UNIVERSITÉ DU QUÉBEC À MONTRÉAL

PEUPLIER HYBRIDE EN ZONE RIVERAINE AGRICOLE : PRODUCTION DE BOIS, SÉQUESTRATION DES NUTRIMENTS ET DU CARBONE, ET EFFET SUR LA DIVERSITÉ VÉGÉTALE

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RÉSUMÉ

L'aménagement de bandes de protection riveraines par le biais de la revégétalisation est considéré comme un des moyens les plus efficaces pour la réduction de la pollution agricole diffuse. Par ailleurs, la restauration de la zone riveraine en milieu agricole a une importance particulière pour la biodiversité, car les habitats riverains abritent des espèces que l'on ne retrouve nulle part ailleurs dans les agroécosystèmes. Pour contrebalancer les coûts liés à l'implantation et à l'entretien de la bande riveraine, il est possible d'utiliser des végétaux qui créeront des biens alternatifs sur la ferme. La récolte des végétaux permet également de maintenir le potentiel d'accumulation des nutriments dans la végétation riveraine. Parmi les essences utilisées en restauration riveraine, le peuplier hybride (*Populus* spp.) est particulièrement intéressant en raison de sa forte productivité et de sa tolérance à l'inondation. Il permet donc de restaurer rapidement plusieurs attributs fonctionnels et structuraux dans l'agroécosystème (accumulation de nutriments, stabilisation du sol et des berges, couvert forestier, microclimat, etc.) tout en permettant la production de biomasse et de bois.

Cette thèse a pour objet l'étude de bandes riveraines de peuplier hybride (4,5 m de largeur et 2222 tiges ha^{-1}) âgées de six ans, comprenant cinq clones non apparentés de peuplier hybride, qui ont été plantées simultanément sur quatre sites agricole de l'Estrie (sud du Québec). Ces bandes riveraines sont toutes situées sur des petits cours d'eau de tête de faible largeur (1 à 2 m). Le premier chapitre a pour objectif d'évaluer la production de bois et de biomasse dans de tels systèmes riverains (4 sites et 5 clones). Cet aspect est un des éléments importants pour évaluer la faisabilité économique des projets de restauration riveraine. Il est donc nécessaire d'identifier les facteurs édaphiques qui influencent la productivité de ces systèmes. Le second chapitre aborde la séquestration du carbone et l'accumulation des nutriments dans la biomasse épigée des peupliers hybrides (4 sites et 5 clones). L'objectif est d'évaluer à quel point les peupliers hybrides sont des puits de carbone, d'azote et de phosphore efficaces dans la zone riveraine agricole et quels sont les facteurs (choix du site, choix des clones) qui influencent cette efficacité. Dans ce chapitre, une comparaison est également réalisée avec des bandes herbacées adjacentes aux plantations. Le troisième chapitre vise à évaluer l'effet des bandes riveraines de peuplier hybride et des différents clones sur la biomasse et la diversité végétale en sous-couvert (3 sites et 2 clones). L'objectif est d'évaluer dans quelle mesure les conditions lumineuses en sous-couvert dans les bandes ont un effet sur la biomasse végétale et sur la richesse et le recouvrement de différents groupes d'espèces. Une comparaison avec des bandes herbacées naturelles adjacentes est également réalisée. Le quatrième chapitre aborde les différences clonales qui peuvent exister au chapitre de l'assimilation de l'azote, un aspect fondamental pour l'adaptabilité des clones de peupliers hybrides à différents milieux de croissance (sol riche vs sol pauvre).

Les résultats montrent le fort potentiel des bandes riveraines de peuplier hybride pour produire du bois et de la biomasse et pour séquestrer du carbone et des nutriments (N et P) dans les parties épigées (tronc, branches et feuilles). Ce potentiel est très variable d'un site à l'autre puisque des écarts de croissance d'environ un ordre de grandeur ont été observés entre les sites, essentiellement en raison de la fertilité du sol. Un rendement en volume de 40 m^3 ha^{-1} an^{-1} a été atteint au site fertile de Bromptonville, un rendement qui n'avait jamais été obtenu auparavant au Québec. Sur ce site la séquestration du carbone, l'accumulation de l'azote et du phosphore s'élevait après 6 ans à 52 t ha^{-1} de C, 770 kg ha^{-1} de N et 82 kg ha^{-1} de P. Au site pauvre de Magog, le rendement en volume était aussi faible que 4 m^3 ha^{-1} an^{-1}, alors que la séquestration du carbone et l'accumulation de l'azote et du phosphore n'était que de 6,4 t ha^{-1} de C, 90 kg ha^{-1} de N et 10 kg ha^{-1} de P. Le principal facteur qui a influencé la croissance des peupliers et, par conséquent, leur capacité à séquestrer du carbone et des nutriments a été la disponibilité en nitrates (NO_3) dans le sol riverain. Des relations hautement significatives ($p<0{,}001$) ont été obtenues entre la disponibilité du nitrate dans le sol et le volume moyen par arbre ($R^2=0{,}58$), la biomasse moyenne (tronc+branches+feuilles) par arbre ($R^2=0{,}54$), la séquestration moyenne du carbone par arbre ($R^2=0{,}54$), l'accumulation moyenne de l'azote par arbre ($R^2=0{,}59$) et l'accumulation moyenne du phosphore par arbre ($R^2=0{,}56$). La forte disponibilité en nitrates a été observée sur les sites (Bromptonville et St-Isidore-de-Clifton) où l'on pratique un élevage plus intensif du bétail (fertilisation annuelle du pâturage, densité élevée d'animaux). Ainsi, le peuplier hybride semble être un arbre idéal pour intercepter la pollution azotée qui provient de la fertilisation agricole. Non seulement le peuplier hybride croît plus vite lorsque l'azote est plus abondant dans le sol, mais on retrouve également l'azote en plus forte concentration dans ses tissus, ce qui produit un effet synergétique sur l'accumulation totale de l'azote dans l'arbre. Cette synergie positive a également été observée pour l'accumulation du phosphore. D'ailleurs, des relations hautement significatives ($p<0{,}001$) ont été observées entre la disponibilité du nitrate dans le sol et la concentration d'azote dans les feuilles de peuplier ($R^2=0{,}47$), de même qu'entre la disponibilité du phosphore et sa concentration foliaire ($R^2=0{,}22$). Au site de Magog, la forte teneur en magnésium dans le sol, la plus faible survie, la fertilité moindre et le drainage imparfait sont tous des facteur pouvant expliquer les faibles valeurs obtenues en termes de production de bois, de séquestration du carbone et des nutriments. Les concentrations de Mg dans les feuilles, les branches et le tronc étaient d'ailleurs environ deux fois supérieures à Magog comparativement aux autres sites. Au sujet des clones, le clone 3729 (*P. nigra* x *P. maximowiczii*) et le clone 915311 (*P. maximowiczii* x *P. balsamifera*) se sont particulièrement démarqués avec une forte croissance en biomasse et en volume, de même que pour leur aptitude à séquestrer du carbone et à accumuler de l'azote et du phosphore. D'importantes différences clonales ont aussi été observées en ce qui concerne la répartition de la biomasse dans les parties épigées. Par ailleurs, lorsque l'on compare les bandes riveraines de peuplier hybrides avec des bandes herbacées qui se développent naturellement, on constate que les bénéfices des bandes riveraines de peuplier hybride en terme de séquestration de carbone et de nutriments (N et P) augmentent davantage en fonction de la fertilité du site que dans le cas des bandes herbacées.

Les bandes riveraines de peuplier hybride créent, à mesure qu'elles croissent, une ambiance forestière en termes de conditions lumineuses. Ce phénomène ne semble pas affecter négativement l'abondance et la richesse des espèces végétales indigènes et de

milieux humides en sous-couvert. D'ailleurs aucune relation significative n'a été observée entre l'ouverture de la canopée et la richesse et le recouvrement de ces deux groupes d'espèces. De plus, aucun effet Site n'a été observé pour la richesse moyenne en espèces indigènes et de milieux humides. Toutefois, à mesure que la canopée se referme, on observe une exclusion des espèces végétales introduites et de milieux mésiques. Ainsi, des relations hautement significatives ($p<0,001$) et positives ont été observées entre l'ouverture de la canopée et le nombre d'espèce introduites ($R^2=0,46$) et de milieux mésiques ($R^2=0,43$), de même qu'entre l'ouverture de la canopée et le recouvrement des espèces introduites ($R^2=0,51$) et de milieux mésiques ($R^2=0,65$). Parallèlement, un effet Site significatif a été observé pour la richesse totale moyenne, la richesse moyenne en espèces introduites et en espèces de milieux mésiques. Ces richesses en espèces étaient plus élevées à Magog où l'ouverture de la canopée est plus importante. À l'échelle de chaque site, la fermeture de la canopée est également significativement ($p<0,001$) et fortement reliée à une diminution de la biomasse végétale en sous-couvert (Bromptonville, $R^2=0,81$; St-Isidore-de-Clifton, $R^2=0,64$; Magog, $R^2=0,51$). Un important effet Clone a également été observé en matière d'ouverture de la canopée et de biomasse végétale en sous-couvert, avec le clone 915311 qui présentait les valeurs les plus faibles comparativement au clone 3570 (*P. deltoides* x *P. nigra*). Sur la plupart des sites, le clone 915311 a réduit également le recouvrement de tous des groupes d'espèces par rapport au clone 3570. Par ailleurs, d'importantes différences en termes de biomasse végétale en sous-couvert sont observées entre les bandes riveraines de peuplier hybride et les bandes herbacées. Ces dernières ont davantage de biomasse végétale au sol, principalement en raison de leur fort ensoleillement. La richesse moyenne totale en espèces n'était toutefois pas différente entre les deux types de bandes riveraines.

