BB (DOY 150). The last stage of BB was synchronized at the 150th DOY at Vlb and Dpq for all clones (Table 4.6). Time required for BB completion was the shortest for clone 915319 at the three sites, and ranged from 25 to 30 days (Fig. 4.1).

Bud set started after 261 DOY (Dpq and Vlb) and 266 DOY (Dhl) (Table 4.6). Difference in BS between the northernmost and southernmost site ranged from five (747215 and 915004) to 17 days (915319) (Table 4.6). Bud set was completed at Vlb and Dpq first, then at Dhl where the last stage of fall phenophases occurred after 300 to 315 DOY depending on clones (Fig. 4.2). Clone 747215 was the first to complete BS at the three sites (293 at Vlb and 300 DOY at Duh) while 915319 was the latest (15 days later). Bud set duration was significantly different ($P < 0.001$) between clones at the southernmost site and ranged between 22 and 37 days (Tables 4.6 and 4.7).

Table 4.6 Phenological traits of the four hybrid poplar clones across the three sites. Values of the same variable labeled with different letters are statistically different ($P > 0.05$).

Clone	747215			915004			915005			915319		
Site	Dhl (47°N)	Dpq (48°N)	Vlb (49°N)	Dhl (47°N)	Dpq (48°N)	Vlb (49°N)	Dhl (47°N)	Dpq (48°N)	Vlb (49°N)	Dhl (47°N)	Dpq (48°N)	Vlb (49°N)
BBLS (DOY)	134 [a]	146 [b]	150 [c]	134 [a]	150 [c]	150 [c]	134 [a]	150 [c]	150 [c]	140 [d]	150 [c]	150 [c]
BBD (phase 0-5, days)	19 [a]	28 [b]	32 [c]	21 [d]	29 [b]	32 [c]	21 [d]	34 [e]	36 [f]	21 [d]	25 [g]	29 [b]
BSS (DOY)	266 [a]	261 [b]	261 [b]	270 [c]	266 [d]	266 [d]	286 [e]	286 [e]	271 [c]	293 [f]	285 [e]	276 [g]
BSD (phase 4-1, days)	34 [a]	32 [b]	32 [b]	37 [c]	41 [d]	34 [a]	29 [e]	41 [d]	20 [f]	22 [g]	31 [b]	21 [f]
GD (days)	132 [a]	115 [b]	111 [c]	136 [d]	116 [e]	116 [e]	152 [f]	136 [d]	121 [g]	153 [f]	135 [d]	126 [h]

BBLS: bud burst last stage, BBD: duration of bud burst, BSD: duration of bud set, GD: length of the growing season duration. Dhl: Duhamel. Dpq: Duparquet. Vlb: Villebois. DOY: day of the year.

Table 4.7 Analysis of variance of physiological and phenological traits in hybrid poplar clones showing degree of freedom (d.f) and *P* value.

		p-value													
Source of variation	d.f	SLA	P_n	N_m	N_a	PNUE	BBLS	BBD	BSS	BSD	GD	J_{max}	Vc_{max}	R_d	J_{max}/V_{cmax}
Site	2	*	**	**	**	ns	**	**	**	**	**	**	**	**	**
Clone	3	*	**	**	**	*	**	**	**	**	**	**	**	ns	ns
Spacing	2	*	**	**	**	**	ns	ns	ns	ns	ns				
Site × Clone	6	ns	ns	**	**	*	**	**	**	**	**	ns	**	**	**
Site × Spacing	4	ns	**	**	**	**		ns	ns	ns	ns				
Clone × Spacing	6	ns	**	ns	ns	ns		ns	ns	ns	ns				
Site × Clone × Spacing	12	ns	*	ns	ns	ns		ns	ns	ns	ns				

SLA: Specific leaf area ($cm^2\ g^{-1}$), N_a: per area nitrogen concentration, N_m: per mass nitrogen concentration ($mg\ g^{-1}$), P_n: net assimilation rate ($\mu mol\ s^{-1}\ m^{-2}$), PNUE : photosynthetic nutrient use efficiency, $\mu mol\ CO_2\ g\ N^{-1}\ s^{-1}$), BBLS: bud burst last stage, BBD: bud burst duration, BSS: bud set start, BSD: bud set duration, GD: growth season duration, J_{max}: maximum rate of photosynthesis electron transport ($\mu mol\ s^{-1}\ m^{-2}$), Vc_{max}: maximum rate of carboxylation limited by Rubisco ($\mu mol\ s^{-1}\ m^{-2}$), R_d: dark respiration ($\mu mol\ s^{-1}\ m^{-2}$).

** $P<0.01$; * $0.05<P<0.01$; ns: non significant ($P > 0.05$)

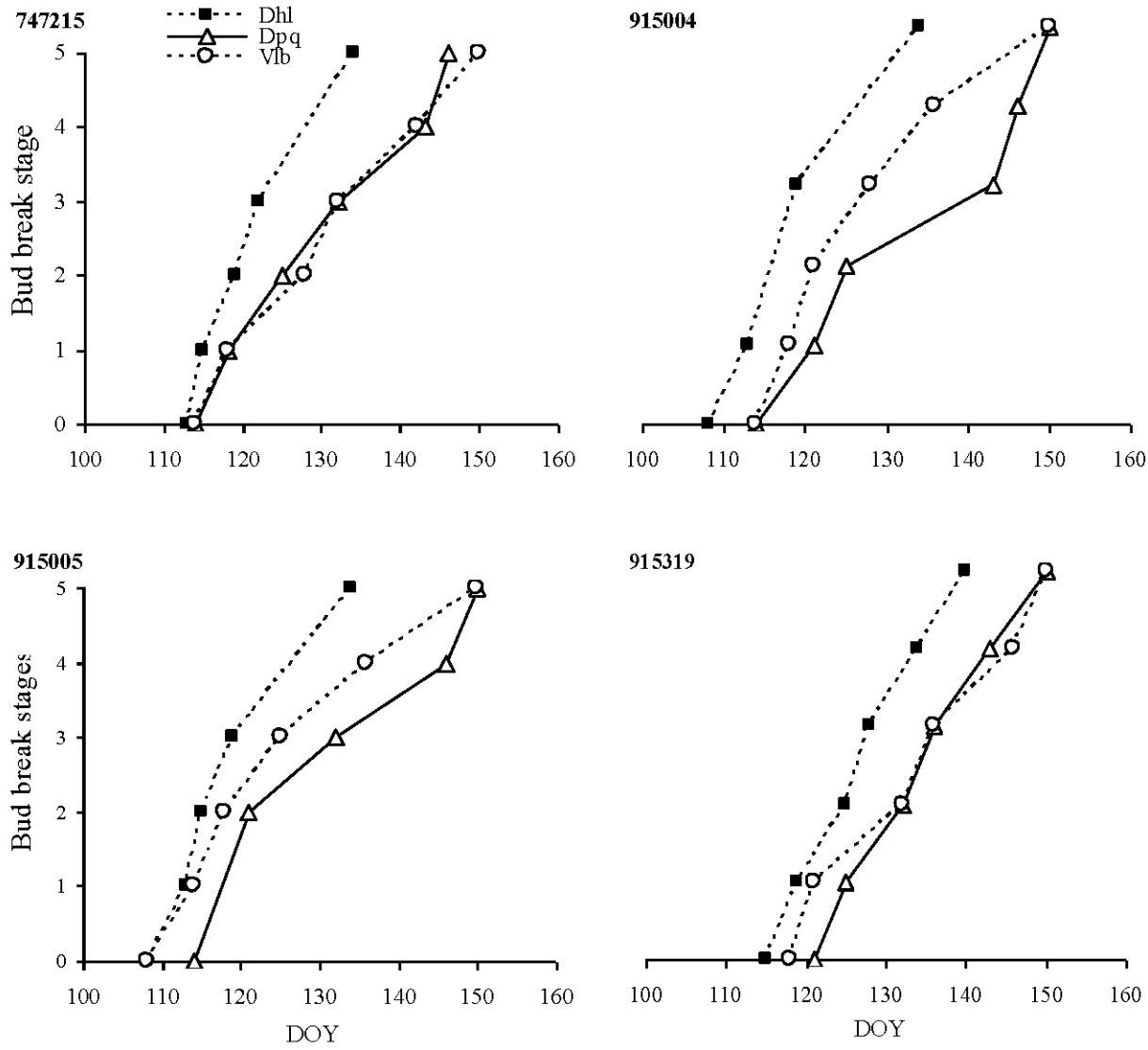

Figure 4.1 Bud burst stages in 2009 for four hybrid poplar clones at the three sites (*) located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity.

(*) Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois. DOY: Day of the year.

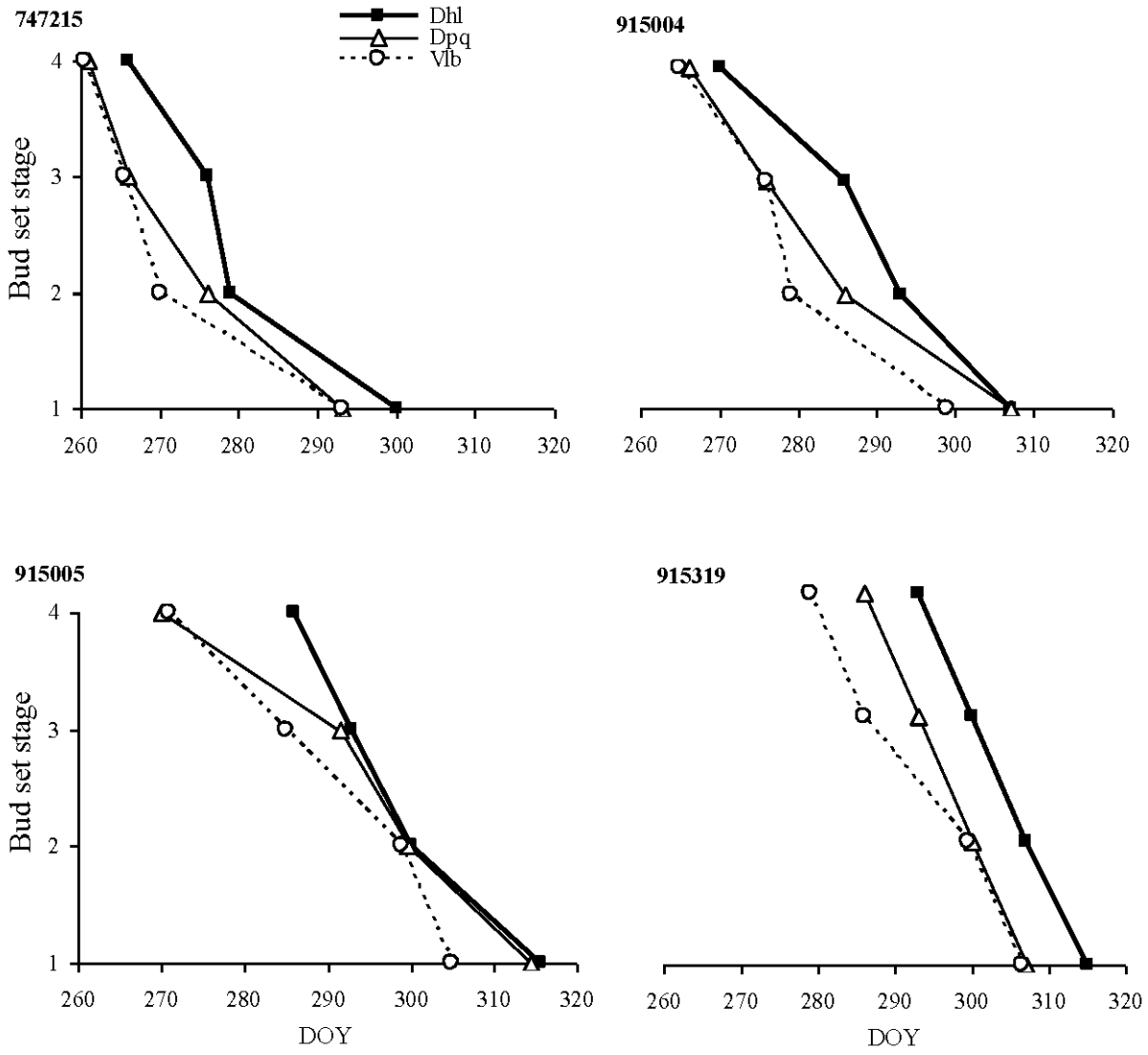

Figure 4.2 Bud set stages in 2009 for four hybrid poplar clones at the three sites (*) located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity.

(*) Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois. DOY: Day of the year.

4.4.5 Physiological response pattern

Net photosynthesis (P_n) decreased from south to north by 17% and 10% for two clones (747215 and 915004) and did not change for clone 915005 being 16.1 μmol s^{-1} m^{-2} on average. P_n of the best performing clone (915319) increased little (4%) from the southernmost (Dhl) to the northernmost site (Table 4.3).

Maximum photosynthetic rate of electron transport (J_{max}) was the highest in the southernmost site (Dhl) where it ranged between 165 to 209 μmol s^{-1} m^{-2}. Then J_{max} decreased to 127 μmol s^{-1} m^{-2} at Dpq (clone 915004) and did not significantly change between Dpq and Vlb except for clone 747215, where it was greater (Fig. 4.3A).

Maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Vc_{max}) was the highest for all clones at the southern site (Dhl) where it ranged between 88 and 113 μmol s^{-1} m^{-2}. Mean Vc_{max} decreased northwards (Vlb) by 8% to 40% except for clone 747215 (Fig. 4.3B). Dark respiration (R_d) was the lowest at Dhl for clones 747215 and 915004 (4 and 5.2 μmol s^{-1} m^{-2} respectively) and increased northwards except for the clone 915005 (Fig. 4.3C). Mean R_d of clone 915319 did not change across the three sites and was 4.8 μmol s^{-1} m^{-2} (Fig. 4.3C).

The ratio J_{max}/Vc_{max} was similar between the four clones at the southernmost site (mean = 1.75). It decreased significantly at Dpq and then increased at Vlb for clones 747215 and 915005 (Fig. 4.3D). Meanwhile J_{max}/Vc_{max} did not vary between Dhl and Dpq (1.74 on average) for the other clones and it increased northwards (Fig. 4.3D).