Il existe enfin d'importantes différences d'activité de la nitrate réductase dans les feuilles des cinq clones de peuplier hybrides non apparentés. Le clone 3570, dont les deux espèces parentales appartiennent à la section des *Aigeiros*, se démarque des autres clones, car son activité nitrate réductase était beaucoup plus élevée sur le site riche en nitrate (Bromptonville) que sur le site pauvre en nitrate (Magog). Peu de différences d'activité de la nitrate réductase ont été observées d'un site à l'autre pour les autres clones, tous apparentés à la section *Tacamahaca*. Ces différences sont probablement liées à l'assemblage génétique des différents clones et suggèrent que les clones ont probablement des préférences différentes pour les formes d'azote dans le sol.

Mots-clés : bandes riveraines, peuplier hybride, séquestration du carbone, accumulation de phosphore et d'azote, biomasse, diversité végétale

INTRODUCTION

I.1 Agriculture intensive, déforestation et pollution diffuse

Au Québec comme ailleurs dans le monde, les activité agricoles se sont intensifiées au cours des 50 à 60 dernières années sur les parties productives du territoire (Pan *et al.*, 1999; Millennium Ecosystem Assessment, 2005; CAAAQ, 2007). L'agriculture intensive a fortement contribué à homogénéiser et modifier la nature physique du territoire (drainage des milieux humides et des terres (fossés et drainage souterrain), redressement des cours d'eau, déforestation, travail du sol, etc.). Par exemple, on estime que les travaux de drainage dans le sud du Québec on permis de doubler la densité du réseau hydrographique par rapport au réseau naturel (Beaulieu, 2001). Dans la vallée du Saint-Laurent où l'agriculture intensive est fortement concentrée, tout comme le développement urbain, on compte huit municipalités régionales de comté (MRC) dont le couvert forestier est inférieur à 20 % (Bélanger et Grenier, 2002). Soulignons qu'en bas de 30 % de couvert forestier, les risques de perte de biodiversité par l'effet de la fragmentation de l'habitat sont éminents (Andrén, 1994). Par ailleurs, pour maintenir une productivité élevée, les systèmes agricoles intensifs nécessitent des apports substantiels de fertilisants, d'amendements et de pesticides. Dans certains cas, on applique au champ des fertilisants même lorsque cela n'est pas nécessaire. Le déséquilibre qui existe entre la totalité des superficies en culture et la taille des élevages porcins et avicoles dans certains bassins versants du sud du Québec fait en sorte qu'on applique année après année des surplus de lisier sur des sols déjà sur-fertilisés, particulièrement en phosphore (CAAAQ, 2007). Sous la force d'entraînement des eaux (fonte des neiges, averses, écoulement souterrain, drainage agricole, etc.), ces intrants, et aussi des particules de sol, provenant de l'ensemble du territoire agricole rejoignent le réseau hydrographique (Carpenter *et al.*, 1998). Ce phénomène est appelé la pollution agricole diffuse.

L'impact combiné des modifications de la nature physique du territoire et de l'application de grandes quantités d'intrants dans une stricte logique productiviste a conduit à un importante dégradation des habitats aquatiques et de la qualité de l'eau, de même qu'à une perte et à une fragmentation des habitats forestiers, avec de nombreuses répercussions négatives sur la biodiversité (Saunders *et al.*, 1991; Sharpley et Withers, 1994; McLaughlin et Mineau, 1995; Carpenter *et al.*, 1998; Bélanger et Grenier, 2002; Di et Cameron, 2002; Sweeney *et al.*, 2004). Il faut souligner que la dégradation de la qualité de l'eau n'affecte pas uniquement la biodiversité aquatique, elle a également des répercussions socioéconomiques (diminution de la potabilité de l'eau, maladies liées à l'exposition aux pesticides et aux nitrates, pertes d'usages récréo-touristiques, dévaluation des propriétés, etc.) (Choe *et al.*, 1996; Cantor, 1997; Leggett et Bockstael, 2000). Parallèlement, le secteur agricole est un grand émetteur de gaz à effet de serre à l'échelle mondiale. Il est estimé que 10 à 12 % des émissions anthropogéniques de carbone sont imputables à ce secteur (Smith *et al.*, 2007). Bref, l'agriculture a des répercussions à différentes échelles (blooms de cyanobactéries dans les cours d'eau québécois vs. réchauffement climatique mondial), sur plusieurs types de milieux naturels (forêts, milieux humides, cours d'eau), mais également sur la qualité de vie des gens. Ces répercussions vont probablement s'accentuer au cours des années à venir, car pour nourrir et approvisionner en matériaux de toutes sortes une population humaine croissante, il faudra intensifier davantage l'agriculture et/ou accroître les superficies cultivées.

Plusieurs solutions ont été mises de l'avant pour atténuer les impacts environnementaux de l'agriculture. D'une part, on retrouve les solutions qui touchent directement la régie des cultures et des élevages (ex : culture sur résidus ou semis direct, lutte antiparasitaire intégrée, alimentation pauvre en phosphore pour le bétail, etc.) (Swanton et Weise, 1991; Karlen *et al.*, 1994; Jongbloed et Lenis, 1998; Paustian *et al.*, 2000). D'autre part, il y a les solutions qui concernent l'aménagement du territoire et des paysages agricoles (aménagement de la zone riveraine, haies brise-vent, cultures intercalaires, sylvopâturages, avaloirs, marais filtrants, afforestation, corridor de conservation, etc.) (Kort et Turnock, 1998; Shutes, 2001; Oelbermann *et al.*, 2004; Peichl *et al.*, 2006; Rivest et Olivier, 2007; Bentrup, 2008).

I.2 L'aménagement de la zone riveraine en milieu agricole

L'aménagement de la zone riveraine est une pratique courante en milieu agricole, car on lui attribue plusieurs bénéfices agro-environnementaux: réduction de la pollution diffuse, stabilisation des berges, création d'un microclimat, pollinisation et lutte biologique, etc. (Osborne et Kovacic, 1993; Lowrance *et al.*, 1997; Boutin *et al.*, 2003; Décamps *et al.*, 2004; Jobin *et al.*, 2004; Sweeney *et al.*, 2004; Altieri *et al.*, 2005).

Les nombreuses fonctions écologiques et biogéochimiques associées aux écosystèmes riverains naturels ne sont pas le fruit du hasard. Elles sont intiment liées a leur emplacement particulier dans le paysage; à l'interface des milieux terrestres et aquatiques (Lowrance *et al.*, 1984; Peterjohn et Correll, 1984; Décamps *et al.*, 2004). Puisqu'ils relient les eaux souterraines aux eaux de surface et qu'ils sont fréquemment perturbés par l'inondation et les fortes crues, ces écosystèmes semi terrestres ont une dynamique complexe qui leur est propre (Naiman *et al.*, 2005; Vidon *et al.*, 2010) (figure I.1). Les écosystèmes riverains ont un rôle paradoxal à jouer puisqu'ils agissent autant comme une barrière que comme un conduit pour la matière, et donc pour les polluants (Burt, 2005). Ils ont ainsi une influence disproportionnée sur le mouvement et la rétention de l'eau, des particules de sol, des nutriments et des intrants agricoles, par rapport à la faible superficie qu'ils occupent dans le paysage (Gregory *et al.*, 1991). Par conséquent, on reconnaît aujourd'hui les écosystèmes riverains comme des éléments clés pour la biodiversité et des « hot spots » biogéochimiques au sein des paysages et des bassins versants (McClain *et al.*, 2003; Naiman *et al.*, 2005). Par exemple, un sol riverain devient un point chaud pour la dénitrification alors qu'il est saturé d'eau et anoxique, et que les eaux de la nappe phréatique, chargées de nitrate (NO_3) et d'ammonium (NH_4), entrent en contact avec une rhizosphère riche en carbone organique (Lowrance *et al.*, 1997). En contrepartie, un sol riverain riche en phosphore, lié aux sédiments, qui devient inondé et anoxique peut également devenir un point chaud pour le transport du P vers le cours d'eau, particulièrement si le mouvement de la nappe phréatique est important (Väänänen *et al.*, 2006; Vidon *et al.*, 2010).

En reconnaissant le rôle particulier des écosystèmes riverains dans le paysage, cela nous porte à revoir nos modes d'aménagement riverain en milieu agricole afin de créer des points chauds pour l'enlèvement des polluants (Vidon *et al.*, 2010). Par ailleurs, la restauration de la zone riveraine en milieu agricole a une importance particulière pour la biodiversité, car les habitats riverains abritent des espèces que l'on ne retrouve nulle part ailleurs dans les agroécosystèmes (Knopf *et al.*, 1988; Boutin *et al.*, 2003; Jobin *et al.*, 2004).

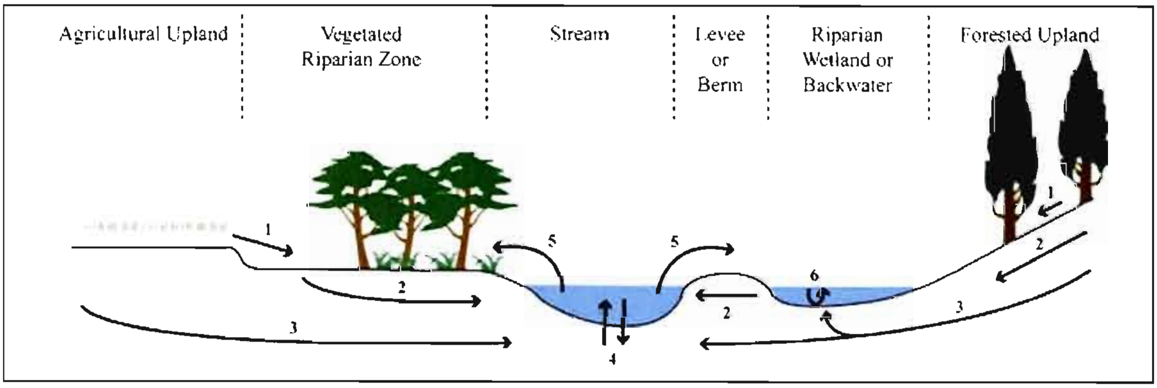

Figure I.1 Schématisation de la dynamique hydrologique complexe qui existe à l'interface entre les milieux terrestres et aquatiques dans les paysages agricoles et forestiers (Vidon *et al.*, 2010). Les flux hydriques dominant sont indiqués: (1) ruissellement de surface; (2) mouvement des eaux de la nappe phréatique; (3) mouvement des aquifères; (4) échanges hydriques entre la zone hyporhéique et le cours d'eau; (5) inondation; (6) mélange des eaux.

L'aménagement de bandes de protection riveraines par le biais de la revégétalisation est considéré comme un des moyens les plus efficaces pour créer des points chauds visant la réduction de la pollution agricole diffuse (Lowrance, 1998; Vidon *et al.*, 2010). L'implantation de végétaux à l'interface de la terre et de l'eau favorise : (1) l'accumulation du P et de l'azote (N) dans la biomasse; (2) le dépôt des sédiments contenus dans les eaux de ruissellement; (3) la stabilisation du sol et des berges; (4) la création d'un environnement propice à la dénitrification et à la dégradation des pesticides; (5) l'infiltration des eaux chargées en polluants dans le sol riverain (Lowrance *et al.*, 1997).

Toutefois, un aménagement précis en terme de largeur de la bande riveraine (en fonction du type d'agriculture et de sol, de la superficie cultivée, de la topographie, du régime des précipitations, etc.) et de choix des végétaux doit être réalisé pour maximiser certaines de ces fonctions et faire en sorte que l'on crée véritablement des points chauds pour l'enlèvement des polluants (Lowrance *et al.*, 1997; Schultz *et al.*, 2004; Dosskey *et al.*, 2008). Les dimensions et la composition en espèces végétales de la bande riveraine auront également une influence importante sur son efficacité si l'on cherche à aménager des corridors riverains dans une perspective de conservation de la biodiversité en milieu agricole (Forman et Baudry, 1984; Boutin *et al.*, 2003; Jobin *et al.*, 2004; Bentrup, 2008).

L'emplacement de la bande riveraine dans le bassin versant a également un effet important sur les fonctions qu'elle pourra remplir. Par exemple, il serait utopique de vouloir protéger la qualité de l'eau de nos lacs et rivières en revégétalisant seulement les berges de ceux-ci. Il faut donc prioriser l'aménagement des cours d'eau situé à la tête des bassins versants (fossés de drainage, petits cours d'eau de tête intermittents et permanents) pour avoir un impact réel sur la qualité de l'eau (Parkyn *et al.*, 2005; Wigington *et al.*, 2005).

En Amérique du Nord, les petits cours d'eau de tête peuvent constituer jusqu'à 85% de la longueur totale du système hydrographique et ils exercent une influence extrêmement importante en matière de rétention et de dénitrification de l'azote (Peterson *et al.*, 2001). Une autre étude réalisée dans cinq bassins versants agricoles de l'Oregon (États-Unis) a montré que la densité du réseau hydrographique durant l'hiver était près de 100 fois supérieure à la densité observée durant l'été (Wigington *et al.*, 2005) (figure 1.2). Cela laisse présager une grande expansion du réseau hydrographique lors d'épisodes de pluies extrêmes et, par conséquent, un transport important des polluants agricoles là où il n'y a souvent aucune bande riveraine (Wigington *et al.*, 2005).

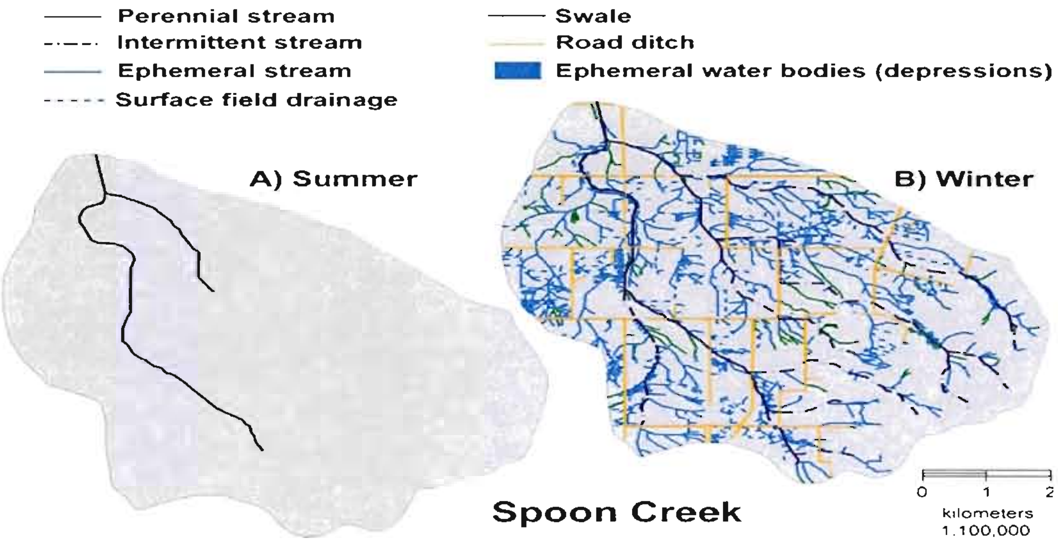

Figure I.2 Réseau hydrographique dans le bassin versant agricole du Spoon Creek en Oregon à l'été 1997 et à l'hiver 1998-99 (Wigington *et al.*, 2005).

Dans bien des cas, ces petits cours d'eau, de même que les fossés de drainage, ne jouissent pas d'une protection adéquate tant sur le terrain que dans la législation (figure I.3). Au Québec, la *Politique de protection des rives du littoral et des plaines inondables* (qui n'a toutefois aucune force de loi) recommande de maintenir ou d'aménager une bande riveraine sur une largeur de 10 à 15 m. En l'absence d'une réglementation municipale en matière d'aménagement riverain, la législation provinciale interdit les activités agricoles (travail du sol et épandage de fertilisant) sur 3 m de largeur en bordure des cours d'eau (Gouvernement du Québec, 2007). Cependant, pour les sections de cours d'eau dont la surface d'écoulement (largeur du cours d'eau x profondeur) est inférieure à 2 m^2, aucune règlementation ne restreint l'application de fertilisant dans la zone riveraine. Il est important de noter que dans le cas particulier des fossés de drainage qui n'existent qu'en raison d'une intervention humaine, la MRC n'est en aucun cas l'autorité compétente en matière de législation. Ainsi, la réglementation provinciale interdit l'épandage de fertilisant sur seulement une largeur de 1 m en bordure des fossés de drainage agricole. Par ailleurs, aucune interdiction ne limite le travail du sol en bordure de ce type de fossé. On estime que la longueur totale de ces fossés de drainage agricole, créés de toutes pièces, c'est-à-dire, les fossés verbalisés, s'élève à environ 10 000 km au Québec (Beaulieu, 2001). Soulignons enfin qu'en milieu agricole aucun règlement provincial en vigueur n'oblige l'aménagement d'une zone de protection riveraine, que ce soit en bordure des cours d'eau ou des fossés verbalisés.

Figure I.3 Exemples du manque d'aménagement riverain en bordure des petits cours d'eau et des fossés de drainage. En haut, absence de bande riveraine et de clôture sur deux cours d'eau de tête dans des pâturages de l'Estrie. En bas, bande riveraine de faible largeur en bordure des fossés qui drainent les cultures annuelles en Montérégie et en Estrie.

I.3 Le choix des végétaux en aménagement riverain

Ce ne sont pas tous les types de végétaux qui ont la même capacité pour restaurer les attributs structuraux et fonctionnels dans la zone riveraine (Osborne et Kovacic, 1993; Wenger, 1999; Lyons *et al.*, 2000). On considère que la végétation herbacée est généralement plus efficace que la végétation ligneuse pour stabiliser le sol en surface et intercepter les eaux de ruissellement et les sédiments provenant des superficies en culture (Wenger, 1999; Lyons *et al.*, 2000). Afin d'éviter que la végétation soit facilement rabattue au sol lors d'une crue ou d'un événement de fort ruissellement (cela réduit considérablement son efficacité), il faut choisir des espèces à tiges rigides formant un couvert dense (Dillaha *et al.*, 1988; Lee *et al.*, 1998). Le panic érigé (*Panicum virgatum* L.) est un exemple de plante herbacée qui peut être utilisée à cette fin (Schultz *et al.*, 2004; Kelly *et al.*, 2007).

Parallèlement, la végétation ligneuse est généralement plus appropriée pour (1) stabiliser le sol et les berges en profondeur, (2) accumuler à long terme une grande quantité de nutriments dans la biomasse, (3) créer un environnement favorable à la dénitrification dans le sol, (4) assimiler les nutriments qui circulent dans les eaux de la nappe phréatique, (5) ralentir la force du courant lors des inondations, (6) créer de l'ombrage sur le cours d'eau, (7) créer un couvert forestier et (8) fournir des débris ligneux et des feuilles qui sont essentiels à de nombreuses fonctions en milieu aquatique (habitats, source de nourriture, dénitrification à l'intérieur du cours d'eau, etc.) (Cooke et White, 1987; Haycock et Pinay, 1993; Abbe et Montgomery, 1996; Canadell *et al.*, 1996; Wallace *et al.*, 1997; Watson *et al.*, 1997; Burckhardt et Todd, 1998; Tufekcioglu *et al.*, 2003; Wynn *et al.*, 2004; Kelly *et al.*, 2007).