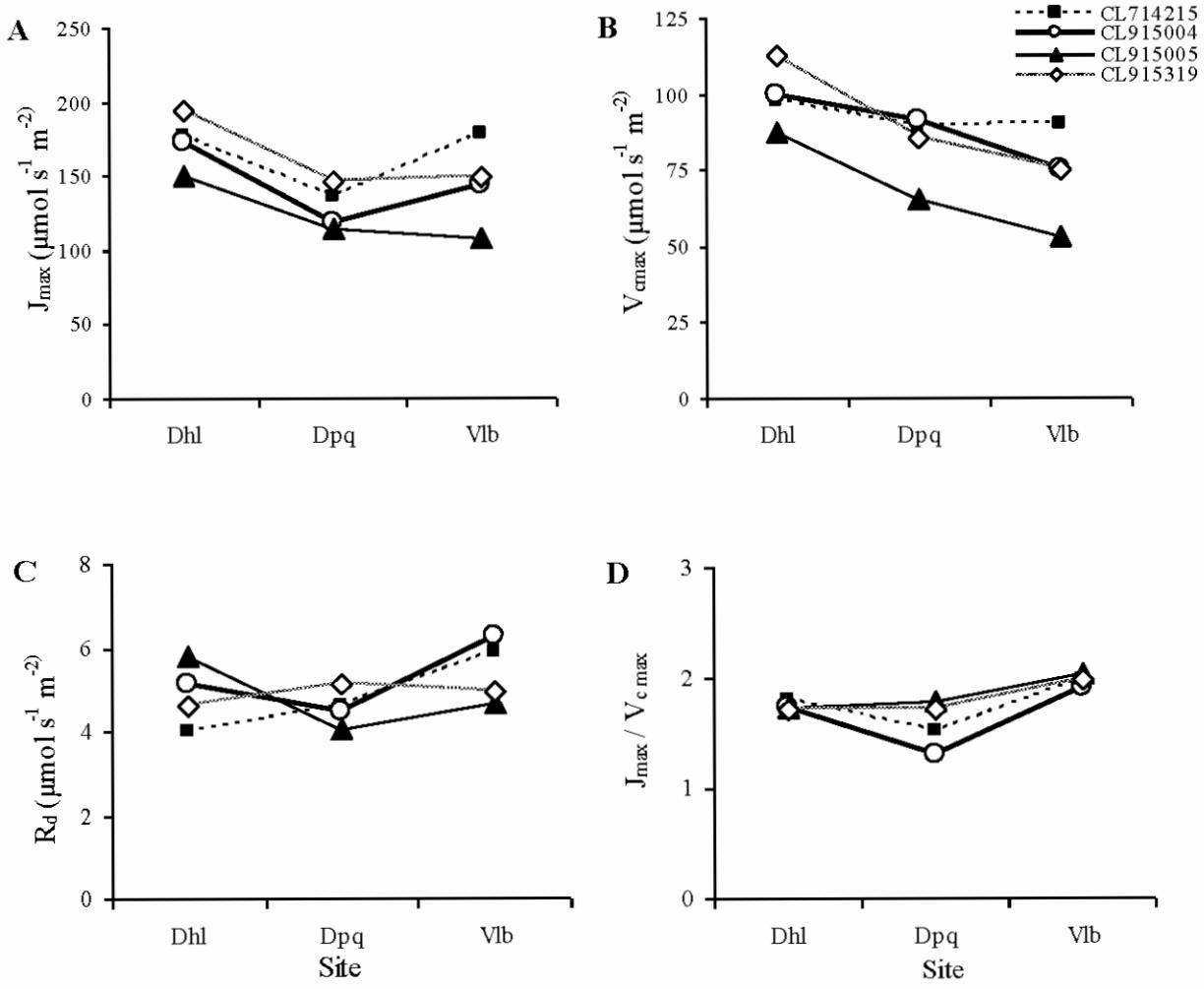

Figure 4.3 Photosynthetic activity measurements in 2009: maximum photosynthetic rate of electron transport (J_{max}), maximum carboxylation rate of ribulose-1.5-bisphosphate carboxylase/oxygenase (Vc_{max}), dark respiration (R_d) and J_{max}/V_{cmax} for four hybrid poplar clones at three sites (*) located along a latitudinal gradient in the boreal region of eastern Canada. Error bars were removed for clarity.

Sites. Dhl: Duhamel; Dpq: Duparquet; Vlb: Villebois.

4.4.6 Plot density and leaf traits

Net photosynthesis (P_n) of clones 915319 and 747215 was significantly greater at 1 × 4 m (5% and 7.3 % respectively), compared to 3 × 4 m, while no difference between spacings

was observed for the two other clones (Table 4.3). Mean N_m generally increased with spacing and ranged between 19.4 to 21.9 mg g^{-1} at 1 × 4 m, and 22.6 to 24.3 mg g^{-1} at 3 × 4 m, depending on sites (Table 4.3). The SLA was usually greater (7% to 9%), and N_a lower (15% to 35%) under the 1 × 4 m spacing compared to 3 × 4 m, depending on clones (Table 4.3). Mean PNUE was often inversely proportional to spacing and ranged between 6.53 to 8.75 µmol CO_2 g N^{-1} s^{-1} at the 1 × 4 m spacing and 5.84 to 7.39 µmol CO_2 g N^{-1} s^{-1} at the 3 × 4 m spacing (Table 4.3).

4.4.7 Relationships between variables

Stem volume (V) was positively correlated with temperature (FFA, MAT, DDA and GDD) but not with mean annual rainfall (Table 4.8). It was also positively correlated with GD, N_m, J_{max} and Vc_{max} ($r = 0.34$, $p = 0.04$, data not shown) but negatively correlated with the DBB (Table 4.8). Leaf nitrogen concentration (N_m) was also negatively correlated with the DBB (Table 4.8). On the other hand, BS was not correlated with any of the variable mentioned above (data not shown). Leaf nitrogen concentration (N_m) was correlated with J_{max} and Vc_{max} (Table 4.8). Maximum rate of electron transfer (J_{max}) was positively correlated to DDA and negatively correlated to precipitations (AR, Table 4.8).

Table 4.8 Pearsons' correlation coefficients (r) and corresponding *p*-values between meteorological and photosynthesis variables, bud phenology traits and leaf nitrogen concentration of the four hybrid poplar clones across the three sites. Significant correlations ($P<0.05$) are in bold.

		Photosynthesis			Bud phenology			N_m
	V (2009)	R_d	V_{cmax}	J_{max}	V_{cmax}/J_{max}	BBLS	BBD	GD	
FFA (days)	**r=0.59**	r=-0.30	**r=0.60**	r=0.03	**r= 0.62**	**r= -0.80**	**r= -0.85**	**r=0.72**	r= 0.27
	***P*=0.04**	*P*=0.32	***P*=0.04**	*P*=0.91	***P*=0.03**	***P*=<0.01**	***P*<0.01**	***P*<0.01**	*P*= 0.39
MAT (°C)	**r=0.70**	r=-0.13	**r=0.62**	r=0.11	r= 0.40	**r = -0.87**	**r= -0.85**	**r=0.72**	r= 0.30
	***P*=0.01**	*P*=0.68	***P*=0.03**	*P*=0.30	*P*=0.20	***P*<0.01**	***P*<0.01**	***P*<0.01**	*P*= 0.35
DDA (°C)	**r=0.65**	r=0.35	r=0.49	**r=-0.68**	r= -0.18	**r= -0.78**	**r= -0.6**	r=0.52	**r= 0.54**
	***P*=0.02**	*P*=0.26	*P*=0.10	***P*=0.01**	*P*=0.56	***P*<0.01**	***P*=0.04**	*P*=0.08	***P*= 0.05**
GDD (°C)	**r=0.61**	r=-0.24	**r=0.68**	r=0.31	r= 0.40	**r= -0.87**	**r= -0.85**	**r=0.72**	r= 0.40
	***P*=0.03**	*P*=0.44	***P*=0.01**	*P*=0.32	*P*=0.18	***P*<0.01**	***P*<0.01**	***P*<0.01**	*P*= 0.19
AR (mm)	r=-0.06	r=-0.53	r=-0.10	**r= -0.57**	**r= 0.71**	r=-0.13	r=-0.26	r=0.22	r= -0.2
	P=0.85	*P*=0.07	*P*=0.76	***P*=0.05**	***P*=0.01**	*P*=0.68	*P*=0.4	*P*=0.48	*P*= 0.51

V: stem volume (10^{-3} m^3 $tree^{-1}$), N_m: per mass nitrogen concentration (mg g^{-1}), BBLS: bud burst last stage, BBD: bud burst duration, GD: growth season duration, J_{max}: maximum rate of photosynthesis electron transport, Vc_{max}: maximum rate of carboxylation limited by Rubisco, R_d: dark respiration, (mm), FFA: frost free days in bud burst month (April, days), MAT: mean annual temperature (°C), DDA: degree days of the bud burst month (°C), GDD: growing season degree days (°C), AR: annual rainfall

4.4.8 Plasticity

Leaf N_m plasticity along the latitudinal gradient (plasticity index TP_i) was greater than the plasticity of SLA (Table 4.4). The variance of the SLA was particularly high for clones 747215 and 915004 (TP_i = 4.9 and 6.8 respectively), compared to clones 915005 and 915319 (TP_i = 1.2, on average). Leaf nitrogen concentration (N_m) variation along the latitudinal gradient was different between clones as TP_i ranged between 9 to 42 (Table 4.4). Plasticity of the photosynthesis variables (J_{max}, Vc_{max} and R_d) was greater than plasticity of the other leaf traits (SLA and N_m) with TP_i values often higher than 50 (Table 4.4). Clones had similar TP_i for R_d and J_{max} (72 and 64 on average, respectively) except for clone 915319 which had

smaller values (TP_i = 22). The plasticity index for Vc_{max} was more variable between clones than J_{max} and R_d (TP_i for Vc_{max} ranged between 18 to 101; Table 4.4).

Bud burst last stage (BBLS) and BSS (Bud set starting) were less influenced by the latitude compared to their duration as TP_i for BBLS and BSS ranged between 14 to 22 and 3 to 12 respectively, while TP_i of bud BBD and BSD ranged between 64 to 99 and 12 to 101, respectively (Table 4.4). Plasticity of BB variables was more similar between clones than plasticity of BS variables. Bud set stages and BSD plasticity for clones 747215 and 915004 were much lower (TP_i = 12.2 and 37.5) than those of the other two clones (TP_i = 81 and 101). Plasticity of GD along the latitudinal gradient differed slightly between clones as TP_i ranged between 33 to 45 (Table 4.4).

The plasticity index for SLA and N_a was greater than the plasticity of P_n and PNUE in response to spacing (Table 4.5). The plasticity of 915005 (TP_i = 8.8) in response to spacing was low, compared to the other clones as their TP_i ranged between 12.85 to 14.07. The plasticity index of P_n was greater for clone 747215 (TP_i = 14) than the other clones as their TP_i ranged between 2.2 to 7.8 while TP_i of PNUE for clone 915319 was noticeably lower (0.13) than for the other clones (0.44 to 0.57).

4.5 Discussion

As expected, tree growth was greater at the southernmost site and decreased towards the north. Stem volume was positively correlated with the number of frost free days in April (FFA) and the mean annual temperature (MAT, Table 4.8). The number of FFA was determinant for the growing season length since bud burst is triggered by warm temperatures while MAT influences growth rate (Sakai and Larcher 1987, Hanninen 1990). Huang *et al.* (2010) reported that growing season temperature had a significant effect on growth of *Populus tremuloides* Michx. and *Betula papyrifera* Marshall, along a latitudinal gradient in the boreal region of Canada. In the boreal zone, bud burst and leaf unfolding start earlier at lower latitudes where temperatures are warmer in early spring, marking the beginning of photosynthetic activity and biomass accumulation (Saxe *et al.* 2001 and references therein). In contrast, day length and thus the photoperiod is longer further north (from March 21 to September 21), which may partially compensate for the shorter growing season (Edmond *et*

al. 1979). In this study the difference in day length between the southernmost and the northernmost site was approximately 24 hours over a growing season (2235 *vs* 2211 hours, respectively). This may not have been long enough to compensate for the colder climate.

In addition to the latitudinal gradient, other environmental factors such as soil characteristics, topography, etc., could affect tree development. In our study, edaphic conditions (elevation soil characteristics) were similar between sites (Chapter 3, Table 3.1) and temperature was the main difference between sites (Table 4.1). Site temperature did affect the timing of bud burst and also its duration. The period required between the start of bud burst and complete unfolding of leaves (phases 0 to 5) was 19, 28 and 32 days from the south to the north for the slowest growing clone (747215) which represents a difference of 13 days. This difference was only eight days for clone 915319. It might reflect clonal difference in plasticity in response to changing temperature at the beginning of the growing season. The speed of bud flushing can be an analogue of an increase in photosynthetic activity in the spring, measuring how fast trees can respond to the changes in temperature (Gu *et al.* 2003). Our results showed that clones with high speed of bud burst also had greater growth (e.g. clone 915319), showing a high level of plasticity to temperature variations which is consistent with previous works on poplar bud phenology (Kramer 2006, Rohde *et al.* 2011). The timing of bud set was less different between sites compared to bud burst, probably because fall phenophases are mainly triggered by photoperiod (<10h) and secondarily affected by temperature (Vegis 1964, Howe *et al.* 1996, Rohde *et al.* 2011). Soolanayakanahally *et al.* (2009) reported that difference in bud set timing of balsam poplar (*Populus balsamifera* L.), grown at two sites with close latitudes but different mean temperatures (9.7 and 2 ℃) was 28 days, while the difference in bud burst date was 44 days. In the present work, bud set duration was shorter northwards but bud set speed was greater for the most productive clones (Table 4.6). Heide (2003) demonstrated that bud burst and bud set are not completely independent processes as he found that warmer temperature during fall phenophases in boreal regions delayed the bud burst dates the following year for *Betula pendula* Roth, *B. pubescens* Ehrh. and *Alnus glutinosa* (L.) Moench. At the same time, when fall temperatures remain relatively warm, respiration rate of roots, in particular, continue to be relatively high in a "pseudo" dormant tree. This "asynchronism" between photoperiod and

temperature at the end of the growing season might counterbalance tree reserves, increase root:shoot ratios and consequently affect the start of growth the following season.

Warmer temperatures at the southern site might affect the magnitude of photosynthetic activity and tree growth. Generally, the photosynthetic rate of cold adapted species increases with increasing temperature to reach an optimum around half of its thermal range (i.e. 15ºC; Larcher 2003). When photosynthesis is not limited by light availability, the optimal temperature corresponds to the maximum thermodynamic activity of the enzymes (Sage and Kubien 2007). In our study, P_n and Vc_{max} often decreased significantly northwards (Table 4.3 and Fig 4.3), which is consistent with the pattern of photosynthetic response to temperature between 0 to 15ºC, described above. Ambient temperature might affect photosynthesis and tree growth of deciduous trees through soil temperature, which controls root system activity. Under boreal climates, where temperatures remain under 0 ºC in early spring, water and nutrient uptake and photosynthesis are inhibited (Bergh and Linder 1999). Root growth and development are also greatly reduced when soil temperature is above and close to 0 ºC (Wan *et al.* 1999). Soil temperatures follow the same trend as air temperatures, and become warmer earlier at southern sites. Consequently, root development and resources uptake should start earlier in the south and result in greater biomass accumulation.