I.4 La récolte des végétaux en milieu riverain agricole

Bien que les dimensions et le choix des végétaux aient une influence importante sur la structure et les fonctions de la bande riveraine, d'autres interventions sont nécessaires pour favoriser certaines de ces fonctions, notamment l'accumulation des nutriments (N et P) dans la biomasse végétale. Parce que tout type de végétation atteint plus ou moins rapidement un stade d'équilibre sur le plan de la croissance, une approche d'aménagement riverain qui n'inclut pas la récolte des végétaux compromettra éventuellement le potentiel de captage et d'accumulation des nutriments par la bande riveraine (Lowrance *et al.*, 1997; Dosskey, 2001; Schultz *et al.*, 2004; Dorioz *et al.*, 2006; Kelly *et al.*, 2007). Il faut souligner que contrairement à l'N qui peut être dénitrifié par les bactéries du sol, le P demeure dans la bande riveraine à moins qu'il ne soit exporté en dehors du système par la récolte ou lessivé dans le cours d'eau. D'ailleurs, plus le sol riverain est saturé en P, plus les risques de perte de ce nutriment dans le cours d'eau augmentent lors d'une inondation ou d'un événement de fort ruissellement (McDowell *et al.*, 2001; Dorioz *et al.*, 2006; Väänänen *et al.*, 2006; Stutter *et al.*, 2009).

Tel que décrit par Vitousek et Reiners (1975), les nutriments sont retenus dans un écosystème lorsque les pools d'accumulation des nutriments croissent dans le sol et dans la biomasse. Toutefois, lorsque la croissance annuelle ralentit pour éventuellement devenir nulle, les pools d'accumulation des nutriments atteignent un état d'équilibre. La quantité de nutriments qui entrent alors dans le système est similaire à la quantité qui en ressort, quoique certains nutriments comme l'azote puissent être immobilisés davantage en raison de l'accumulation du C organique (Homyak *et al.*, 2008). Par conséquent, une bande riveraine dont la végétation atteint cet état d'équilibre sera probablement moins efficace pour prévenir les pertes de nutriments dans le cours d'eau. De plus, si la végétation n'est pas récoltée, les nutriments accumulés dans la biomasse seront libérés à mesure que la végétation meurt et se décompose (Bedard-Haughn *et al.*, 2005; Dorioz *et al.*, 2006). Pour ces raisons, une récolte périodique des végétaux est recommandée pour maintenir un potentiel élevé de captage et d'accumulation des nutriments dans la bande riveraine (Dosskey, 2001).

I.5 Aspects économiques de la récolte des végétaux en bande riveraine

Bien que la revégétalisation de la zone riveraine soit un moyen efficace pour contrer la pollution agricole diffuse et créer des habitats naturels ou semi-naturels, il n'en demeure pas moins que cette pratique est relativement coûteuse (achat des végétaux, préparation de terrain, pose de clôture dans les pâturages, mise en terre des végétaux, répression de la compétition végétale, protection contre le cerf ou le castor, etc.) (Sweeney et Czapka, 2004).

Il faut également garder à l'esprit que l'aménagement de la zone riveraine se fait généralement au détriment de la superficie cultivée, ce qui engendre des pertes économiques pour l'agriculteur. Au Québec, il est possible d'obtenir du financement par le biais du programme Prime-Vert pour aménager une bande riveraine dans une perspective de réduction de la pollution diffuse, mais seulement à l'intérieur des bassins versants ciblés (Gouvernement du Québec, 2009).

Pour contrebalancer les coûts liés à l'implantation et à l'entretien de la bande riveraine, il est toutefois possible d'utiliser des végétaux qui créeront des biens alternatifs sur la ferme (Rockwood *et al.*, 2004; Licht et Isebrands, 2005). La production de biens alternatifs (biomasse, bois, fourrage, petits fruits, plantes ornementales, etc.) dans la zone riveraine est d'ailleurs un moyen pour diversifier l'économie régionale et augmenter la résilience économique des fermes face aux fluctuations des marchés (Valdivia *et al.*, 1996; Josiah *et al.*, 2004; Rockwood *et al.*, 2004). Bref, la récolte des végétaux en zone riveraine génère à la fois des bénéfices environnementaux et économiques.

I.6 Le peuplier hybride dans les systèmes agroforestiers riverains

Les espèces ligneuses de la famille des Salicacées (famille du saule) sont largement utilisées pour revégétaliser la zone riveraine, notamment en raison de leur grande tolérance à l'inondation (Licht, 1992; Schultz *et al.*, 1995; Watson *et al.*, 1997; Kuzovkina et Quigley, 2005; Farrar, 2006; Kelly *et al.*, 2007). Parmi celles-ci, le peuplier hybride (*Populus* spp.) est particulièrement intéressant en raison de sa forte croissance, qui peut atteindre 45 m^3 ha^{-1} an^{-1} et 30 t ha^{-1} an^{-1} (Heilman *et al.*, 1994; Riemenschneider *et al.*, 2001). Sa croissance rapide et ses exigences nutritionnelles élevées (Heilman et Stettler, 1986) font en sorte que le peuplier hybride devient en quelques années un puit très important pour l'azote et le phosphore dans la bande riveraine.

Dans le sol, le peuplier hybride peut déployer son réseau racinaire à plus de 3 m de profondeur après seulement 4 ans (Heilman *et al.*, 1994). Cela permet une stabilisation accrue du sol et des berges, de même qu'un puisage en profondeur des nutriments contenus dans le sol et la nappe phréatique. Par ailleurs, en comparaison avec d'autres espèces ligneuses, le système racinaire des peupliers contient une forte proportion de racines fines (Heilman *et al.*, 1994). Une biomasse de racines fines semblables a également été observée lorsque qu'une bande riveraine contenant des plantes fourragères a été comparée à une bande riveraine de peuplier hybride (Tufekcioglu *et al.*, 1999). Puisqu'elles ont un taux de renouvellement élevé, les racines fines contribuent à enrichir le sol en matière organique et en carbone (Block *et al.*, 2006). Ces apports de C organique dans le sol riverain constituent une source d'énergie essentielle aux bactéries qui réalisent la dénitrification (Hill *et al.*, 2000; Blazejewski *et al.*, 2005). Le C organique permet également la création de macro-agrégats dans le sol. Ces derniers améliorent l'infiltration de l'eau et augmentent l'activité biologique du sol, ce qui favorise la rétention et la dégradation de certains polluants (Lowrance *et al.*, 2002). Parallèlement, les peupliers hybrides ont la capacité de développer des racines adventives qui peuvent puiser l'azote et le phosphore directement dans le cours d'eau (Krasny *et al.*, 1988).

La croissance rapide du peuplier hybride en fait également un puits de carbone intéressant lorsqu'il est utilisé dans un contexte d'afforestation et d'agroforesterie (Kort et Turnock, 1998; Oelbermann *et al.*, 2004; Updegraff *et al.*, 2004; Peichl *et al.*, 2006). Enfin, cet arbre produit rapidement une grande quantité de litière, source de matière organique pour le sol, mais également pour la chaîne trophique aquatique. Ces apports allochtones peuvent représenter jusqu'à 95% des apports totaux dans les cours d'eau de tête de l'est de l'Amérique du Nord, ils permettent donc de restaurer ou de maintenir les liens trophiques dans le cours d'eau (Webster *et al.*, 1995; Wallace *et al.*, 1997).

Sur le plan économique, le peuplier hybride offre de multiples possibilités du fait qu'on peut le cultiver en très courte rotations (3 à 4 ans) avec des densité très élevées (10 000 à 20 000 tiges ha^{-1}) ou en plus longues rotation (8 à 30 ans) avec des densité de moyennes à faibles (156-2500 tiges ha^{-1}) (Boysen et Strobl, 1991; Stanturf *et al.*, 2001; Labrecque et Teodorescu, 2005). On cultive principalement le peuplier hybride pour la biomasse énergétique, les pâtes et papiers, les panneaux de composites, le contre-plaqué, les bois d'ingénierie, le bois de sciage et de déroulage, les allumettes et les baguettes (Balatinecz *et al.*, 2001). Sur le plan agronomique, le bois raméal de peuplier est également intéressant pour la fertilisation des terres et l'alimentation du bétail (McWilliam *et al.*, 2004; Singh et Sharma, 2007).

Par contre, sur le plan sociopolitique, le peuplier ne fait pas toujours l'unanimité en milieu agricole. Par exemple, une certaine partie de la population française a une perception négative des peupleraies alluviales du fait qu'elles referment des paysages agricoles jadis ouverts ou qu'elles constituent une menace pour l'avenir agricole du territoire (Le Floch et Terrasson, 1999; Le Floch *et al.*, 2005). Rappelons aussi que les premiers agriculteurs ont travaillé très fort pour défricher leurs terres, alors le reboisement peut représenter un énorme paradoxe; comme si on laissait la terre revenir à ce qu'elle était avant la colonisation (Neumann *et al.*, 2007).

Au Québec, la populiculture n'est d'ailleurs pas encore reconnue comme une culture agricole, contrairement à ce que l'on observe dans certaines provinces canadiennes, en France ou aux États-Unis. Cela constitue un obstacle majeur à l'utilisation de cette essence en milieu agricole du fait que les travaux sylvicoles sont non subventionnés si le projet de reboisement n'est pas autorisé par le MAPAQ et l'UPA (Marchand et Masse, 2007). Par exemple, sur les terres agricoles de la région de Lanaudière (incluant les friches), il sera probablement impossible d'avoir du financement pour réaliser des plantations mono spécifique de peuplier hybride à compter de 2010 (P. Moreau, communication personnelle, 2009). Bref, l'acceptabilité sociale du peuplier hybride en milieu agricole québécois semble à l'heure actuelle relativement faible, du moins dans les régions où l'agriculture occupe une place importante. Nos rencontres avec certains intervenants du Ministère du Développement Durable de l'Environnement et des Parcs (MDDEP), nous ont également permis de constater une forte désapprobation quant à l'utilisation de cette essence en milieu riverain agricole. Cette situation pourrait jouer en défaveur des projets de restauration avec le peuplier hybride, car les projets d'aménagement riverain admissibles au programme Prime-Vert doivent obtenir l'aval du MDDEP (Gouvernement du Québec, 2009).

Par ailleurs, l'aménagement de plantation avec des espèces « exotiques » comme le peuplier hybride (même si souvent les 2 parents ou 1 des 2 sont indigènes) n'est pas toujours bien perçu tant du côté des groupes environnementaux que de la part de certains écologistes.

On reproche aux bandes riveraines constituées de peupliers hybrides d'être moins diversifiées par rapport à la forêt naturelle (Potton, 1994; Stephens et Wagner, 2007). On craint également que le peuplier hybride soit une menace pour l'intégrité génétique des populations de peupliers indigènes (Broeck *et al.*, 2005). Néanmoins, dans un contexte d'afforestation, les plantations de peupliers hybrides peuvent contribuer à augmenter la diversité des paysages dominés par l'agriculture (Weih *et al.*, 2003). Elles peuvent également être utilisées comme un outil de restauration, car elles permettent de redémarrer la succession forestière (Laquerbe, 1999; Lust *et al.*, 2001; Gardiner *et al.*, 2004; Boesch *et al.*, 2007).

I.7 Objectifs et hypothèses de la thèse

Actuellement, au Québec, il existe très peu d'études qui se sont intéressées aux bandes riveraines de peuplier hybride. La seule étude qui existe dans le domaine arrive à la conclusion que l'inclusion de peupliers hybrides âgés de deux ans n'améliore pas l'efficacité de filtration d'une bande où une couverture herbacées avait été établie (Duchemin et Hogue, 2009). Cela n'a rien de surprenant compte tenu de la faible taille des peupliers à cet âge. Parallèlement, les connaissances sur le potentiel du peuplier hybride à produire du bois et de la biomasse dans le milieu agricole cultivé sont très limitées à ce jour, car la majorité des études sont réalisées en milieu forestier, dans des friches agricoles ou dans des systèmes de culture intercalaire à très faible densité (Coll *et al.*, 2007; Lteif *et al.*, 2007; Rivest *et al.*, 2009). Jusqu'à présent, aucune étude québécoise n'a mesuré la croissance du peuplier sur plusieurs sites aménagés simultanément. Par conséquent, on en connaît bien peu sur la croissance des différents clones recommandés pour le sud du Québec.

Dans le domaine de la restauration riveraine en général, au niveau mondial, on connaît également peu sur le potentiel régional des différents clones de peuplier hybride à produire de la biomasse, à séquestrer du C et des nutriments. Les études qui ont évalué certains de ces aspects ont été réalisées sur un site unique et avec un seul clone de peuplier (Haycock et Pinay, 1993; O'Neill et Gordon, 1994; Tufekcioglu *et al.*, 2003; Kelly *et al.*, 2007).

De plus, aucune étude québécoise ne s'est intéressée aux effets des plantations de peuplier hybride sur la diversité végétale en sous-couvert. On connaît par contre l'importance des différents types d'habitats riverains naturels et semi-naturels (bandes boisées, arbustives et herbacées) pour la conservation de la biodiversité en milieu agricole (Boutin *et al.*, 2003; Jobin *et al.*, 2004).

Dans ce contexte, l'étude de bandes riveraines de peuplier hybride (4,5 m de largeur et 2222 tiges ha^{-1}) âgées de six ans, comprenant cinq clones non apparentés, qui ont été plantées simultanément sur quatre sites agricole du sud du Québec est d'un grand intérêt, et ce, tant pour la recherche en restauration riveraine que pour la recherche sur le peuplier hybride. Ces bandes riveraines sont toutes situées sur des petits cours d'eau de tête de faible largeur (1 à 2 m). Trois de ces bandes sont en marge de pâturages dans les municipalités de Bromptonville, Magog et St-Isidore-de-Clifton, et une autre est située dans une culture fourragère à Roxton Falls. Ces sites sont tous situés dans la région de l'Estrie.

Le premier chapitre de cette thèse a pour objectif d'évaluer la production de bois et de biomasse dans de tels systèmes riverains (4 sites et 5 clones). Comme nous l'avons mentionné, la production de biens alternatifs dans la bande riveraine est un moyen de rentabiliser les investissements liés à la restauration de la zone riveraine. Cet aspect est possiblement essentiel à la faisabilité économique des projets de restauration riveraine, particulièrement dans les bassins versants qui ne sont pas jugés prioritaires sur le plan de la lutte à la pollution diffuse (donc exclus du programme Prime-Vert). Il est donc nécessaire d'évaluer la capacité des systèmes agroforestiers riverains à produire des biens, comme le bois et la biomasse, tout en identifiant les facteurs édaphiques qui influencent la productivité de ces systèmes. Il existe également un intérêt grandissant au Québec pour la production de biomasse énergétique en général, que ce soit en forêt naturelle ou en plantation (Labrecque et Teodorescu, 2005; Samson *et al.*, 2005; Gouvernement du Québec, 2008).

Le second chapitre aborde la séquestration du C et l'accumulation des nutriments dans la biomasse épigée des peupliers hybrides (4 sites et 5 clones). L'objectif est d'évaluer à quel point les peupliers hybrides sont des puits de C, d'N et de P efficaces dans la zone riveraine agricole et quels sont les facteurs (choix du site, choix des clones) qui influencent cette efficacité. La capacité de séquestration de C et d'accumulation des nutriments est également comparée, à l'échelle du site, entre les bandes riveraines de peuplier et des bandes riveraines naturelles essentiellement composées de végétation herbacée. Cette comparaison a pour objectif de montrer si la revégétalisation de la zone riveraine avec le peuplier hybride favorise la séquestration des nutriments et du C, par rapport à une stratégie plus conventionnelle où on laisse la végétation recoloniser d'elle-même la zone riveraine. Ce chapitre a donc un intérêt particulier dans un contexte où l'on cherche des solutions pour réduire la pollution agricole diffuse et les émissions de C du secteur agricole (CAAAQ, 2007; Gouvernement du Québec, 2009).

Le troisième chapitre vise à évaluer l'effet des bandes riveraines de peuplier hybride et des différents clones sur la biomasse et la diversité végétale en sous-couvert (3 sites et 2 clones). Dans ce chapitre, nous évaluons dans quelle mesure les conditions lumineuses en sous-couvert dans les bandes ont un effet sur la biomasse végétale et sur la richesse et l'abondance de différents groupes d'espèces (espèces indigènes, introduites, de milieux humide, de milieu mésique, et espèces de mauvaises herbes). Nous comparons également, à l'échelle du site, la biomasse et la diversité végétale sous les peupliers et dans les bandes herbacées naturelles adjacentes. Cette comparaison met en évidence quels seraient les effets réels sur la diversité végétale en sous-couvert d'implanter des bandes riveraines de peuplier hybrides, plutôt que de laisser la zone riveraine se faire coloniser naturellement par la végétation.

Finalement, le quatrième chapitre aborde les différences clonales qui peuvent exister chez le peuplier hybride au chapitre de l'assimilation de l'azote, un aspect fondamental pour l'adaptabilité des différents clones de peupliers hybrides à différents milieux de croissance. L'objectif est d'évaluer et de comparer l'assimilation de l'azote de cinq clones de peuplier hybride, en termes d'activité de la nitrate réductase, dans deux environnements riverains agricoles différents sur le plan édaphique (un sol riche et un sol pauvre).

L'objectif général de cette thèse est donc d'évaluer dans quelle mesure le peuplier hybride est un outil de restauration riveraine intéressant, pour le sud du Québec et ailleurs en région tempérée, dans une perspective de production de bois et de biomasse, de création de « points chauds » pour l'enlèvement des polluants agricoles, de réduction des émissions de C du secteur agricole, ainsi que de conservation de la biodiversité dans les paysages ruraux.

Voici les hypothèses de départ sur lesquelles s'appuie cette thèse:

(1) Puisque les peupliers hybrides répondent fortement à la richesse édaphique (Stanturf *et al.*, 2001), leur croissance en volume et en biomasse augmentera avec la fertilité du site, et leur capacité de séquestration (C, N et P) augmentera de manière linéaire avec la croissance en biomasse des arbres. Cette hypothèse sera testée dans les chapitres 1 et 2 de la thèse.