The shifts in photosynthetic capacity of higher plants in response to lower temperatures help maintain carbon assimilation homeostasis (Schlichting 1986, Sultan 2000). Numerous studies have shown that photosynthetic rates of northern populations are greater than those of southern populations in the temperate and boreal regions (Benowicz *et al.* 2000, Gornall and Guy 2007, Soolanayakanahally *et al.* 2009). Other studies also demonstrated a decrease in the optimal temperature of photosynthesis when trees are moved from warmer to colder environments (Jonas and Geber 1999). In our study, the plasticities of J_{max} and V_{cmax} were greater than plasticity of the other leaf traits (SLA and N_m) and were also significantly different between clones across the three sites (Table 4.4). Mean J_{max} and Vc_{max} decreased northwards for all clones, except 747215, for which these parameters changed little across the latitudinal gradient. This suggests the presence of photosynthetic acclimation to lower temperatures (Jonas and Geber 1999, Way and Yamori 2013), but at the price of a slower growth rate. Indeed, the increasing R_d of clone 747215 (and 915004) northwards shows a

greater plasticity but implies greater carbon losses by respiration for biosynthesis and maintenance processes at the expense of growth (Atkin and Tjoelker 2003, Yamori *et al.* 2009). This finding is consistent with the lower productivity of these clones northwards, compared to the best performing clones (915319 and 915005) for which R_d was steady or decreased. Remote sensing analysis showed that the duration of the growing season in the northern hemisphere has increased on average by 5 days per °C of temperature rise between 1981 and 1991 (Zhang *et al.* 2004). If we consider the effect of global warming, clone 747215, in contrast with the other clones, was too conservative and may not benefit from rising temperatures at northern latitudes.

Specific leaf area plasticity along the latitudinal gradient (measured at 1×4 m spacing) might also contribute in increasing photosynthetic assimilation rate as greater SLA increases light interception area and reduces leaf thickness (Gun *et al.* 1999, Niinemets 2001, 2004). Our results showed that mean SLA increased by 24% and 6% northwards for two of our clones (747215 and 915005), suggesting an acclimation to lower temperatures. This result is consistent with the findings of Groom and Lamont (1997) and Prior *et al.* (2005), who showed that leaf mass per area (inverse of SLA) was lower and leaves were thicker when temperatures were higher or precipitations lower. Lower SLA reflects a greater investment in leaf structure (e.g. cell wall) and then leaf thickness for longer lifespan but also represents a limit for CO_2 diffusion from stomata to chloroplasts (Wright *et al.* 2002). This acclimation did not lead to similar yields between the northern and southern sites in our study, most probably because the growing season length overcame SLA changes.

The effect of increasing density on basal diameter growth of trees was often negative as a consequence of increasing competition for resources, particularly at the belowground level of single genotype stands (Takeneka 2000, Medhurst *et al.* 2001, Dillen *et al.* 2010, Benomar *et al.* 2013). Height on the contrary, increased as spacing between trees was lowered showing an acclimation to competition for light as trees of the same clone have similar crown geometry. Mean SLA increased significantly when spacing between trees was reduced from 3×4 to 1×4 m which is consistent with the effect of narrow spacing on tree height (Benomar *et al.* 2012). Increased SLA was accompanied by leaf allocation of nitrogen to light capture and electron transfer apparatus via Rubisco particularly, rather than investment in structural

proteins (Evans 1989). This allocation results in reducing the effect of N limitation on photosynthesis (Ellsworth *et al.* 2004, Takashima *et al.* 2004). In our study, despite the lower N leaf concentration at 1×4 m spacing (around 20 mg g^{-1}) net photosynthesis (P_n) did not decrease. This reflected a more efficient mobilization of N to photosynthesis (PNUE), which increased with density (Table 4.3). It was previously shown that PNUE is sensitive to external factors and strongly correlated to specific leaf area (Lambers and Poorter 1992, Garnier *et al.* 1995, Poorter and Evans 1998, Grassi and Bagnaresi 2000). Thus, N limitations in poplars, because of their high N requirements and low N availability in soils of boreal regions, might be substantially reduced by selecting clones with greater PNUE (Stanturf *et al.* 2001). Even though root development response to increasing density of trees was not examined in our study, we think that trees also acclimated to crowding by increasing root biomass and modifying their distribution. Intraclonal competition of four hybrid poplar clones increased root:shoot ratio and roots extension far from the stem, compared to the four clones' mixture (see Chapter 3). Root plasticity is however not limitless and could not completely compensate a high competition, hence the lower productivity under narrow spacings (Coomes and Grubb 2000). Benomar *et al.* (2013) found that root density of hybrid poplar clones was greater at high (10000 tree ha^{-1}), compared to lower densities (1111 and 400 tree ha^{-1}). Morphological, more than physiological adjustments were reported as a response to aboveground competition (light), while plasticity to belowground competition (nutrients) was morphological and physiological (Schwinning and Weiner 1998, Ballaré 1999, Grams and Andersen 2007).

Previous studies on tree acclimation to unfavourable environments showed that modulation of developmental traits can be at the expense of biomass production (Nolet *et al.* 2008). In our study, the least productive clone had the lowest mean plasticity index (of all the traits) to latitudinal gradient (although greater TP_i for some leaf traits, Table 4.4), while the other clones (more productive) had greater mean TP_is. Taulavuori *et al.* (2010) found no growth reduction for southern provenances of *Pinus sylvestris* L. transplanted to northern latitudes in Finland. Our results showed that greater growth was often linked to greater clonal plasticity along the latitudinal gradient, particularly for phenological traits and SLA, suggesting a positive effect of plasticity on growth. However, we could not find a

relationship between plasticity of photosynthetic capacity and growth performance of the clones across the three sites.

In response to reduced spacing, no relationship was found between the mean TP_i (of all the traits) and the growth performance of clones. The fastest growing clone (915319) had greater N_a and SLA plasticities, but low Pn and PNUE plasticities, while the slowest growing clone (747215) had the greatest P_n and PNUE plasticities. This may reflect different genotype-specific strategies to overcome increasing competition as some clones had more noticeable morphological *vs* physiological adjustments (SLA and height) and *vice-versa* for other clones. The type of adjustment might originate from the clone's sensitivity and tolerance to different resources limitations. For example some clones might be more tolerant to nutrient limitation but intolerant to shading while other clones might be intolerant to nutrient and light limitations altogether.

In conclusion, the plasticity of bud phenology was noticeable and correlated to stem volume along the latitudinal gradient. Best performing clones had a longer growing season, due to a faster development of bud burst (but not earlier) and a later bud set. Most clones did not show photosynthetic acclimation to colder temperatures along the latitudinal gradient as their Vc_{max} and J_{max} were low in the northern site and increased southwards. Consequently, establishing these clones at northern sites could be advantageous in the future since their photosynthetic capacity should increase in response to global rising temperatures. Clone 747215, however, had a steady photosynthesis capacity and a more stable growth across sites which suggest a greater adaptative photosynthesis for this clone, but at the cost of growth rate. In response to increasing stand density, SLA and tree height increased showing aboveground acclimation to competition. These adjustments, most likely, contributed in the greater photosynthetic nitrogen use efficiency under the tighter spacing.

5. CONCLUSION GÉNÉRALE

Les plantations forestières d'essences améliorées à haut potentiel productif sont d'ores et déjà une composante des plans d'aménagement forestiers au Québec. En effet, la nouvelle loi sur l'aménagement durable du territoire forestier, entrée en vigueur en 2013, exige la création de zones dites « aires d'intensification de la production ligneuse » (AIPL) qui occuperaient 2 % du territoire forestier à moyen terme et 15 % à long terme (ministère des Ressources Naturelles du Québec 2013). Le peuplier hybride, une espèce à croissance rapide, est particulièrement intéressant pour la production ligneuse intensive à courte rotation. L'établissement des AIPL a été recommandé sur des sites productifs en région boréale pour atteindre les rendements escomptés. Cela est d'autant plus important pour le peuplier hybride dont les exigences nutritionnelles sont relativement élevées. Dans ce contexte, il est important de mieux connaître et d'une façon précise les caractéristiques nutritionnelles des clones de peuplier à planter et leur tolérance à la compétition. Par ailleurs, on en connaît peu sur leur réponse à la variation des conditions du milieu le long de gradients climatiques, un paramètre particulièrement important sur le territoire forestier du Québec.

5.1 Synthèse des résultats

Notre travail a permis d'acquérir des connaissances nouvelles sur la nutrition du peuplier hybride en région boréale et sur la réponse des clones à différentes traitements de fertilisation. Nous avons démontré que la fertilisation basée sur la méthode de diagnostique foliaire (DRIS) était généralement efficace dans la détection et la correction de la carence azotée. Elle a permis d'accroitre la croissance de 7% en moyenne, comparativement aux arbres non fertilisés. Néanmoins, la dose conventionnelle de fertilisants (40N-20P-20K) a parfois été plus efficace que la méthode DRIS mais contenait une quantité de fertilisants beaucoup plus importante. Dans la perspective d'une exploitation commerciale à grande échelle dans le futur, une fertilisation non basée sur les besoins réels en nutriments ne serait pas une pratique viable car elle contient souvent trop de fertilisants sans prendre en considération les ratios de nutriments et les interactions entre eux (Fageria 2001). La détermination précise des besoins nutritionnels et des ratios de minéraux dans les fertilisants à l'aide des analyses foliaires permet un apport équilibré et évite la fertilisation excessive et

par conséquent, réduit le coût de production et augmente la profitabilité des plantations. Par ailleurs, nous avons constaté que si la fertilisation azotée permettait de corriger les carences en azote, les indices de phosphore demeuraient déséquilibrés après la fertilisation, quel que soit le traitement. Ceci était vraisemblablement lié à des interactions avec d'autres minéraux, car l'ion phosphate, de charge négative dans la solution du sol, se lie facilement aux cations présents comme le calcium (Ca^{2+}) et l'aluminium (Al^{3+}) et se trouve ainsi immobilisé et peu disponible (DesRochers *et al.* 2007). Dans les deux sites étudiés, la concentration du sol en calcium relativement élevée (7,2 mg g^{-1} en moyenne) a probablement immobilisé une quantité du phosphore et réduit son prélèvement par les arbres (Tisdale *et al.* 1985, Lteif *et al.* 2008). En effet, les sols argileux des deux sites (luvisol et brunisol) sont connus pour être riches en calcium (McKeague et Stonehouse 2008). Ainsi, l'analyse des nutriments du sol permet de détecter les concentrations en certains nutriments tels que le calcium et il serait utile dans ce cas de majorer la quantité de fertilisants phosphatés pour contrer l'effet de leur immobilisation.

Ce travail a également permis de mettre en évidence les différences en besoins nutritionnels entre les clones, alors que le diagnostic pré-fertilisation avait montré que les clones avaient des statuts nutritifs similaires. Le prélèvement de nutriments par les arbres est généralement proportionnel au taux de croissance (Reich *et al.* 1999, Comas *et al.* 2002, Li *et al.* 2012) et les clones les plus productifs puisent souvent plus de nutriments et ont par conséquent des teneurs foliaires plus élevées (mais parfois des concentrations faibles à cause de l'effet de dilution). La différence de la réponse à la fertilisation azotée entre les clones pourrait être liée à des différences dans l'efficience de l'utilisation de l'azote entre les clones, un mécanisme fréquemment observé chez le genre *Populus spp* (Blackmon *et al.* 1979, Stanturf *et al.* 2001). Ainsi, la sélection de clones à haute efficience d'utilisation d'azote (NUE) permettrait de minimiser l'effet des carences en azote sur la croissance et de réduire les apports en fertilisants le long du cycle de rotation. Cette caractéristique pourrait être utile pour valoriser des sites peu productifs sans trop compromettre la productivité en sélectionnant des clones à NUE supérieure. L'historique des deux sites étudiés semble par ailleurs avoir affecté la réponse des clones à la fertilisation; Sur le site agricole initialement exploité pour des cultures fourragères, la fertilisation a permis d'avoir un réservoir équilibré

en nutriments, notamment en N, P et K. En effet, les besoins nutritifs des peupliers ne sont possiblement pas très différents de ceux des cultures conventionnelles telles que les céréales surtout en termes d'exigences élevées en azote et en phosphore (Stanturf *et al.* 2001). Les indices nutritionnels obtenus avec DRIS ont montré que les carences des arbres établis sur ce site agricole étaient inférieures à celles du site forestier. Les arbres semblaient avoir trouvé dans le sol du site agricole des teneurs en nutriments proches de leurs besoins et leur réponse à la fertilisation en termes de concentration foliaire et de croissance a été à peine détectable, comparativement au site forestier. Sur ce dernier, le sol était plus pauvre en nutriments, notamment en azote, et l'effet positif de la fertilisation sur la croissance des clones a été plus marqué. La corrélation entre l'indice de la balance des nutriments (NBI), un paramètre qui intègre les indices DRIS des différents nutriments, et la croissance en volume a été plus forte que les corrélations entre la croissance et chacun des indices DRIS. Il représente par conséquent un indicateur plus fiable de l'effet de la fertilisation sur la productivité des peupliers, conformément avec l'effet largement documenté des interactions entre les nutriments sur la croissance des végétaux (Fageria 2001, Nachtigall and Dechen 2007).

En définitive, le taux de croissance des jeunes plantations de peupliers a été améliorée par les différents traitements de fertilisation (7,5% en moyenne), mais ceux basés sur le diagnostique foliaire DRIS ont été globalement plus efficaces comparativement à la fertilisation conventionnelle, communément utilisée en sylviculture (40N-20P-20K). La compétition croissante, notamment pour les espacements étroits, aurait tendance à accroitre les carences particulièrement en fin de la rotation. En sylviculture intensive, plusieurs apports de fertilisants tout au long de la rotation sont recommandés afin de subvenir aux besoins croissants des arbres et atteindre de hauts rendements (Stanturf *et al.* 2001). Dans le contexte de notre étude, il serait alors recommandé d'appliquer un second apport de fertilisants afin de réduire l'effet de la compétition pour les nutriments qui s'ajoute aux faibles concentrations en nutriments du sol, notamment en N et P, en région boréale (Weih 2004, Cooke et al. 2005). Des amendements organiques à moindre coût issus de matières résiduelles municipales ou industrielles (compost ou boues de papetières, notamment) pourraient également être utilisés (Larchevêque *et al.* 2011). Au Québec, la politique en matière de gestion des déchets organiques prévoit le recyclage d'une part importante de matières résiduelles d'ici 2012, qui

pourrait être utilisée pour la fertilisation des plantations de peuplier hybride. La forte compétition dans les plantations d'espèces à croissance rapide est attribuable, entre autres, à la monoculture où les arbres de même génotype exploitent les mêmes ressources, simultanément. Ils se trouvent ainsi contraints à allouer plus de biomasse aux racines pour capter les nutriments, aux dépens de la croissance du houppier. Ainsi et en partant du principe du partage des niches écologiques dans les écosystèmes (Menalled *et al.* 1998, Loreau *et al.* 2001), les plantations composées de plusieurs clones ont été proposées comme un outil pour un partage optimal des ressources.