(2) Les hybrides DxN, NxM et TxD ont une forte productivité sur les sites riches en milieu tempéré (Heilman *et al.*, 1994; Stanturf *et al.*, 2001), ils seront donc plus productifs que les hybrides MxB et DNxM, développés pour les conditions de cultures au Québec, en termes de climat de sol. Cette hypothèse sera testée dans le chapitre 1 de la thèse

(3) La fermeture du couvert arborescent affectera négativement l'abondance des plantes introduites, sans affecter négativement l'abondance des plantes indigènes puisque celles-ci sont généralement plus tolérantes à l'ombre (Humbert *et al.*, 2007). Cette hypothèse sera testée dans le chapitre 3 de la thèse

(4) Par rapport à une bande riveraine herbacée, la création rapide d'une structure arborescente en zone agricole génèrera plus de services écosystémiques (biens, séquestration C, N et P, d'habitat) (Lyons *et al.*, 2000; Josiah *et al.*, 2004). Cette hypothèse sera vérifiée dans les chapitres 1,2 et 3 de la thèse.

(5) Tel que montré par les travaux de Dykstra (1974), les clones qui auront la plus forte activité de la nitrate réductase dans les feuilles seront également ceux qui auront la plus forte croissance en biomasse. Cette hypothèse sera testée dans le chapitre 4 de la thèse.

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CHAPITRE I

BIOMASS AND VOLUME YIELD AFTER 6 YEARS IN MULTICLONAL HYBRID POPLAR RIPARIAN BUFFER STRIPS

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Abstract

In this paper the potential of five hybrid poplar clones (*Populus* spp.) to provide biomass and wood volume in the riparian zone is assessed in four agroecosystems of southern Quebec (Canada). For all variables measured, significant site effects were detected. Survival, biomass yield and volume yield were highest at the Bromptonville site. After 6 years of growth, total aboveground biomass production (stems+branches+leaves) reached 112.8 tDM/ha and total leafless biomass production (stems+branches) reached 101.1 tDM/ha at this site, while stem wood volume attained 237.5 m^3/ha. Yields as low as 14.2 tDM/ha for total biomass and 24.8 m^3/ha for total stem volume were also observed at the Magog site. Highest yields were obtained on the most fertile sites, particularly in terms of NO_3 supply rate. Mean stem volume per tree was highly correlated with NO_3 supply rate in soils (R^2=0.58, $p<0.001$). Clone effects were also detected for most of the variables measured. Total aboveground biomass and total stem volume production were high for clone 3729 (*P. nigra* x *maximowiczi*) (73.1 tDM/ha and 134.2 m^3/ha), although not statistically different from clone 915311 (*P. maximowiczi* x *balsamifera*). However, mean whole-tree biomass (including leaves) was significantly higher for clone 3729 (38.8 kgDM/tree). Multifunctional agroforestry systems such as hybrid poplar riparian buffer strips are among the most sustainable ways to produce a high amount of biomass and wood in a short time period, while contributing to alleviate environmental problems such as agricultural non-point source pollution.

Keywords

Riparian buffer strip, agroforestry, streambank restoration, hybrid poplar, biomass, wood production.

1.1 Introduction

Riparian ecosystems are considered as keystone elements of watersheds and landscapes (Naiman *et al.*, 2005). Conservation and restoration of these landscape features are important for non-point source pollution control, water quality protection, streambank stabilisation, flood control, species conservation, aesthetic value, recreation, etc. (Schlosser and Karr, 1981; Peterjohn and Correll, 1984; Osborne and Kovacic, 1993; Lowrance *et al.*, 1997; Décamps *et al.*, 2004).

However, restoration of the riparian zone generally implies important investments (buffer plantation and management, streambank stabilisation structures, etc.), particularly in landscapes where agricultural practices have led to severe alterations of the land-water ecotone. Hence, riparian buffer installation or restoration is often unrealistic at both farm and watershed levels without proper financial and technical support to landowners. This is particularly true in a context where landscapes under intensive agricultural pressures are expected to expand in order to meet an increasing global demand for food and other goods (textiles, biofuels, fibre) (Millennium Ecosystem Assessment, 2005). One way to overcome costs of buffer plantation and management is to create economic opportunities from biomass and wood production in the riparian zone (Rockwood *et al.*, 2004). As they provide environmental benefits, these multifunctional systems help to diversify the regional economy by the production of alternate goods on the farm (Licht and Isebrands, 2005). Moreover, the use of the riparian zone for poplar biomass and wood production is an interesting way for offsetting the economic loss of converting it from more traditional agricultural uses such as annual row crops.

Like other trees from the Salicaceae family, poplars were identified by several authors as potential species for the restoration of the agricultural riparian zone (Licht, 1992; O'Neill and Gordon, 1994; Schultz *et al.*, 1995; Schultz *et al.*, 2004; Kelly *et al.*, 2007). Because these flood-tolerant pioneer species get established rapidly and grow very fast, they can restore some functional and structural attributes within agroecosystems in a short time period (forest cover, nutrient accumulation, microclimate, soil stability, windbreak, etc.). Fast-growing hybrid poplars are also very effective carbon sinks and can be planted to offset CO_2 emissions (Oelbermann *et al.*, 2004; Updegraff *et al.*, 2004; Yemshanov and McKenney, 2008).

From an economic perspective, hybrid poplars are extremely versatile since different tree parts produce different kinds of marketable products. Woody parts (branches and stems) can be chipped to produce bioenergy and particle boards, whereas wood from the stems can be used for pulp (Balatinecz *et al.*, 2001; Labrecque and Teodorescu, 2005; Yu *et al.*, 2008). Higher quality wood from stems can also be sawn or peeled to provide solid wood products such as veneer and pallets (Balatinecz *et al.*, 2001; Yu *et al.*, 2008). In times of drought, leaves and branches can be pruned from hybrid poplars to create an inexpensive livestock feed (McWilliam *et al.*, 2004). Poplar leaves and ramial wood can also be used for agricultural land fertilisation (Singh and Sharma, 2007). Depending on the end product needed, different cultural systems can be designed because hybrid poplars can be managed on very short rotations like many *Salix* species, but also on longer ones (15-20 years) (Colletti *et al.*, 1991; Berthelot *et al.*, 2000) . Hence, hybrid poplars have the potential to create diverse ecosystem goods and services when they are used in riparian agroforestry systems.

Although hybrid poplars show interesting qualities for restoration and income creation in the land-water ecotone, very few studies have assessed biomass and wood production of these species in riparian agroforestry systems. Moreover, studies that have attempted to quantify some of these variables have generally taken place on a single research site (Schultz *et al.*, 1995; Tufekcioglu *et al.*, 2003; Kelly *et al.*, 2007). Furthermore, in Quebec (Canada), no study has assessed biomass and volume yield of hybrid poplars across a variety of agricultural sites since most plantations are established on abandoned farmland or forest land rather than on prime agricultural land (Lteif *et al.*, 2007).

So far, few studies done in southern Quebec compared biomass yield of clones of different parentages (Rivest *et al.*, 2009). In addition, the growth potential of clones developed for this region has never been tested extensively in the field. Little is known about the productivity of clones from different parentages in contrasted riparian environments since studies on hybrid poplar agricultural buffers have generally used a single clone (Tufekcioglu *et al.*, 2003; Kelly *et al.*, 2007). This aspect is particularly important given that large growth differences among clones of different parentages have been reported in the literature (Brown *et al.*, 1996; Lo and Abrahamson, 1996; Brown and Driessche, 2002).

In order to make regional predictions about hybrid poplar yield in the riparian zone of agroecosystems, it is also imperative to understand how site factors such as soil fertility are influencing the growth of hybrid poplars. This is a major issue because hybrid poplar growth is known to respond strongly to soil richness, competing vegetation and climate (Boysen and Strobl, 1991; Czapowskyj and Safford, 1993; Tabbush and Beaton, 1998; Stanturf *et al.*, 2001; Coleman *et al.*, 2006).

In addition, because different poplar tree parts produce different kinds of economic products, there is also a need for measuring biomass production in these different tree compartments (stems, branches and leaves), and for evaluating stem volumes that can be produced in hybrid poplar plantations. Moreover, because different poplar clones have different tree architectures and branching habits (Boysen and Strobl, 1991), separate compartment biomass data can be helpful to evaluate which clone is best suited for a particular end-use. Compartment biomass data are also very useful for eventual studies on nutrient accumulation and carbon sequestration in hybrid poplar buffers, as nutrient concentrations in different poplar compartments tend to differ considerably (Swamy *et al.*, 2006).

In this study, the potential of hybrid poplars to produce biomass from different tree compartments and stem wood volume is assessed in the riparian zone of southern Quebec (Canada) agroecosystems. The three main objectives are: (1) to determine biomass and volume growth of hybrid poplars in different riparian sites of agricultural watersheds in Quebec, (2) to compare growth of five unrelated clones, and (3) to determine if different riparian site conditions affect poplar growth and the relative growth among the clone

1.2. Materials and methods

1.2.1 Study sites

In May 2003 four hybrid poplars riparian buffer strips were established along small headwater streams in the Eastern Townships region of southern Quebec, Canada. The buffers had cumulated 6 years of growth in the year of the study (2008). Three of the four buffers are located in pastures with different cattle densities (Bromptonville, 0.6 cow/ha; Magog, 0.2 cow/ha; St-Isidore-de-Clifton, 0.5 cow/ha). The other buffer (Roxton Falls) occupies the riparian zone of a hayfield. Bromptonville and St-Isidore-de-Clifton sites are fertilized each year with cow manure, while Magog and Roxton Falls sites are not fertilized. Every 5 years, 0.8 t/ha of lime is applied at the St-Isidore-de-Clifton site.

Three study sites (Bromptonville, Magog and Roxton Falls) are located in a hilly landscape (Sherbrooke unit), which is characterised by gentle slopes and a continental subhumid moderate climate (Robitaille and Saucier, 1998). Land use in this landscape unit is 71 % natural and managed forest (mostly private), 28 % agricultural and 1 % urban. Agricultural activities are concentrated in larger valley bottoms; pastures are frequently found on the poorer hillside soils. The St-Isidore-de-Clifton site is located in the Mont Mégantic landscape unit, which is characterised by continental subhumid-subpolar climate, higher elevation, steeper hillside slopes and lower agricultural land use (9 % of land use) (Robitaille and Saucier, 1998). Both landscape units are covered by a thick surface deposit of till and share a similar precipitation regime (1000-1100 mm). St-Isidore-de-Clifton, Magog, and Bromptonville sites are located in the St-François River watershed, while the Roxton Falls site is in the Yamaska River watershed. These watersheds both drain into the St-Lawrence River. The natural vegetation of southern Quebec is characterised by hardwood tree species, mainly sugar maple (*Acer saccharum*), and two native poplars species are found within riparian corridors in the region (*P. deltoides* and *P. balsamifera*). A summary of site characteristics is presented in Table 1.1.

Table 1.1

Site and soil characteristics of the 4 riparian buffer strips. Nutrient supply rate (μg/10 cm^2) measured with PRS-probes in the soil of the four riparian hybrid poplar buffer strips are also presented along with NO_3:NH_4 and Ca:Mg molar ratios. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Site and soil characteristics .	Sites					
	Bromptonville	Magog	Roxton Falls	St-Isidore-de-Clifton	SE	$p<$
Land use	Pasture	Pasture	Hayfield	Pasture	-	-
Soil texture	Silty clay	Clay	Clay	Silty clay	-	-
Yearly fertilization	Cow manure	None	None	Cow manure	-	-
Cattle density (cow/ha)	0.6	0.2	None	0.5	-	-
Elevation (m)	140	208	147	360	-	-
pH	6.36 b	5.81 c	6.54 a	5.52 d	0.04	0.001
Organic matter (%)	6.21	7.47	4.69	7.46	-	NS
NO_3	80.5 a	17.4 b	18.8 b	87.9 a	8.2	0.001
NH_4	5.52 c	9.09 b	3.30 c	14.07 a	1.47	0.001
NO_3:NH_4 (molar ratio)	4.2	0.6	1.7	1.8	-	-
P	7.28 a	5.14 b	3.98 b	6.90 a	0.81	0.05
K	383.6 a	77.6 b	43.7 c	74.3 b	13.6	0.001
Ca	860 b	540 c	1308 a	1220 a	44	0.001
Mg	204 b	388 a	176 c	142 d	12	0.001
Ca:Mg (molar ratio)	2.5	0.8	4.4	5.1	-	-
Mn	1.41 b	24.03 a	3.84 b	5.34 b	4.37	0.001

At each site, riparian buffers weere installed on both sides of the streams for a total length of 90 m and a width of 5.5 m on each streambank. A row of silver maple was planted directly on the streambank, following recommendations made by Schultz *et al.* (Schultz *et al.*, 1995). A meter and a half away from the silver maple row, 3 hybrid poplar rows where planted with a spacing of 1.5 m between the rows and 3 m between trees within a same row (4.5 m^2/hybrid poplar or ~ 2222 hybrid poplars/ha).

Rooted cuttings with approximately 2 m-long stems were planted manually with a shovel at 30 to 40 cm depth. This type of planting stock was preferred to standard cuttings, in order to improve initial survival (Zsuffa *et al.*, 1977). The planting stock was provided by the Berthierville nursery of the Ministère des Ressources Naturelles et de la Faune (MRNF) of Quebec.

No site preparation was done prior to planting and a fence was installed one meter away from the third hybrid poplar row in pasture sites to prevent grazing from livestock. Weed control was done only once, one month after planting in June 2003. Glyphosate was spayed locally at the base of each hybrid poplar ($1 m^2$/tree) using a backpack sprayer (4 L/ha) and a cardboard tube to protect trees from herbicide drift. Hence, herbicide application was done on approximately 25% of the entire buffer surface. This targeted weed control strategy, along with fencing, led to the rapid recolonisation of the buffer by natural herbaceous and shrubby vegetation. The recolonisation of the herbicide-treated patches by some herbaceous species was already observed in late summer of the year of herbicide treatment (2003). Depending on the landscape context of the sites, some indigenous trees have also begun to colonise the planted buffer (*Larix laricina*, *Pinus strobus*, *Acer saccharum*, *Alnus rugosa*, etc.).

Five unrelated hybrid poplar clones were used in this study: *P. trichocarpa* x *deltoides* (TxD, 3230; also named *P.* x *generosa*); *P. deltoides* x *nigra* (DxN, 3570; also named *P.* x *canadensis*); *P. canadensis* x *maximowiczii* (DNxM, 915508); *P. nigra* x *maximowiczi* (NxM, 3729) and *P. maximowiczi* x *balsamifera* (MxB, 915311). Name, parentage and origin of planted hybrid poplar clones are presented in Table 1.2 The 5 poplar clones were chosen because they had different growth patterns, physiological characteristics, and because they had been selected for superior disease resistance/tolerance and growth characteristics in MRNF genetic selection trials in southern Quebec (Périnet *et al.*, 2001).

Table 1.2
Name, parentage and origin of planted hybrid poplar clones.

Clone number	Scientific name (common name)	Parentage	Origin
3230	*P.* x *generosa* A. Henry (Boelare)	T x D	Belgium
3570	*P.* x *canadensis* Moench	D x N	Belgium
3729	*P. nigra* x *P. maximowiczii* (NM6)	N x M	Germany
915311	*P. maximowiczii* x *P. balsamifera*	M x B	Québec
915508	*P.* x *canadensis* x *P. maximowiczii*	DN x M	Québec

1.2.2 Experimental design

A randomized block design was used at each of the 4 sites (factor A), with 4 blocks (replicates) and 5 hybrid poplar clones (factor B) for a total of 80 experimental plots (n=80). Each block contains 5 experimental plots (one clone per plot). Dimensions of a plot are 4.5 m wide and 9 m long (40.5 m^2). Each plot contains 9 trees from a single clone (3 rows, 3 trees/row). Each tree is spaced 3 m on the row and the rows are 1.5 m apart. A total of 180 hybrid poplars were planted at each site (36 trees of each clone) for a total of 720 hybrid poplars. This design allowed us to test 5 poplar clones in 4 different riparian environments simultaneously, a common procedure in crop cultivar evaluations (Steel and Torrie, 1980).

1.2.3 Soil characteristics

Soil samples were taken at 15 cm depth in each plot in 2007 at Bromptonville and Magog sites and in 2008 at the St-Isidore-de-Clifton and Roxton Falls sites (total of 80 samples). All samples were analysed for pH. A composite sample was made by pooling samples from 5 plots in order to determine soil texture and organic matter content at the block level. Soil samples where air dried prior to analysis. The determination of soil pH was made using a 2:1 ratio of water to soil. The Bouyoucos (Bouyoucos, 1962) method was used to analyse soil particle size, and textural class was determined in accordance with the Canadian Soil Classification Committee (Comité d'experts sur la prospection pédologique d'Agriculture Canada, 1987). Soil organic matter content was determined by loss on ignition at 550°C. Soil characteristics are presented in Table 1.1.

1.2.4 Soil nutrient availability

Nutrient availability in the hybrid poplar buffers was determined using Plant Root Simulator (PRS^{TM}-Probes) technology from Western Ag Innovations Inc. Saskatoon, Canada. The PRS-probes consist of an ion exchange membrane encapsulated in a thin plastic probe, which is inserted into the ground with little disturbance of soil structure. The membrane surface exhibits surface and sorption characteristics similar to those of a plant root. The PRS-probes are an ideal tool to assess nutrient supply rates (ions fluxes) by continuously adsorbing ions over the burial period. Nutrient availability predicted with this method is generally significantly correlated with conventional soil extraction methods over a wide range of soil types (Qian *et al.*, 1992). This technology has also been previously used in agronomic, forestry and environmental studies (Adderley *et al.*, 2006; Coll *et al.*, 2007; Nelson *et al.*, 2007).

Three pairs of probes (an anion and a cation probe in each pair) were buried along the first row of poplars (closest to the stream) and three other pairs were buried along the third row of poplars (field side), for a total of six pairs of probes in each experimental plot (80 plots). For the Magog and Bromptonville sites, probes were buried on August 11 and removed on August 26, 2008. For the Roxton Falls and St-Isidore de Clifton sites, probes were buried from August 12 to August 27, 2008. The burial duration was 15 days at the four sites. After probe removal from the ground they were washed in the field with deionised water, and returned to Western Ag Labs for analysis (NO_3, NH_4, P, K, Ca, Mg and several micronutrients). Composites were made by averaging the data of three pairs of probes. Two composites were taken from each experimental treatment; one from the first poplar row and one from the third poplar row. Probe supply rates are reported as μg of nutrient /10 cm^2 and are presented in Table 1.1.

1.2.5 Sampling and regression procedures

Near the end of the 6th growing season (from August 30 to September 17, 2008), we selected one representative hybrid poplar in each experimental plot, for a total 80 trees (each tree represents 4.5 m^2 of plot area). In each plot, this representative tree was selected because it was the closest to the average diameter at breast height of all hybrid poplars in the plot. The diameter at breast height (DBH) range for these 80 trees was 3.6 - 25.1 cm. Trees were cut and aboveground compartments (leaves, branches and stem) were separated and weighed fresh using a tripod scale. Leaves and branches were completely separated in 40 trees (8 trees per clone). Sub-samples from stem, branches and leaves were immediately weighed in the field and taken back to the lab for determining dry weight.