Les plantations mixtes se composent généralement d'espèces différentes plus ou moins apparentées. En foresterie à courte rotation, le mélange de plusieurs clones s'avère utile étant donné que la différence du taux de croissance et du produit récolté n'est pas considérable, comparativement à un mélange feuillues/conifères, par exemple (Benomar *et al.* 2012). Aussi, des parcelles composées de clones différents seraient moins vulnérables à la propagation de ravageurs en cas d'infestation (Miot *et al.* 1999, Jactel and Brockerhoff 2007). L'effet du mélange clonal sur la productivité des plantations a été peu étudié, comparativement à l'intérêt phytosanitaire des plantations mélangées. Nos résultats ont montré que cinq années après l'établissement des plantations, le volume moyen du tronc dans les parcelles polyclonales était 21% supérieur à celui des parcelles monoclonales et le gain en rendement a été plus élevé sur les sites les moins productifs. Ainsi, les combinaisons de clones qui montrent un effet positif de la mixture sur la croissance pourraient accroitre le rendement global sur des sites peu productifs; Il est probable que, comme pour la fertilisation, la réponse des arbres à la mixture soit plus manifeste sur des sites pauvres. Des études ont montré que les conditions limitantes du milieu favorisent les interactions positives telles que la facilitation et la complémentarité (Cardinale *et al.* 2000, Eisenhauer 2012). L'effet positif du mélange clonal sur la croissance que nous avons observé semble être dû à une complémentarité entre les clones via un partage des ressources au niveau racinaire. Les clones de peuplier hybride ont montré des exigences nutritionnelles différentes dans une étude sur l'effet de la fertilisation réalisée dans la région de l'Abitibi-Témiscamingue (Elferjani *et al.* 2013). En effet, l'allocation de biomasse aux racines était moindre dans le mélange polyclonal et le système racinaire se développait à proximité des arbres, ce qui

suggère que la compétition intraclonale pour la capture des nutriments entre les arbres a été réduite. De nombreux travaux ont montré que des racines se trouvant dans un milieu pauvre en nutriments (N surtout), explorent un volume plus important de sol et s'étendent davantage en longueur et en profondeur, comparativement à des arbres établis sur des sites riches (Bhatti *et al.* 1998, Hodge *et al.* 1999, Wu *et al.* 2004).

L'effet significatif du mélange clonal sur la distribution racinaire des clones de peuplier est probablement lié à la complexité et la diversité particulière de l'architecture racinaire du genre *Populus* (Dickmann *et al.* 2001). Aussi, la phénologie du bourgeon terminal a montré des différences significatives entre les quatre clones en termes de date de débourrement et d'aoûtement ce qui aurait différencié le cycle de croissance des clones et réduit la compétition sur les nutriments, notamment au début et à la fin de la saison de croissance (Kelty 2006). La concentration en glucides totaux non-structuraux (TNC) des racines dans les parcelles polyclonales était également généralement supérieure à celle dans les parcelles monoclonales. Ceci pourrait montrer que le mélange des différents clones aurait réduit la compétition pour les nutriments. Wargo *et al.* (2002) ont montré que la correction des carences nutritives d'une plantation d'érable par une fertilisation a permis de réduire la concentration des polyamines (indicateurs de stress) et d'accroitre la concentration racinaire en amidon. La grande majorité de l'amidon est stockée dans les racines au cours de la saison de croissance et est par la suite transformée en sucres solubles au cours de la période de dormance pour assurer la survie de l'arbre (Kobe *et al.* 2010). La teneur en TNC dans les racines est soumise à des variations saisonnières et est également affectée par des facteurs tels que la disponibilité en nutriments dans le sol (Von Fircks et Sennerby-Forsse 1998). Le maintien d'une concentration optimale en TNC est ainsi crucial pour une meilleure protection des arbres aux effets du gel hivernal, surtout pour les plantations commerciales établies en régions boréales. Les TNC sont aussi essentiels au démarrage de la croissance au printemps avant que la photosynthèse ne puisse répondre aux besoins des arbres. Par conséquent, des réserves en amidon faibles pourraient ralentir le démarrage de la croissance des arbres et diminuer le rendement des plantations (Canham *et al.* 1999). Ces résultats pourraient suggérer d'intégrer la concentration racinaire en TNC parmi les attributs d'intérêt dans les programmes d'amélioration des clones de peuplier hybride et dans le choix de clones à

déployer dans les stations les plus nordiques afin d'assurer leur survie et accroitre leur productivité.

Le suivi de la phénologie du débourrement et de l'aoûtement du bourgeon terminal a permis de mieux comprendre la différence de productivité entre les clones le long d'un gradient latitudinal allant du Témiscamingue en passant par l'Abitibi et jusqu'au Nord-du-Québec. Dans l'ensemble, les variables relatives à la température ont été les paramètres distinguant les sites les uns des autres, avec une saison de croissance plus longue dans le site méridional et diminuant le long du gradient latitudinal.

L'écart de la date du début du débourrement entre les extrémités du gradient latitudinal variait de 10 à 16 jours selon les clones. Ceci suggère que, dans la perspective du réchauffement climatique global, le début de la saison de croissance de certains clones serait peu affecté par l'augmentation de la température. En contrepartie, ceci pourrait être un avantage vis-à-vis du risque de gels printaniers tardifs qui peuvent endommager les jeunes pousses vulnérables et compromettre la croissance par la suite. La durée du débourrement, de l'émergence du bourgeon terminal jusqu'au déploiement total des feuilles a augmenté du sud vers le nord et ce pour tous les clones. Ceci démontre que la latitude affecte non seulement la chronologie du débourrement du bourgeon terminal, mais aussi la durée des différentes phases. La durée des phases de débourrement aux extrémités du gradient variait de 8 à 13 jours selon les clones. On peut déduire que certains clones ont une orientation plus « conservatrice » vis-à-vis des températures printanières plus froides sur le site septentrional, en étalant le débourrement sur une plus longue période ce qui pourrait réduire les risques de dégâts causés par les gels printaniers tardifs. A l'opposé, d'autres clones plus productifs (ex. 915319) ont minimisé la durée du démarrage de la croissance. La date de l'aoûtement du bourgeon terminal a suivi les mêmes tendances que le débourrement et au site méridional, le clone le moins productif a été le premier à entrer en dormance (261 jour julien) alors que le clone le plus productif a été le dernier avec 293 jour julien. Ainsi, il semble que la productivité des clones soit liée à une saison de croissance maximale avec un débourrement rapide et une entrée en dormance tardive. Soolanayakanahally *et al.* (2009) ont montré que des températures plus douces au début du printemps plutôt qu'a la fin de l'automne allongent la saison de croissance du peuplier baumier (*Populus balsamifera* L.).

On a également observé une plasticité des composantes de la capacité photosynthétique (Vc_{max} et J_{max}) et, avec une moindre importance, de la surface foliaire spécifique (SLA) le long du gradient latitudinal. Des travaux sur l'acclimatation thermique des plantes ont rapporté une flexibilité de la température optimale de l'activité photosynthétique en réponse à la variation de la température ambiante (Kattge et Knorr 2007, Yamori *et al.* 2010). Cette flexibilité a été expliquée par une plasticité des taux de carboxylation et de régénération du ribulose-1,5-diphosphate (Vc_{max} et J_{max}). Dans le présent travail, la variation de température le long du gradient latitudinal a eu des effets différents selon les clones. Certains clones (915005 et 915319) ont eu une réponse similaire avec des valeurs du J_{max} qui ont baissé le long du gradient latitudinal (sud–nord) alors que pour les autres clones (747215 et 915004), J_{max} a peu ou pas varié. Les valeurs de Vc_{max} ont généralement diminué le long du gradient. Des travaux précédents ont montré que Vc_{max} et J_{max} pouvaient s'acclimater à la température ambiante en modifiant leur température optimale sur les intervalles 0 - 40°C et 0 - 30°C respectivement (Hikosaka *et al.* 2006). Globalement, nos résultats ont montré qu'à l'exception du clone 747215, Vc_{max} et J_{max} ont baissé du sud vers le nord, démontrant une absence d'ajustement à l'effet du gradient thermique.

La variation de la surface foliaire spécifique (SLA) était significative le long du gradient, mais moins importante que celle de la capacité photosynthétique. La SLA a augmenté du sud vers le nord pour deux des quatre clones, suivant ainsi une tendance inverse à celle du gradient thermique (ou de la longueur de la saison de croissance). Ceci suggère que la variation de SLA était un ajustement morphologique au gradient latitudinal afin d'accroitre la captation de la lumière et la photosynthèse, et de réduire ainsi l'effet de la basse température et de la courte saison de croissance. La plasticité de la morphologie foliaire a été plus importante en réponse à la réduction de l'espacement entre les arbres de 3×4 m à 1×4 m, alors que la surface foliaire spécifique (SLA) et la hauteur des arbres étaient proportionnelles à la densité de plantation. Ceci représente un ajustement morphologique à la compétition pour la lumière afin d'accroitre la quantité de radiation interceptée, réduite par l'effet de l'ombrage et du chevauchement des houppiers des arbres voisins. Cet effet a été observé sur différentes espèces (Gunn *et al.* 1999, Niinemets 2004, Benomar *et al.* 2012). L'ajustement du SLA a également permis d'accroitre l'efficience de l'utilisation de l'azote en

photosynthèse (PNUE) ainsi que la photosynthèse nette (P_n). Dans les espacements étroits, le diamètre à la base du tronc a diminué, ce qui montre que la pression de compétition était forte et que son effet sur la croissance a été supérieur à l'effet des ajustements du SLA et de la hauteur des arbres. Le volume du tronc des arbres espacés de 1×4 m était par conséquent généralement inférieur à celui des arbres espacés de 2×4 m ou de 3×4 m.

5.2 Applications à l'aménagement des plantations forestières

Cette thèse a couvert trois aspects-clés de la sylviculture intensive du peuplier hybride en région boréale, à savoir : (i) la gestion de la nutrition minérale au moment de l'établissement de la plantation (ii) les interactions entre les arbres à l'échelle racinaire et l'effet positif d'un déploiement polyclonal sur la productivité (iii) la plasticité des clones le long d'un gradient latitudinal et en réponse à une compétition croissante au niveau physiologique (photosynthèse) et morphologique. La prise en considération de l'ensemble de ces trois aspects lors du choix du site, de la densité et des clones à déployer permet de mieux réussir la sylviculture des plantations du peuplier hybride; on a démontré par exemple que l'effet positif du déploiement polyclonal sur la croissance était lié à l'amélioration du statut nutritif et était plus manifeste sur les sites les plus pauvres. Ceci pourrait permettre d'établir les plantations sur des sites marginaux ou peu productifs avec un supplément de fertilisants sur le territoire forestier et agricole et la sélection de cultivars ayant, par exemple, une efficience de l'utilisation de l'azote élevée. Dans ce contexte, le recours à une méthode de diagnostique telle que DRIS est utile pour déterminer avec précision les ratios de nutriments et par la suite la quantité de fertilisants à ajouter. Le mélange clonal pourrait ainsi réduire les quantités en fertilisants requises et les coûts de production, dépendamment du rendement escompté, et accroître ainsi la profitabilité économique des plantations. L'utilisation d'une dose conventionnelle de fertilisants ne serait pas à recommander étant donné la grande hétérogénéité bioclimatique et édaphique de la région boréale de l'est canadien. En effet, la réponse des arbres à la fertilisation est fortement liée à la fertilité du site (ex. Welham *et al.* 2007). Néanmoins, les caractéristiques du bois (contenu en H_2O, longueur des fibres et densité du bois) et du volume à la récolte sont souvent différents entre les clones du peuplier

hybride (Zhang *et al.* 2003). Cet inconvénient pourrait être réduit en sélectionnant les clones qui présentent les plus faibles différences, surtout en termes de caractéristiques du bois.

Pour ce qui de la densité de plantation, le choix de l'espacement optimal à laisser entre les arbres devrait varier en fonction de la finalité du produit récolté. En laissant 4 m entre les rangées pour le désherbage mécanique, deux scénarios pourraient être envisagés d'après nos résultats sur la productivité; (i) un espacement de 1×4 m au départ, suivi d'une première éclaircie après la 3^{ième} ou la 4^{ième} saison de croissance, ramenant l'espacement à 2×4 m et une deuxième éclaircie à la 7^{ième} pour avoir un espacement de 4 x 6 m. La première récolte pourrait servir à la production de copeaux de bois ou de pâte à papier, la deuxième pour produire du bois de sciage et la 3^{ième} pour avoir un bois de qualité (déroulage et bois d'œuvre); (ii) un espacement de 2×4 m permet d'épargner les coûts d'une première éclaircie et d'obtenir du bois pour le sciage et le déroulage, et un bois de qualité après une éclaircie à 4×6 m. Nos résultats ont montré que la plasticité variait entre les clones vis-à-vis d'une compétition croissante à un espacement réduit entre les arbres. Ainsi, les clones ayant une meilleure efficacité de l'utilisation des ressources pourraient mieux supporter la compétition intraclonale et être plantés à des densités élevées sans compromettre la croissance, augmentant ainsi le rendement à l'hectare. Au Canada, le rendement moyen des plantations de peuplier hybride en région boréale varie de 3 à 9 $m^3 ha^{-1} an^{-1}$ selon la qualité des sites et le régime sylvicole utilisé (Lieffers *et al.* 2003). Le rendement obtenu dans notre étude variait entre 1,5 – 3,8 $m^3 ha^{-1} an^{-1}$ avec une densité de 1250 arbres ha^{-1}. Ce rendement est supérieur à celui obtenu par des travaux précédents effectués dans la région boréale au Québec (Abitibi-Témiscamingue et Saguenay-Lac Saint-Jean) qui variait de 0,7 à 1 $m^3 ha^{-1} an^{-1}$ après 5 - 6 années de croissance et une densité de plantation similaire à celle de notre étude (Benomar *et al.* 2012, Bilodeau-Gauthier *et al.* 2011). Des rendements de l'ordre de 2 - 3 $m^3 ha^{-1} an^{-1}$ à 10 $m^3 ha^{-1} an^{-1}$ après 20 ans et 16 $m^3 ha^{-1} an^{-1}$ après 6 ans ont été rapportés au centre et au sud du Québec sur des sites agricoles (Rainville *et al.* 2003, Fortier *et al.* 2012, Delagrange et Lorenzetti, 2008, Truax *et al.* 2012). Les meilleurs rendements ont souvent été obtenus sur des sites agricoles, comparés aux sites forestiers (après coupe) où le sol est souvent plus acide (Bona *et al.* 2008). Nous estimons que l'écart de rendement entre les sites forestiers *vs* agricoles et ceux du sud *vs* du nord pourrait être réduit, entre autres, par l'amélioration

génétique des cultivars, la sélection de sites productifs, l'amélioration de l'efficacité des traitements sylvicoles tels que la préparation du terrain, le désherbage et la fertilisation. Dans le présent travail, même si la productivité a globalement baissé du sud vers le nord, les clones les plus « flexibles » ont eu des rendements satisfaisants quand ils ont été établis sur le site septentrional. Sur ce site, situé au-delà de la 49ème parallèle, les rendements obtenus à une densité de 1250 arbres/ha ont atteint 3 m^3 ha^{-1} an^{-1} après cinq années de croissance pour le clone le plus productif. Ceci est près du triple de productivité des forêts naturelles de la région, considérant que leur rendement à maturité se situe autour de 1 m^3 ha^{-1} an^{-1} (Pothier et Savard, 1998). Il est à noter que le rendement du peuplier hybride à maturité dépasserait largement 3 m^3 ha^{-1} an^{-1} et serait par conséquent supérieur à celui du peuplier de la forêt naturelle. Si un apport de fertilisants avait été fait au moment de la plantation, le volume du tronc aurait pu augmenter de 10% en moyenne, selon des résultats obtenus dans des sites de la même région (Elferjani *et al.* 2013). Sachant le réchauffement global prévu de 1,5 - 2 °C d'ici 2050 (IPCC 2007), nos résultats sur la plasticité de la phénologie et de la capacité photosynthétique le long du gradient latitudinal pourront servir à planifier l'établissement des clones selon la réponse de leur croissance à l'augmentation prévue des températures à moyen et à long termes. En d'autres termes, un clone comme 915319 sensible au gradient thermique serait plus productif tout au long du gradient que ce qu'il est en ce moment, alors que la productivité du 747215 changera peu. Il sera aussi important de revoir les recommandations des clones de peupliers pour chaque région, car avec l'augmentation de températures, des clones initialement recommandés pour les sites méridionaux pourraient « migrer » vers le nord sans compromettre la croissance.

5.3 Limites et perspectives

La compétition entre les arbres d'une plantation s'accroît au fil des années et deviendrait aussi importante au niveau racinaire qu'au niveau du houppier. Il serait alors intéressant d'explorer l'évolution de la nature et du degré d'acclimatation et leur effet sur la productivité au cours de la rotation afin de choisir la densité optimale pour chacun des clones et en fonction de la finalité du bois récolté. L'exploration du système racinaire nous a permis d'en savoir davantage sur l'effet de la diversité clonale sur la distribution des racines et leur acclimatation au voisinage, un paramètre difficile à observer avec des carottes de sol.

Toutefois, on ignore si l'effet positif de la mixture des clones va se maintenir, baisser ou disparaitre quand la compétition sera plus importante dans les prochaines années. Les métabolites primaires tels que les glucides totaux non-structuraux ont également été affectés par la compétition, notamment la concentration en amidon qui est cruciale pour le démarrage de la croissance l'année suivante et la protection contre le froid. Nos résultats ont montré un effet non significatif de l'espacement sur le débourrement et l'aoûtement, mais il est fort probable que la compétition qui devrait accroitre dans les prochaines années avec l'accroissement en volume des arbres, affecterait la phénologie du bourgeon terminal. La répartition des glucides totaux non-structuraux et leur dynamique entre la partie aérienne tout au long de l'année à différents degrés de compétition entre les arbres serait une piste à explorer afin de mieux caractériser la stratégie des clones en réponse au stress induit par la compétition et d'identifier les clones les plus performants sous des conditions défavorables. Dans ce contexte, on suggère le dosage de métabolites secondaires liés au stress tels que les polyamines pour mesurer le degré de compétition et identifier les clones qui la tolèrent mieux (Gupta *et al*. 2013). Il serait également intéressant d'évaluer la réponse des clones selon la latitude avec un plus large gradient afin de tester la limite de leur plasticité à la baisse de température en allant plus vers le nord que Villebois ainsi que leur réponse à des températures plus élevées sur des sites situés plus au sud que Duhamel. Ceci permettrait de mesurer la plasticité des clones aux importantes fluctuations climatiques interannuelles (ex. hivers exceptionnellement froids) et leurs conséquences sur la croissance.

BIBLIOGRAPHIE

Adler, P.R., Grosso, S.J.D., and Parton, W.J. 2007. Life-cycle assessment of net greenhouse gas flux for bioenergy cropping systems. Ecological Applications 17: 675-691.

Agriculture and Agri-food Canada. 2012. Soils landscapes of Canada. http://sis.agr.gc.ca/cansis/publications/maps/slc/1m/v1/index.html. Site consulted in October 2012.

Agriculture and Agri-food Canada. 2013. Plant hardiness zones of Canada. http://atlas.agr.gc.ca/agmaf/. Site consulated in May 2013.

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., and King, J.S. 1998. Leaf area and above-and belowground growth responses of loblolly pine to nutrient and water additions. Forest Science 44: 317-328.

Allison, S.D., Czimczik, C.I., and Treseder, K.K. 2008. Microbial activity and soil respiration under nitrogen addition in Alaskan boreal forest. Global Change Biology 14: 1156-1168.

Allison, S.D., LeBauer, D.S., Ofrecio, M.R., Reyes, R., Ta, A.-M., and Tran, T.M. 2009. Low levels of nitrogen addition stimulate decomposition by boreal forest fungi. Soil Biology and Biochemistry, 41: 293-302.

Archibald, S., and Bond, W.J. 2003. Growing tall vs grwing wide: tree architecture and allometry of Acacia karroo in forest, savanna, and arid environments. Oikos 102: 3-14.

Ballaré, C.L. 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. Trends in Plant Science 4: 97-102.

Balvanera, P., and Aguirre, E. 2006. Tree diversity, environmental heterogeneity, and productivity in a mexican tropical dry forest. Biotropica 38: 479-491.

Barber, V.A., Juday, G.P., and Finney, B.P. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405: 668-673.

Beaufils, E.R. 1973. Diagnosis and recommendation integrated system (DRIS). Soil Sciences Bulltein 1: 1–132.

Benbrahim, M., Gavaland, A., and Gauvin, J. 2000. Growth and yield of mixed polyclonal stands of *Populus* in short-rotation coppice. Scandinavian Journal of Forest Research 15: 605-610.

Benomar, L., DesRochers, A., and Larocque, G.R. 2011. Changes in specific leaf area and photosynthetic nitrogen-use efficiency associated with physiological acclimation of two hybrid poplar clones to intraclonal competition. Canadian Journal of Forest Research 41: 1465-1476.

Benomar, L., DesRochers, A., and Larocque, G.R. 2012. The effects of spacing on growth, morphology and biomass production and allocation in two hybrid poplar clones growing in the boreal region of Canada. Trees 26: 939-949.

Benomar, L., DesRochers, A., and Larocque, G.R. 2013. Comparing growth and fine root distribution in monocultures and mixed plantations of hybrid poplar and spruce. Journal of Forestry Research 24: 247-254.

Benowicz, A., Guy, R.D., and El-Kassaby, Y.A., 2000. Geographic pattern of genetic variation in photosynthetic capacity and growth in two hardwood species from British Columbia. Oecologia, 123: 168-174.

Bergh, J., and Linder, S. 1999. Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. Global Change Biology 5: 245-253.

Berthelot, A. 2001. Mélange de clones en taillis à courtes rotations de peuplier: influence sur la productivité et l'homogénéité des produits récoltés. Canadian Journal of Forest Research 317: 1116-1126.

Bhatti, J., Foster, N., and Hazlett, P. 1998. Fine root biomass and nutrient content in a black spruce peat soil with and without alder. Canadian Journal of Soil Science 78: 163-169.

Bilodeau-Gauthier, S., Paré, D., Messier, C., and Bélanger, N. 2011. Juvenile growth of hybrid poplars on acidic boreal soil determined by environmental effects of soil preparation, vegetation control, and fertilization. Forest Ecology and Management 26: 620-629.

Binkley, D. 1986. Forest nutrition management. Wiley, New York, pp 289-290.

Blackmon, B., Baker, J.B., and Cooper, D. 1979. Nutrient use by three geographic sources of eastern cottonwood. Canadian Journal of Forest Research 9: 532-534.

Block, R.M.A., Knight, J.D., Booth, N.W.H., and Van Rees, K.C.J. 2009. Nursery stock type, nitrogen fertilization and shoot pruning effects on the growth of juvenile hybrid poplar in Saskatchewan. Canadian Journal of Plant Science 89: 289-301.

Boivin, J.R., Salifu, K.F., and Timmer, V.R. 2004. Late-season fertilization of Picea mariana seedlings: intensive loading and outplanting response on greenhouse bioassays. Annals of Forest Science 61 737-745.

Bollmark, L., Sennerby-Forsse, L., and Ericsson, T. 1999. Seasonal dynamics and effects of nitrogen supply rate on nitrogen and carbohydrate reserves in cutting-derived *Salix viminalis p*lants. Canadian Journal of Forest Research 29: 85-94.

Bona, K.A., Burgess, M.S., Fyles, J.W., Camiré, C., and Dutilleul, P. 2008. Weed cover in hybrid poplar (*Populus*) plantations on Quebec forest soils under different lime treatments. Forest Ecology and Management 255: 2761-2770.

Bonduelle, P., 1983. Taillis de peuplier à courtes rotations : tarifs de poids. Annales de Recherches Sylvicoles: 375-401.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Advances In Genetics 13: 115-155.

Bradshaw, A., and Hardwick, K. 1989. Evolution and stress—genotypic and phenotypic components. Biological Journal of the Linnean Society 37: 137-155.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., and Sayer, J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodiversity and Conservation 17: 925-951.

Brown, K., and van den Driessche, R. 2002. Growth and nutrition of hybrid poplars over 3 years after fertilization at planting. Canadian Journal of Forest Research 32: 226-232.

Brown, K., and van den Driessche, R. 2005. Effect of nitrogen and phosphorus fertilization on the growth and nutrition of hybrid poplars on Vancouver islands. New Forests 29: 89-104

Bruno, J.F., Stachowicz, J.J., and Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18: 119-125.

Callahan, H.S., Maughan, H., and Steiner, U.K. 2008. Phenotypic plasticity, costs of phenotypes, and costs of plasticity. Annals of the New York Academy of Sciences 1133: 44-66.

Campion, J., and Scholes, M. 2008. Diagnosing foliar nutrient dynamics of Eucalyptus grandis in KwaZulu-Natal, South Africa, using optimal element ratios and the diagnosis and recommendation integrated system (DRIS). Southern Hemisphere Forestry Journal 69:137-150.

Canham, C.D., Kobe, R.K., Latty, E.F., and Chazdon, R.L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121: 1-11.

Cannell, M., and Smith, R. 1986. Climatic warming, spring budburst and forest damage on trees. Journal of Applied Ecology: 177-191.

Cardinale, B.J., Nelson, K., and Palmer, M.A. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos 91: 175-183.

Chapin, F.S. 1980. The mineral nutrition of wild plants. Annual review of ecology and systematics 11: 233-260.

Chmielewski, F.M., and Rötzer, T. 2001. Response of tree phenology to climate change across Europe. Agriculture For Meteorology 108:101–112.

Chow, P.S., and Landhäusser, S.M. 2004. A method for routine measurements of total sugar and starch content in woody plant tissues. Tree Physiology 24: 1129-1136.

Chuine, I., and Beaubien, E.G. 2001. Phenology is a major determinant of tree species range. Ecology Letters 4: 500-510.

Coleman, M., Tolsted, D., Nichols, T., Johnson, W.D., Wene, E.G., and Houghtaling, T. 2006. Post-establishment fertilization of Minnesota hybrid poplar plantations. Biomass and Bioenergy 30: 740-749.

Comas, L., Bouma, T., and Eissenstat, D. 2002. Linking root traits to potential growth rate in six temperate tree species. Oecologia 132: 34-43.

Cooke, J.E.K., Martin, T.A., and Davis, J.M. 2005. Short-term physiological and developmental responses to nitrogen availability in hybrid poplar. New Phytologist 167: 41-52.

Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70: 171-207.

Curtis, P.S., Vogel, C.S., Wang, X., Pregitzer, K.S., Donald, R., Zak, D.R., Lussenhop, J., Kubiske, M., and Teeri, J.A,. 2000. Gas exchange, leaf nitrogen, and growth efficiency of *Populus tremuloides* in a CO_2-enriched atmosphere. Ecological Applications 10: 3-17.

de Mazancourt, C., and Schwartz, M.W. 2012. Starve a competitor: evolution of luxury consumption as a competitive strategy. Theoretical Ecology 5: 37-49.

Delagrange, S., Montpied, P., Dreyer, E., Messier, C., and Sinoquet, H. 2006. Does shade improve light interception efficiency? A comparison among seedlings from shade-tolerant and -intolerant temperate deciduous tree species. New Phytologist 172: 293-304.

Delagrange, S., et F. Lorenzetti, F., 2008. Inventaire et évaluation de la performance de plantations de peupliers hybrides implantées par FPS Canada Inc. en Outaouais. Institut Québécois d'Aménagement de la Forêt feuillue, Ripon, Qc. 23 p.

DesRochers, A., van den Driessche, R., and Thomas, B.R. 2007. The interaction between nitrogen source, soil pH, and drought in the growth and physiology of three poplar clonesThis article is one of a selection of papers published in the Special Issue on Poplar Research in Canada. Canadian Journal of Botany 85: 1046-1057.

DeWitt, T.J., Sih, A., and Wilson, D.S. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13: 77-81.

Diaz, S., and Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16: 646-655.

Dickmann, D.I., Isebrands, J., Blake, T.J., Kosola, K., and Kort, J. 2001. Physiological ecology of poplars. In Poplar culture in North America. Edited by D.I. Dickmann, J.G. Isebrands, J.E. Eckenwalder and R. Richardson. NRC Research Press, Ottawa, 77-118.

Dillen, S.Y., Rood, S.B., and Ceulemans, R. 2010. Growth and physiology. In Genetics and genomics of *Populus*. Edited by S. Jansson , R.P. Bhalerao RP and A.T. Groover. Springer, pp. 39-66. New York.

Domzl H., Hodara, J., Słowińska-Jurkiewicz, A., and Turski, R. 1993. The effects of agricultural use on the structure and physical properties of three soil types. Soil and Tillage Research 27: 365-382.

Drechsel, P., and Zech, W. 1994. DRIS evaluation of teak (*Tectona grandis* L.) mineral nutrition and effects of nutrition and site quality on teak growth in West Africa. Forest Ecology and Management 70: 121-133.

Duggan, B.L., Yeates, S.J., Gaff, N., and Constable, G.A. 2007. Phosphorus Fertilizer Requirements and nutrient uptake of irrigated dry-season cotton grown on virgin soil in tropical Australia. Communications in Soil Science and Plant Analysis 39: 282-301.

Edmond, J.B., Senn, T., Andrews, F., and Halfacre, R., 1979. Fundamentals of horticulture. Tata McGraw-Hill Publishing Co.

Eisenhauer, N., Beßler, H., Engels, C., Gleixner, C., Habekost, M,. Milcu A., Partsch S., Sabais, A.C.W., Scherber, C., and Steinbeiss, S. 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. Ecology 91:485-96.

Eisenhauer, N. 2012. Aboveground–belowground interactions as a source of complementarity effects in biodiversity experiments. Plant and soil 351: 1-22.

Elferjani, R., DesRochers, A., and Tremblay, F. 2013. DRIS-based fertilization efficiency of young hybrid poplar plantations in the boreal region of Canada. New Forests 44: 487-508.

Ellis, A.R., Hubbell, S.P., and Potvin, C. 2000. In situ field measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. Canadian Journal of Botany 78: 1336-1347.

Ellsworth, D.S., Reich, P.B., Naumburg, E.S., Koch, G.W., Kubiske, M.E., and Smith, S. D. 2004. Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated CO_2 across four free - air CO2 enrichment experiments in forest, grassland and desert. Global Change Biology 10: 2121-2138.

Environment Canada. 2013. http://climate.weatheroffice.gc.ca. Accessed on May 2013.

Ericsson, T. 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability, Nutrient Uptake and Cycling in Forest Ecosystems. Springer Netherlands pp. 205-214.

Erskine, P.D., Lamb, D., and Bristow, M. 2006. Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? Forest Ecology and Management 233: 205-210.

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. Oecologia 78: 9-19.

Evans, J., and Turnbull, J.W. 2004. Plantation forestry in the tropics: the role, silviculture, and use of planted forests for industrial, social, environmental, and agroforestry purposes, 3rd Edition. Oxford University Press, Oxford.

Fabbrini, F, Gaudet, M., Bastien, C., Zaina, G., Harfouche, A., Beritognolo, I., Beritognolo, I., Marron, N., Morgante, M., Scarascia-Mugnozza, G., and Sabatti, M. 2012. Phenotypic plasticity, QTL mapping and genomic characterization of bud set in black poplar. BMC Plant Biology 12: 47.

Fageria, V. 2001. Nutrient interactions in crop plants. Journal of Plant Nutrition 24: 1269-1290.

FAO 2010. http://www.fao.org/docrep/013/i1757e/i1757e.pdf. Accessed in January 2013.

Fargione, J. Tilman, D., Dybzinski, R., Lambers, J.H.S., Clark, C., Harpole W.S., Knops J.M.H., Reich, P.B., and Loreau, M. 2007. From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. Proceedings of the Royal Society B: Biological Sciences 274: 871-876.

Farquhar, G.D., von Caemmerer, S., and Berry, J.A. 1980. A biochemical model of photosynthetic $C0_2$ assimilation in leaves of C3 species. Planta 149: 78-90.

Flint, C.M., Harrison, R.B., Strahm, B.D., and Adams, A.B. 2008. Nitrogen Leaching from Douglas-fir Forests after Urea Fertilization. Journal of Environmental Quality 37:1781-1788.

Forrester, D.I., Bauhus, J., and Cowie, A.L. 2006. Carbon allocation in a mixed-species plantation of *Eucalyptus globules* and *Acacia mearnsii*. Forest Ecology and Management 233: 275-284.

Forrester, D.I., Theiveyanathan, S., Collopy, J.J., & Marcar, N.E. 2010. Enhanced water use efficiency in a mixed *Eucalyptus globules* and *Acacia mearnsii* plantation. Forest Ecology and Management, 259: 1761-1770.

Fortier, J., Truax, B., Gagnon, D., and Lambert, F. 2012. Hybrid poplar yields in Québec: Implications for a sustainable forest zoning management system. The Forestry Chronicle 88: 391-407.

Francis, T., and Kannenberg, L. 1978. Yield stability studies in short-season maize. I. A descriptive method for grouping genotypes. Canadian Journal of Plant Science 58: 1029-1034.

Garber, S.M., and Maguire, D.A. 2004. Stand productivity and development in two mixed-species spacing trials in the central Oregon Cascades. Forest Science 50: 92-105.

Garnier, E., Gobin, O., and Poorter, H. 1995. Nitrogen productivity depends on photosynthetic nitrogen use efficiency and on nitrogen allocation within the plant. Annals of Botany 76: 667-672.

Gedroc, J.J., McConnaughay, K.D. M., and Coleman, J.S. 1996. Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? Functional Ecology 44-50.

Gersani, M., O'Brien, E.E., Maina, G.M., and Abramsky, Z. 2001. Tragedy of the commons as a result of root competition. Journal of Ecology 89: 660-669.

Gornall, J.L., and Guy, R.D. 2007. Geographic variation in ecophysiological traits of black cottonwood (*Populus trichocarpa*) This article is one of a selection of papers published in the Special Issue on Poplar Research in Canada. Botany 85: 1202-1213.

Grams, T.E., and Andersen, C.P. 2007. Competition for resources in trees: physiological versus morphological plasticity, Progress in botany. Springer, pp. 356-381.

Grassi, G., and Bagnaresi, G. 2000. Influence of nutrient supply on shade–sun acclimation of *Picea abies* seedlings: effects on foliar morphology, photosynthetic performance and growth. Tree physiology 20: 645-652.

Gregoire, N., and Fisher, R.F. 2004. Nutritional diagnoses in loblolly pine (*Pinus taeda*L.) established stands using three different approaches. Forest ecology and management 203 : 195-208.

Grondin P. 1996 Ecologie forestière. In Manuel de foresterie. Edited by J. Bérard and M. Côté M Presses de l'Université Laval, Québec. pp 135–279.

Groom, P., and Lamont, B.B. 1997. Xerophytic implications of increased sclerophylly: interactions with water and light in *Hakea psilorrhyncha* seedlings. New Phytologist 136: 231-237.

Gu, L., Post., W.M., Baldocchi, D., Black, T.A., Verma, S.B., Vesala, T., and Wofsy, S.C. 2003. Phenology of vegetation photosynthesis. In Phenology: An Integrative Environmental Science. Edited by M.D. Schwartz, pp. 467–486. Kluwer, Dordrecht.

Guillemette, T,. and DesRocher,s A. 2008. Early growth and nutrition of hybrid poplars fertilized at planting in the boreal forest of western Quebec. Forest Ecology and Management 255: 2981-2989.

Gundersen, P., Schmidt, I.K., and Raulund-Rasmussen, K. 2006. Leaching of nitrate from temperate forests – effects of air pollution and forest management. Environmental Reviews 14 1-57.

Gunn, S., Farrar, J.F., Collis, B.E., and Nason, M. 1999. Specific leaf area in barley: individual leaves versus whole plants. New Phytologist 143: 45–51.

Gupta, K., Dey, A., and Gupta, B. 2013. Plant polyamines in abiotic stress responses. Acta Physiologiae Plantarum 35: 2015-2036.

Güsewell, S. 2004. N : P ratios in terrestrial plants: variation and functional significance. New Phytologist 164: 243-266.

Hall, D., Luquez, V., Garcia, V.M., St Onge, K.R., Jansson, S., and Ingvarsson, P.K. 2007. Adaptive population differentiation in phenology across a latitudinal gradient in European aspen (*Populus tremula,* L.): a comparison of neutral markers, candidate genes and phenotypic traits. Evolution 61: 2849-2860.

Hanninen, H. 1990. Modelling bud dormancy release in trees from cool and temperate regions (No. 213). Finnish Forest Research Institute

Hanninen, H., and Kramer, K. 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. Silva Fennica 41: 167.

Hansen, J., Sato, M., and Ruedy, R., 2012. Perception of climate change. Proceedings of the National Academy of Sciences, 109: 2415-2423.

Harley, P.C., Thomas, R.B., Reynolds, J.F., and Strain, B.R. 1992. Modelling photosynthesis of cotton grown in elevated $C0_2$. Plant, Cell & Environment 15: 271-282.

Hartz, T.K., Johnstone, P., Williams, E., and Smith, R. 2007. Establishing lettuce leaf nutrient optimum ranges through DRIS analysis. HortScience 42: 143-146.

Harvey, C.A., Gonzalez, J., and Somarriba, E., 2006. Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in

Talamanca, Costa Rica. Biodiversity & Conservation 15: 555-585.

Harvey, H., and Van Den Driessche, R. 1997. Nutrition, xylem cavitation and drought resistance in hybrid poplar. Tree Physiology 17: 647-654.

Heide, O. 2003. High autumn temperature delays spring bud burst in boreal trees, counterbalancing the effect of climatic warming. Tree Physiology 23: 931-936.

Heilman, P.E. 1992. Sustaining production: nutrient dynamics and soils. In Ecophysiology of short rotation forest crops. Edited by C.P. Mitchell, J.B. Ford-Robertson, T.M. Hinckley and L Sennerby Forsse. Elsevier Science Publishers Ltd., New York, pp 216–230.

Heilman, P.E., and Xie, F.G. 1993. Influence of nitrogen on growth and productivity of short-rotation *Populus trichocarpa*× *Populus deltoides* hybrids. Canadian Journal of Forest Research 23: 1863-1869.

Heilman, P.E., Ekuan, G., and Fogle, D. 1994. Above-and below-ground biomass and fine roots of 4-year-old hybrids of *Populus trichocarpa* × *Populus deltoides* and parental species in short-rotation culture. Canadian Journal of Forest Research 24: 1186-1192.

Heilman, P., and Norby, R.J. 1998. Nutrient cycling and fertility management in temperate short rotation forest systems. Biomass and Bioenergy 14: 361-370.

Hikosaka, K., Ishikawa, K., Borjigidai, A., Muller, O., and Onoda, Y. 2006. Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. Journal of Experimental Botany 57: 291-302.

Hodge, A., Robinson, D., Griffiths, B., and Fitter, A. 1999. Why plants bother: root proliferation results in increased nitrogen capture from an organic patch when two grasses compete. Plant, Cell & Environment 22: 811-820.

Hogg, E., Brandt, J., and Michaelian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. Canadian Journal of Forest Research, 38: 1373-1384.

Hooper, D.U., and Vitousek, P.M., 1997. The effects of plant composition and diversity on ecosystem processes. Science 277: 1302-1305.

Hooper, D.U., and Dukes, J.S. 2004. Overyielding among plant functional groups in a long-term experiment. Ecology Letters 7: 95-105.

Hooper, D.U. Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., Gonzalez, A., Emmett Duffy, J., Gamfeldt, L., and O'Connor, M. I. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486: 105-108.

Horner-Devine, M., Leibold, M.A., Smith, V.H., and Bohannan, B.J. 2003. Bacterial diversity patterns along a gradient of primary productivity. Ecology Letters 6: 613-622.

Howe, G.T., Gardne,r G., Hackett, W.P., and Furnier G.R. 1996. Phytochrome control of short-day induced bud set in black cottonwood. Physiologica Plantarum 97: 95–103.

Huang, J., Tardif, J.C., Bergeron, Y., Denneler, B., Berninger, F., and Girardin, M.P. 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Global Change Biology 16: 711-731

Hundal, H., Singh, D., and Singh, K. 2007. Monitoring nutrient status of guava fruit trees in Punjab, northwest India through the diagnostic and recommendation integrated system approach. Communications in Soil Science and Plant Analysis 38: 2117-2130.

Hüner, N.P.A., and Hopkins, W.G. 2008 Introduction to plant physiology, 4th edn. Wiley, New York.

Hutchings, M.J., and John, E.A. 2004. The effects of environmental heterogeneity on root growth and root/shoot partitioning. Annals of Botany 94: 1-8.

Hüttl, R.F., and Schaaf, W. 1995. Nutrient supply of forest soils in relation to management and site history. Plant and Soil 168-169: 31-41.

Inno, M., and Timmer, V.R., 1997. Vector diagnosis of nutrient dynamics in mesquite seedlings. Forest Science 43: 268-273.

IPCC (Intergovernmental Panel on Climate Change). Climate Change 2007: The Physical Science Basis. Cambridge University Press, Cambridge, UK.

Jacobs, D.F., and Timmer, V.R. 2005. Fertilizer-induced Changes in Rhizosphere Electrical Conductivity: Relation to Forest Tree Seedling Root System Growth and Function. New Forests 30: 147-166.

Jactel, H., and Brockerhoff, E.G. 2007. Tree diversity reduces herbivory by forest insects. Ecology Letters 10: 835-848.

Jarecki, M.K., and Lal, R. 2003. Crop management for soil carbon sequestration. Critical Reviews in Plant Sciences 22: 471-502.

Jonas, C.S., and Geber, M.A. 1999. Variation among populations of Clarkia unguiculata (Onagraceae) along altitudinal and latitudinal gradients. American Journal of Botany 86: 333-343.

Joshi, J., Schmid, B., Caldeira, M.C., Dimitrakopoulos, P.G., Good, J., Harris, R., Hector,

A., Huss - Danell, K., Jumpponen, A., and Minns, A. 2001. Local adaptation enhances performance of common plant species. Ecology Letters 4: 536-544.

Junior, R., dos Anjos, R., and Monnerat, P.H. 2003. Norms establishment of the Diagnosis and Recommendation Integrated System (DRIS) for nutritional diagnosis of sugarcane. Pesquisa Agropecuária Brasileira 38: 277-282.

Kalliokoski, T., Nygren, P., and Sievanen, R. 2008. Coarse root architecture of three boreal tree species growing in mixed stands. Silva Fennica 42: 189.

Kasuga, J., Arakawa, K., and Fujikawa, S. 2007. High accumulation of soluble sugars in deep supercooling Japanese white birch xylem parenchyma cells. New Phytologist 174: 569-579.

Kattge, J., and Knorr, W. 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. Plant, Cell & Environment 30: 1176-1190.

Kelty, M.J. 2006. The role of species mixtures in plantation forestry. Forest Ecology and Management 233: 195-204.

Keskitalo, J., Bergquist, G., Gardeström, P., and Jansson, S., 2005. A cellular timetable of autumn senescence. Plant Physiology 139: 1635-1648.

King, J.S., Pregitzer, K.S., and Zak, D.R. 1999. Clonal variation in above-and below-ground growth responses of *Populus tremuloides* Michaux: influence of soil warming and nutrient availability. Plant and Soil 217: 119-130.

Knops, J., Bradley, K., and Wedin, D. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecology Letters 5: 454-466.

Kobe, R.K., Iyer, M., and Walters, M.B. 2010. Optimal partitioning theory revisited: Non-structural carbohydrates dominate root mass responses to nitrogen. Ecology 91: 166-179.

Kozlowski, T., and Pallardy, S. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. The Botanical Review 68: 270-334.

Kramer, K. 1995. Phenotypic plasticity of the phenology of seven European tree species in relation to climatic warming. Plant, Cell & Environment 18: 93-104.

Lambers, H., and Poorter, H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Advances in Ecological Research 23: 187-261.

Landhäusser, S.M., and Lieffers, V.J. 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above - ground disturbance. Journal of Ecology 90: 658-665.

Larcher, W. 2003. Physiological plant ecology: Ecophysiology and stress physiology of functional groups. 4th ed. Springer, Berlin, Germany

Larchevêque, M., DesRochers, A. and Larocque, G.R., 2011. Comparison of manure compost and mineral fertilizer for hybrid poplar plantation establishment on boreal heavy clay soils. Annals of Forest Sciences 68:849-860.

Larocque, G. DesRochers, A., Larchevêque, M., Tremblay, F., Beaulieu, J., Mosseler, A., Major, J. E., Gaussiran, S., Thomas, B.R., Sidders, D. Périnet, P., Kort, J., Labrecque, M., Savoie, P., Masse, S., Bouman, O.T., Kamelchuk, D., Benomar, L., Mamashita, T., and Gagné, P. 2013. Research on hybrid poplars and willow species for fast-growing tree plantations: Its importance for growth and yield, silviculture, policy-making and commercial applications. The Forestry Chronicle. 89: 32-41.

Leco Corp. 1986. CHN-600 elemental analyzer for macrosamples system 785-500. Application Bull. CHNP2-84. LECO Corp., St. Joseph, MI.

Leech, R., and Kim, Y. 1981. Foliar analysis and DRIS as a guide to fertilizer amendments in poplar plantations. The Forestry Chronicle 57: 17-21.

Lei, X., Wang, W., and Peng, C. 2009. Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. Canadian Journal of Forest Research 39: 1835-1847.

Li, H., Li, M., Luo, J., Cao, X., Qu, L., Gai, Y., Jaing, X., Liu, T., Bai, H., Janz, T., Polle, Peng, C., and Luo, Z. 2012. N-fertilization has different effects on the growth, carbon and nitrogen physiology, and wood properties of slow-and fast-growing Populus species. Journal of Experimental Botany 63: 6173-6185.

Lieffers, V., Messier, C., Burton, P., Ruel, J. and Grover, B., 2003. Nature-based silviculture for sustaining a variety of boreal forest values. In Towards Sustainable Management of the Boreal Forest. Edited by P.J. Burton, C. Messier, D.W. Smith and W.L. Adamowicz. NRC research Press. Ottawa, Canada. 481-530.

Löfgren, S., Ring, E., von Brömssen, C., Sørensen, R., and Högbom, L. 2009. Short-term Effects of Clear-cutting on the Water Chemistry of Two Boreal Streams in Northern Sweden: A Paired Catchment Study. Ambio 38: 347-356.

Loreau, M. and Hector, A. 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412: 72-76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U.,

Huston, M.A., Rafaelli, D., Schmid, B., Tilman, D., and Wardle, D.A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294: 804-808.

Lteif, A., Whalen, J.K., Bradley, R.L., and Camiré, C. 2008. Diagnostic tools to evaluate the foliar nutrition and growth of hybrid poplars. Canadian Journal of Forest Research 38: 2138-2147.

Luquez, V., Hall, D., Albrectsen, B.R., Karlsson, J., Ingvarsson, P., and Jansson, S. 2008. Natural phenological variation in aspen (*Populus tremula*): the SwAsp collection. Tree Genetics & Genomes, 4: 279-292.

Malamy, J. 2005. Intrinsic and environmental response pathways that regulate root system architecture. Plant, Cell & Environment 28: 67-77.

Marenco, R., Gonçalves, J.D.C., and Vieira, G. 2001. Photosynthesis and leaf nutrient contents in *Ochroma pyramidale* (Bombacaceae). Photosynthetica 39: 539-543.

Marron, N., Bastien, C., Sabatti, M., Taylor, G., and Ceulemans, R. 2006. Plasticity of growth and sylleptic branchiness in two poplar families grown at three sites across Europe. Tree physiology 26: 935-946.

Marron N., Ricciotti, L., Bastien, C., Beritognolo, I., Gaudet, M., Paolucci, I., Fabbrini, F., Salani F., Dillen, S.Y., Ceulemans, R., Pinel, M.P.C., Taylor, G., Scarascia-Mugnozza, G., and Sabatti, M. 2010. Plasticity of growth and biomass production of an intraspecific *Populus alba* family grown at three sites across Europe during three growing seasons. Canadian Journal of Forest Research 40 : 1887-1903.

Marschner, H. 1996. Mineral nutrition of higher plants. Academic Press, London.

Martinelli, L.A., Piccolo, M.C., Townsend, A.R., Vitousek, P.M., Cuevas, E., McDowell, W., Robertson, G.P., Santos, O.C., and Treseder, K. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. Biogeochemistry 46: 45–65.

Masson, P., and Esvan, J. 1995. Simultaneous determination by inductively coupled plasma spectrometry N, P, K, Ca, Cu, Mg, Fe, Mn and Zn in plant samples. Analysis, 23, 437-440.

Mattson, W.J., Hart, E.A., and Volney, W.J.A. 2001. Insect pests of *Populus*: coping with the inevitable. In Poplar culture in North America. Edited by D.I. Dickmann, J.G. Isebrands, J.E. Eckenwalder and R. Richardson. NRC Research Press, Ottawa, 219-248.

McCracken, A., and Dawson, W. 1997. Growing clonal mixtures of willow to reduce effect of *Melampsora epitea* var. epitea. European Journal of Forest Pathology 27: 319-329.

McKeague, JA, and Stonehouse, H.B. 2008 The Canadian encyclopedia, soil classification. Online edition. http://www.thecanadianencyclopedia.com/index.cfm? PgNm=TCE &Params=A1SEC8787

McLaughlin, J.W., Reed, D.D., Jurgensen, M.F., Mroz, G.D., and Bagley, S.T. 1996. Relationships between soluble sugar concentrations in roots and ecosystem stress for first year sugar maple seedlings. Water, Air, and Soil Pollution 88: 1-19.

Medhurst, J., Beadle, C., and Neilsen, W. 2001. Early-age and later-age thinning affects growth, dominance, and intraspecific competition in *Eucalyptus nitens* plantations. Canadian Journal of Forest Research 31: 187-197.

Medhurst, J.L., and Beadle, C.L. 2005. Photosynthetic capacity and foliar nitrogen distribution in Eucalyptus nitens is altered by high-intensity thinning. Tree Physiology 25: 981-991.

Menalled, F.D., Kelty, M.J., and Ewel, J.J. 1998. Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures. Forest Ecology and Management 104: 249-263.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, Ø., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Stritz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., ZACH, S., and ZUST, A. 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12: 1969-1976.

Messier, C. Tittler, R., Kneeshaw, D.D., Gélinas, N., Paquette, A., Berninger, K., Rheault, H., Meek, P., and Beaulieu, N. 2009. TRIAD zoning in Quebec: Experiences and results after 5 years. The forestry chronicle 85: 885-896.

Millar, C.I., Stephenson, N.L., and Stephens, S.L. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17: 2145-2151.

Ministère des Ressources Naturelles du Québec. http://www.mrn.gouv.qc.ca/ forets/gestion/nouveau-regime-2013.jsp. Site consulted in October 2013.

Miot, B.S., Frey, P., and Pinon, J. 1999. Varietal mixture of poplar clones: Effects on infection by *Melampsora larici - populina* on plant growth. European Journal of Forest Pathology 29: 411-423.

Monclus, R., Dreyer, E., Villar, M., Delmotte, F.M., Delay, D., Petit, J.M., Le Thiec, D., Bréchet, C., and Brignolas, F. 2006. Impact of drought on productivity and water-use efficiency in 29 genotypes of *Populus deltoides* × *Populus nigra* . New Phytologist 169:765-777.

Montagnini, F., González, E., Porras, C., and Rheingans, R. 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. In IUFRO Tropical Silviculture Subject Group, S1-07-00, IUFRO 20th World Congress, Tampere, Finland.

Montagnini, F. 2000. Accumulation in above-ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland. Forest Ecology and Management 134: 257-270.

Morris, L., Moss, S., and Garbett, W. 1993. Competitive interference between selected herbaceous and woody plants and *Pinus taeda* L. during two growing seasons following planting. Forest Science 39: 166-187.

Mourão-Filho, A.D.D. 2005. DRIS and sufficient range approaches in nutritional diagnosis of "Valencia" sweet orange on three rootstocks. Journal of Plant Nutrition 28: 691-705.

Mousseau, M., and Saugier, B. 1992. The direct effect of increased CO2 on gas exchange and growth of forest tree species. Journal of Experimental Botany 43: 1121-1130.

Mulder, C., Uliassi, D., and Doak, D. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. Proceedings of the National Academy of Sciences 98: 6704-6708.

Muth, C.C., and Bazzaz, F. 2003. Tree canopy displacement and neighborhood interactions. Canadian Journal of Forest Research 33: 1323-1330.

Nachtigall, G.R., and Dechen, A.R. 2007. DRIS use on apple orchard nutritional evaluation in response to potassium fertilization. Communications in Soil Science and Plant Analysis 38: 2557-2566.

Naeem, S., Thompson, L.J., Lawler, S.P., and Lawton, J.H. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368: 21.

Nichols, J.D., Bristow, M., and Vanclay, J.K. 2006. Mixed-species plantations: prospects and challenges. Forest Ecology and Management 233: 383-390.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. Ecology 82: 453-469.

Niinemets, Ü. 2004. Adaptive adjustments to light in foliage and whole - plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. New phytologist 162: 683-696.

Nikitishen, V.I., and Lichko, V.I. 2008. Nitrogen budget in agroecosystems on gray forest soils under long-term fertilization. Eurasian Soil Science 41: 429-440.

Nolet, P., Delagrange, S., Bouffard, D., Doyon, F., and Forget, E. 2008. The successional

status of sugar maple (*Acer saccharum*), revisited. Annals of forest science 65: 208-208.

Oelmann, Y., Potvin, C., Mark, Werther, Lisa., Tapernon, S., and Wilcke W. 2010. Tree mixture effects on aboveground nutrient pools of trees in an experimental plantation in Panama. Plant and Soil 326: 199-212.

Ollinger, S. Richardson, A.D., Martin, M.E., Hollinger, D.Y., Frolking, S.E., Reich, P.B., Plourde, L.C., Katul, G.G., Munger, J.W., Oren, R., Smith, M.-L., Paw, K.T., Bolstad, P.V., Cook, B.B., Day, M.C., Martin, T.A., Molson, R.K., and Schmid, H.P. 2008. Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: functional relations and potential climate feedbacks. Proceedings of the National Academy of Sciences 105: 19336-19341.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer, K., McCarthy, H., Hendrey, G., McNulty, S.G., and Katul, G. G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411: 469-472.

Oskarsson, H., and Brynleyfsdottir, S.J. 2009. The interaction of fertilization in nursery and field on survival growth and the frost heaving of birch and spruce. Icelandic Agricultural Science, 22: 59-68.

Ouimet, R., and Camiré, C. 1995. Foliar deficiencies of sugar maple stands associated with soil cation imbalances in the Quebec Appalachians. Canadian Journal of Soil Science 75: 169-175.

Ouimet, R., Camiré, C., Brazeau, M., and Moore, J.-D. 2008. Estimation of coarse root biomass and nutrient content for sugar maple, jack pine, and black spruce using stem diameter at breast height. Canadian Journal of Forest Research 38: 92-100.

Paquette, A., and Messier, C. 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecology and Biogeography 20: 170-180.

Paquette, Bastien Fontaine, A., Berninger, F., Karine Dubois, K., Lechowicz, M.J., Christian Messier, C., Posada, J., Valladares, F., and Brisson, J. 2012. Norway maple displays greater seasonal growth and phenotypic plasticity to light than native sugar maple. Tree physiology 32: 1339-1347.

Partelli, F.L., Vieira, H.D., de Carvalho, V.B., and Mourão-Filho, A.D.D. 2007. Diagnosis and recommendation integrated system norms, sufficiency range, and nutritional evaluation of Arabian coffee in two sampling periods. Journal of Plant Nutrition 30: 1651-1667.

Pellis, A., Laureysens, I., and Ceulemans, R. 2004. Genetic variation of the bud and leaf phenology of seventeen poplar clones in a short rotation coppice culture. Plant Biology 6: 38-46.

Persson, J., Gardeström, P., and Näsholm, T. 2006. Uptake, metabolism and distribution of organic and inorganic nitrogen sources by *Pinus sylvestris*. Journal of Experimental Botany 57: 2651-2659.

Petchey, O.L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos 101: 323-330.

Petit, B., and Montagnini, F. 2006. Growth in pure and mixed plantations of tree species used in reforesting rural areas of the humid region of Costa Rica, Central America. Forest Ecology and Management 233: 338-343.

Piirainen, S., Finér, L., Mannerkoski, H., and Starr, M. 2007. Carbon, nitrogen and phosphorus leaching after site preparation at a boreal forest clear-cut area. Forest Ecology and Management 243: 10-18.

Pinno, B., and Bélanger, N. 2009. Competition control in juvenile hybrid poplar plantations across a range of site productivities in central Saskatchewan, Canada. New Forests 37: 213-225.

Piotto, D. 2008. A meta-analysis comparing tree growth in monocultures and mixed plantations. Forest Ecology and Management 255: 781-786.

Pitre, F.E., Pollet, B., Lafarguette, F., Cooke, J.E.K., MacKay, J.J., and Lapierre, C. 2007. Effects of increased nitrogen supply on the lignification of poplar wood. Journal of Agricultural and Food Chemistry, 55, 10306-10314.

Poorter, H., and Evans, J.R. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia 116: 26-37.

Pothier, D., et F. Savard. 1998. Actualisation des tables de production pour les principales espèces forestières du Québec. Ministère des Ressources Naturelles, Direction de l'environnement forestier. 184 p

Potvin, C. and Gotelli, N.J. 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. Ecology Letters 11: 217-223.

Potvin, C., and Dutilleul, P. 2009. Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. Ecology 90: 321-327.

Pretzsch, H., and Schütze, G. 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. European Journal of Forest Research 128: 183-204.

Pretzsch, H., Block, J., Dieler, J., Dong, P. H., Kohnle, U., Nagel, J., Spellmann, H., and Zingg, A. 2010. Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. Annals of Forest

Science 67: 712.

Prior, L., Bowman, D., and Eamus, D. 2005. Intra-specific variation in leaf attributes of four savanna tree species across a rainfall gradient in tropical Australia. Australian Journal of Botany 53: 323-335.

Rainville, A., Desponts, M., Beaudoin, R., Périnet, P., Mottet, M-J., and Perron, M. 2003. Tree Improvement in Québec: A Tool for Industrial and Environmental Productivity. Research Note. Tabled at the XII World Forestry Congress. Québec, Canada 2003.

Rathcke, B., and Lacey, E.P. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16: 179-214.

Regier, N., Streb, S., Zeeman, S.C., and Frey, B. 2010. Seasonal changes in starch and sugar content of poplar (*Populus deltoides*× *nigra* cv. Dorskamp) and the impact of stem girdling on carbohydrate allocation to roots. Tree physiology 30: 979-987.

Reich, P.B. Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., and Bowman, W. D. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80: 1955-1969.

Reich, P.B., Oleksyn, J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. PNAS 101: 11001-11006.

Richards, A.E., Forrester, D.I., Bauhus, J., and Scherer-Lorenzen, M. 2010. The influence of mixed tree plantations on the nutrition of individual species: a review. Tree Physiology 39: 1192-1208.

Riemenschneider, D.E. Isebrands, J. G., Berguson, W. E., Dickmann, D. I., Hall, R. B., Mohn, C. A., Stanosz, G.R. and Tuskan, G. A. 2001. Poplar breeding and testing strategies in the north-central US: demonstration of potential yield and consideration of future research needs. The Forestry Chronicle 77: 245-253.

Ripullone, F., Grassi, G., Lauteri, M., and Borghetti, M. 2003. Photosynthesis–nitrogen relationships: interpretation of different patterns between *Pseudotsuga menziesii* and *Populus*× *euroamericana* in a mini-stand experiment. Tree Physiology 23: 137-144.

Rivest, D., Cogliastro, A., and Olivier, A. 2009. Tree-based intercropping systems increase growth and nutrient status of hybrid poplar: A case study from two Northeastern American experiments. Journal of Environmental Management. 91: 432-440.

Robinson, D.E., Wagner, R.G., Bell, F.W., and Swanton, C.J. 2001. Photosynthesis, nitrogen-use efficiency, and water-use efficiency of jack pine seedlings in competition with four boreal forest plant species. Canadian Journal of Forest Research 31: 2014-2025.

Rohde, A., Bastien, C., and Boerjan, W., 2011. Temperature signals contribute to the timing of photoperiodic growth cessation and bud set in poplar. Tree physiology, 31: 472-482.

Rompré, M., and Carrier, D. 1997. Étude pédologique des sols défrichés de l'Abitibi-Témiscamingue. Centre de recherche et d'expérimentation en sols, ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec.

Rossi, S., Deslauriers, A.., Anfodillo, T., Morin, H., Saracino, A., Motta, R., and Borghetti, M. 2006. Conifers in cold environments synchronize maximum growth rate of tree ring formation with day length. New Phytologist 170: 301-310.

Rothe, A., and Binkley, D. 2001. Nutritional interactions in mixed species forests: a synthesis. Canadian Journal of Forest Research 31: 1855-1870.

Ruiz-Bello, A., and Cajuste, L.J. 2002. Controlling fertilizer applications through plant analysis. Communications in soil science and plant analysis 33: 2793-2802.

Sadras, V.O., and Trentacoste, E.R. 2011. Phenotypic plasticity of stem water potential correlates with crop load in horticultural trees. Tree physiology 31: 494-499.

Sage, R.F., and Kubien, D.S. 2007. The temperature response of C3 and C4 photosynthesis. Plant, Cell & Environment 30: 1086-1106.

Sakai, A., and Larcher, W., 1987. Frost survival of plants. Responses and adaptation to freezing stress. Springer-Verlag, Berlin, Germany.

Salifu, K.F., Jacobs, D.F., and Birge, Z.K.D. 2009. Nursery Nitrogen Loading Improves Field Performance of Bareroot Oak Seedlings Planted on Abandoned Mine Lands. Restoration Ecology 17: 339-349.

Saxe, H., Cannell, M.G., Johnsen, Ø., Ryan, M.G., and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. New Phytologist 149: 369-399.

Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. Annual review of ecology and systematics 17: 667-693.

Schlichting, C.D., and Smith, H. 2002. Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. Evolutionary Ecology 16: 189-211.

Schmid, B. 2002. The species richness-productivity controversy. Trends in Ecology & Evolution 17: 113-114.

Schmid, I., and Kazda, M. 2002. Root distribution of Norway spruce in monospecific and mixed stands on different soils. Forest Ecology and Management 159: 37-47.

Schwinning, S., and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113: 447-455.

Sedjo, R.A. 2001. From foraging to cropping: the transition to plantation forestry and implications for wood supply and demand.Unasylva 52: 24–32

Shafer, S.L., Bartlein, P.J., and Thompson, R.S. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems 4: 200-215.

Sharkey, T.D. 1985. O_2-insensitive photosynthesis in C3 plants. Its occurrence and a possible explanation. Plant Physiology 78: 71-75.

Simansky, V., Tobiašová, E., and Chlpík, J. 2008. Soil tillage and fertilization of Orthic Luvisol and their influence on chemical properties, soil structure stability and carbon distribution in water-stable macro-aggregates. Soil and Tillage Research 100: 125-132.

Smethurst, P., Holz, G., Moroni, M., and Baillie, C. 2004. Nitrogen management in *Eucalyptus nitens* plantations. Forest ecology and management 193: 63-80.

Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Drewes, E.C., and Schroeder, W.R. 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). Plant, Cell & Environment 32: 1821-1832.

Stanton, B.J., Neale, D.B., and Li, S. 2010. *Populus* breeding: from the classical to the genomic approach, In Genetics and genomics of *Populus*. Edited by S. Jansson , R. Bhalerao and A.T. Groover. Springer New York, NY, USA: 309–348.

Stanturf, J.A., van Oosten, C., Netzer, D.A., Coleman, M.D., and Portwood, C.J. 2001, Ecology and silviculture of poplar plantations. In Poplar culture in North America. Edited by D.I. Dickmann, J.G. Isebrands, J.E. Eckenwalder and R. Richardson. NRC Research Press, Ottawa, pp 153–206.

Steinaker, D.F., and Wilson, S.D. 2008. Phenology of fine roots and leaves in forest and grassland. Journal of Ecology 96: 1222-1229.

Stephan, A., Meyer, A.H., and Schmid, B. 2000. Plant diversity affects culturable soil bacteria in experimental grassland communities. Journal of Ecology 88: 988-998.

Sultan, S.E. 1987. Evolutionary implications of phenotypic plasticity in plants, Evolutionary Biology. Springer, pp. 127-178.

Sultan, S.E. 2000. Phenotypic plasticity for plant development, function and life history. Trends in Plant Science 5: 537-542.

Sumner, M.E. 1979. Interpretation of Foliar Analyses for Diagnostic Purposes1. Agronomy Journal 71: 343-348.

Takashima, T., Hikosaka, K. and Hirose, T., 2004. Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. Plant, Cell & Environment 27: 1047-1054.

Takei, K., Takahashi, T., Sugiyama, T., Yamaya, T., and Sakakibara, H. 2002. Multiple routes communicating nitrogen availability from roots to shoots: a signal transduction pathway mediated by cytokinin. Journal of Experimental Botany 53: 971-977.

Takenaka, A. 2000. Shoot growth responses to light microenvironment and correlative inhibition in tree seedlings under a forest canopy. Tree Physiology 20: 987-991.

Taulavuori, E., Taulavuori, K., Niinimaa, A., and Laine, K. 2010. Effect of ecotype and latitude on growth, frost hardiness, and oxidative stress of south to north transplanted Scots pine seedlings. International Journal of Forestry Research 2010: 162084.

Thomas, C.D. 2010. Climate, climate change and range boundaries. Diversity and Distributions 16: 488-495.

Tilman, D. Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a research for general principals. Ecology 80:1455–1474.

Tisdale, S.L., Nelson, W.L., and Beaton, J.D. 1985. Soil fertility and fertilizers. Collier Macmillan Publishers, New York.

Tissue, D., Thomas, R., and Strain, B. 1997. Atmospheric CO2 enrichment increases growth and photosynthesis of *Pinus taeda*: a 4 year experiment in the field. Plant, Cell & Environment 20: 1123-1134.

Toth, Z., Jolánkai, P., Hermann, T., and Kismanyoky, T. 2009. Observation of nutrient status of maize monoculture as a major stressor in long-term field experiment over 38 years. Cereal Research Communications 37:193-196.

Truax, B., Gagnon, D., Fortier, J., and Lambert, F. 2012. Yield in 8 year-old hybrid poplar plantations on abandoned farmland along climatic and soil fertility gradients. Forest Ecology and Management 267: 228-239.

Tullus, A., Tullus, H., Vares, A., and Kanal, A. 2007. Early growth of hybrid aspen (*Populus x wettsteinii* Hamet-Ahti) plantations on former agricultural lands in Estonia. Forest ecology and management 245: 118-129.

Tuskan, G.A, Difazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U.,.. and Henrissat, B. 2006. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). Science, 313: 1596-1604.

Valladeras, F., Wright, S.J., Lasso, E., Kitajima, K., and Pearcy, R.W. 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a panamian rainforest.

Ecology 81: 1925-1936.

van den Driessche, R. 1999. First-year growth response of four *Populus trichocarpa*× *Populus deltoides* clones to fertilizer placement and level. Canadian Journal of Forest Research 29: 554-562.

van den Driessche, R., Niemi, F., and Charleson, L. 2005. Fourth year response of aspen seedlings to lime, nitrogen and phosphorus applied at planting and 1 year after planting. Forest Ecology and Management 219: 216-228.

van den Driessche, R., Thomas, B., and Kamelchuk, D. 2008. Effects of N, NP, and NPKS fertilizers applied to four-year old hybrid poplar plantations. New Forests 35: 221-233.

van Dijk, A.I., and Keenan, R.J. 2007. Planted forests and water in perspective. Forest Ecology and Management 251: 1-9.

Van Kleunen, M., and Fischer, M. 2005. Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytologist 166: 49-60.

Van Miegroet, H., and Jandl, R. 2007. Are Nitrogen-Fertilized Forest Soils Sinks or Sources of Carbon? Environmental Monitoring and Assessment 128: 121-131.

Van Wijk, M.T., Williams, M., Gough, L., Hobbie, S.E., and Shaver, G.R. 2003. Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? Journal of Ecology 91: 664-676.

Vance, E.D. 2000. Agricultural site productivity: principles derived from long-term experiments and their implications for intensively managed forests. Forest Ecology and Management 138: 369-396.

Varallyay, G. 2007. Soil resilience (is soil a renewable natural resource?). Cereal Research Communications 35: 1277-1280.

Vegis, A. 1964. Dormancy in higher plants. Annual review of plant physiology 15: 185-224.

Verwijst, T. 1996. Cyclic and progressive changes in short-rotation willow coppice systems. Biomass and Bioenergy 11: 161-165.

Visser, M.E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275: 649-659.

Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., and Kremer, A. 2009. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. Canadian Journal of Forest Research 39: 1259-1269.

Von Caemmerer, S.V., and Farquhar, G.D. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153 : 376-387.

Von Fircks, Y., and Sennerby-Forsse, L. 1998. Seasonal fluctuations of starch in root and stem tissues of coppiced Salix viminalis plants grown under two nitrogen regimes. Tree Physiology 18: 243-249.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M, Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature, 416: 389-395.

Walworth, J., and Sumner, M. 1987. The diagnosis and recommendation integrated system (DRIS). Advances in soil science 6: 149-188.

Wan, X., Landhäusser, S.M., Zwiazek, J.J., and Lieffers, V.J. 1999. Root water flow and growth of aspen (*Populus tremuloides*) at low root temperatures. Tree physiology 19: 879-884.

Wang, Q.C. 2002. Spatial distribution of fine roots of larch and ash in the mixed plantation stand. Journal of Forestry Research 13: 265-268.

Wang, Z.-H., Li, S.-X., and Malhi, S. 2008. Effects of fertilization and other agronomic measures on nutritional quality of crops. Journal of the Science of Food and Agriculture 88: 7-23.

Wargo, P.M., Rakesh Minocha, P.M., Wong, B.L, Long, R.P., Horsley, S.B., and Hall, T.J. 2002. Measuring changes in stress and vitality indicators in limed sugar maple on the Allegheny Plateau in north-central Pennsylvania. Canadian Journal of Forest Research 32: 629-641.

Way, D.A., and Yamori, W. 2013. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynthesis Research: 1-12.

Weih, M. 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. Canadian Journal of Forest Research 34: 1369-1378.

Welham, C., Van Rees, K., Seely, B., and Kimmins, H. 2007. Projected long-term productivity in Saskatchewan hybrid poplar plantations: weed competition and fertilizer effects. Canadian Journal of Forest Research 37: 356-370.

Wright, I.J. Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F.,.. and Villar, R. 2004. The worldwide leaf economics spectrum. Nature 428: 821-827.

Wright, I.J., Westoby, M., and Reich, P.B. 2002. Convergence towards higher leaf mass per area in dry and nutrient - poor habitats has different consequences for leaf life span. Journal of Ecology 90: 534-543.

Wu, R., and Stettler, R. 1998. Quantitative genetics of growth and development in *Populus*. III. Phenotypic plasticity of crown structure and function. Heredity, 81: 299-310.

Wu, R., Grissom, J., McKeand, S., and O'Malley, D. 2004. Phenotypic plasticity of fine root growth increases plant productivity in pine seedlings. BMC Ecology 4: 14.

Yamori, W., Noguchi, K., Hikosaka, K., and Terashima, I. 2009. Cold-tolerant crop species have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. *Plant and Cell Physiology. 50*: 203-215.

Yamori, W., Noguchi, K., Hikosaka, K., and Terashima, I. 2010. Phenotypic plasticity in photosynthetic temperature acclimation among crop species with different cold tolerances. Plant Physiology 152: 388-399.

Zasada, J., David, A., Gilmore, D., and Landhausser, S. 2001. Ecology and silviculture of natural stands of *Populus* species. In Poplar culture in North America. Edited by D.I. Dickmann, J.G. Isebrands, J.E. Eckenwalder and R. Richardson. NRC Research Press, Ottawa. pp 119-151.

Zeugin, F., Potvin, C., Jansa, J., and Scherer-Lorenzen, M. 2010. Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation? Forest Ecology and Management 260: 1424-1433.

Zhang, S.Y., Yu, Q., Chauret, G., and Koubaa, A. 2003. Selection for both growth and wood properties in hybrid poplar clones. Forest Science 49: 901-908.

Zhang, X., Friedl, M.A., Schaaf, C.B., and Strahler, A.H. 2004. Climate controls on vegetation phenological patterns in northern mid and high latitudes inferred from MODIS data. Global Change Biology 10: 1133-1145.

Zhang, Y. Duan, B., Qiao, Y., Wang, K., Korpelainen, H., and Li, C. 2008. Leaf photosynthesis of *Betula albosinensis* seedlings as affected by elevated CO_2 and planting density. Forest Ecology and Management 255: 1937-1944.

Zhu, J., Goldstein, G., and Bartholomew, D. 1999. Gas exchange and carbon Isotope composition of *Anonas comosus* in response to elevated CO_2 and temperature. Plant Cell and Environment 22: 999-1008.