In order to calculate stem volume (outside of the bark) for the 80 sampled trees the following measurements were taken outside of the bark: tree base diameter, DBH, length from the tree base to 10 cm diameter, and length from tree base to 3 cm diameter. For larger trees (DBH > 10 cm), stem volume was calculated for three sections of the stem: (1) tree base diameter to DBH, (2) DBH to 10 cm diameter, and (3) 10 cm diameter to 3 cm diameter. For smaller trees (DBH < 10 cm) volume was calculated for two sections of the stem: (1) tree base diameter to DBH and (2) DBH to 3 cm diameter. Volumes of different stem sections were then summed to obtain total stem volume for each of the sampled hybrid poplars. Volume calculations were made using the following equation (Perron, 1996):

$$V = \pi/12(D_1^2+D_2^2+D_1D_2)\ L$$

Where V is the volume of a stem section, D_1 is the base diameter of the stem section, D_2 is the diameter at the top of the stem section, and L is the length of the stem section.

With data from the stems of 16 trees per clone and branches and leaves from 8 trees per clone, regression models for volume and biomass vs. DBH were developed. Residuals were plotted and compared to a normal distribution in order to determine the goodness-of-fit. According to the Shapiro Wilk W test, all our regressions had a good fit. These regressions were then used to estimate aboveground biomass and volume yield for the entire experimental design. The DBH measurements and survival determinations were made from late October to early November 2008, at the end of the 6th growing season. Regressions used for biomass and volume yield calculation are presented in Table 1.3. All biomass and volume yield data were scaled up to one hectare (ha) area for purposes of comparison with other studies. Based on hybrid poplar plot dimensions (see section 1.2.2), one hectare of hybrid poplar riparian buffer would represent three rows of hybrid poplars (total width = 4.5 m) on each side of the stream and would cover 1.11 km of streambank (4.5 m + 4.5 m x 1.11 km of stream = 1 ha).

Table 1.3

Regressions between DBH (cm) and dry mass (kg) for stems, branches, and leaves of the 5 hybrid poplar clones (stems, $n = 16$; branches and leaves, $n = 8$; $p<0.001$). Regression models between DBH (cm) and stem volume (dm^3) for the 5 hybrid poplar clones ($n=16$, $p<0.001$) are also presented. For all regressions, the x variable is the DBH and the Y variable is the biomass or the volume.

Tree components and clone number	Model	R^2	F-value
Stem biomass			
3230	$Y = 0.0662x^{2.2014}$	0.997	4591
3570	$Y = 0.0531x^{2.2445}$	0.989	1261
3729	$Y = 0.0753x^{2.197}$	0.985	936
915311	$Y = 0.1295x^2 - 0.1544x$	0.980	936
915508	$Y = 0.0815x^{2.1408}$	0.991	1472
Branches biomass			
3230	$Y = 0.0276x^2 + 0.1177x$	0.977	382
3570	$Y = 0.0386x^2 - 0.0602x$	0.989	574
3729	$Y = 0.0622x^{1.9956}$	0.967	173
915311	$Y = 1.3127\exp^{0.1576x}$	0.882	45.0
915508*	$Y = 0.0024x^3 + 0.0057x^2 + 0.1614x$	0.989	320
Leaves biomass			
3230	$Y = 0.0931x^{1.4189}$	0.970	193
3570	$Y = 0.0669x^{1.5336}$	0.986	422
3729	$Y = 0.0125x^2 + 0.2343x$	0.962	284
915311	$Y = 1.2637\exp^{0.0944x}$	0.893	50.1
915508	$Y = 0.072x^{1.4855}$	0.971	203
Stem volume			
3230	$Y = 0.1441x^{2.3529}$	0.997	3986
3570	$Y = 0.1466x^{2.3423}$	0.997	4779
3729	$Y = 0.1757x^{2.3005}$	0.990	1445
915311	$Y = 0.4726x^2 - 0.8815x$	0.993	2558
915508	$Y = 0.1773x^{2.3016}$	0.994	2155

In this study the term «total biomass» represents the sum of stems, branches and leaves biomass on a per hectare basis, which is the total harvestable aboveground biomass, while the term «whole-tree biomass» represents the sum of stems, branches and leaves biomass on a per tree basis. The term «leafless biomass» represents the sum of stems and branches biomass which is the harvestable aboveground woody biomass. The term «volume» refers to the stem wood volume.

1.2.6 Statistical analysis

ANOVA tables were constructed in accordance with Petersen (Petersen, 1985), where degrees of freedom, sum of squares, mean squares and *F*-values were computed. When a factor was declared statistically significant (Sites, Clones and Sites x Clones interactions), the standard error of the mean (SE) was used to determine differences between means for three levels of significance ($p<0.05$, $p<0.01$ and $p<0.001$) (Petersen, 1985). Only significant effects (Petersen, 1985) were retained and compiled for all of the parameters measured, and they are presented in respective tables or figures by indicating the level of significance and standard errors each time. All of the ANOVAs were run with the complete set of data (4 sites, 5 clones, 4 blocks = 80 experimental plots). All statistical analyses were done with JMP 6 from SAS Institute (Cary, NC).

1.3. Results

In this study, the only Site x Clone interaction detected by the ANOVA was for survival, but this interaction was weak ($p<0.05$) compared to the Site effect ($p<0.001$), which was the largest effect. Moreover, the biological explanation of this interaction was unclear. Hence, in the presentation of survival data, we have preferred to show only Site and Clone effects, which are more relevant in this study.

For all other variables measured in this study, no Site x Clone interaction was detected by the ANOVA. Therefore, we only report Site and Clone effects. In all cases, the largest effect was by far the Site effect, followed by the Clone effect (not always significant).

1.3.1 Soil nutrient availability

Results in Table 1.1 show significantly different soil nutrient availability across the four sites. No Clone effect was detected by the ANOVA. Nitrate (NO_3) availability was more than 4 times greater at Bromptonville and St-Isidore-de-Clifton sites compared to Magog and Roxton Falls sites. Ammonium (NH_4) availability was greater at St-Isidore-de-Clifton and Magog. The NO_3:NH_4 molar ratio was higher at the Bromptonville site (4.2), followed by St-Isidore-de-Clifton (1.8), Roxton Falls (1.7) and Magog (0.6). Phosphorus (P) availability was also higher at Bromptonville and St-Isidore-de-Clifton sites, while calcium (Ca) availability was higher at Roxton Falls and St-Isidore-de-Clifton sites. In comparison with the three other sites, potassium (K) availability was more than 5 times higher at Bromptonville, while magnesium (Mg) and manganese (Mn) availability were by far the highest at the Magog site. This site showed a particularly low Ca:Mg molar ratio (0.8) compared to Bromptonville (2.5), Roxton Falls (4.4) and St-Isidore-de-Clifton (5.1). Generally, it seemed that nutrient availability, or site fertility, was highest in two of the riparian plantation sites, Bromptonville and St-Isidore-de-Clifton.

1.3.2 Hybrid poplar survival after 6 years

Survival was significantly higher ($p<0.001$) at Bromptonville (87.2%) and Roxton Falls sites (82.2%) (Table 1.4). The St-Isidore-de-Clifton site has an intermediate position (71.1%), while the lowest survival rate was observed at Magog (57.2%). The low survival at the Magog site can be partly attributed to livestock browsing trees nearest the fence. In May 2006, it was estimated that 34.5% of living trees were browsed by livestock. This situation was not observed at the other pasture sites (Bromptonville and St-Isidore-de-Clifton), because the hybrid poplar buffer is protected with an electric fence. Hence, during buffer installation in pastures, it is important to place the fence more than a meter away from the tree row, particularly if electrical fencing is not used.

After 6 years of growth, survival rates were comparable for clones 3230, 3729, 915311 and 915508, with values ranging from 75 % to 78.5% (Table 1.4). However, survival rate for clone 3570 (63.9%) was significantly lower ($p<0.05$) than what was observed for the four other clones.

Table 1.4

Mean survival rate of each hybrid poplar clone and mean survival rate at each site at the end of the 6th growing season. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Clones	Survival (%)	Sites	Survival (%)
3230	75.0 a	Bromptonville	87.2 a
3570	63.9 b	Magog	57.2 c
3729	77.8 a	Roxton Falls	82.2 a
915311	78.5 a	St-Isidore-de-Clifton	71.1 b
915508	77.1 a		
SE	3.9		3.5
$p <$	0.05		0.001

1.3.3 Regression models for biomass and volume production

Using linear and non linear regression models (including Logarithmic, Power, Exponential and Polynomial), regression equations for predicting biomass in different aboveground compartments (stem, branches and leaves) and stem volume were fitted for each clone, with DBH being the predictor variable (x) and biomass (stem, branches or leaves) and volume (stem) being the response variables (Y). Final models developed using only non linear regression models had R^2 ranging from 0.980 to 0.997 for stem biomass, 0.882 to 0.989 for leaves' biomass, 0.893 to 0.970 for branches' biomass and 0.990 to 0.997 for stem volume, all were highly statistically significant at $p<0.001$ (Table 1.3). Since tree architecture varies from one poplar clone to the other, the use of different regression models for each clone is a common procedure to evaluate hybrid poplar yields (Heilman *et al.*, 1994; Laureysens *et al.*, 2004).

1.3.4 Aboveground biomass yield after 6 years

Highly significant ($p<0.001$) Site effects were observed for total aboveground biomass production per ha and mean aboveground biomass production per tree (Tables 1.5 and 1.6). For all these variables, the Bromptonville site was statistically more productive than the three other sites, while the Magog site was statistically less productive than the three other sites. In order to simplify data presentation, only total aboveground biomass per ha and mean whole-tree biomass will be used in the discussion on Site effects.

Table 1.5

Total aboveground biomass yield (tDM ha^{-1}) at the 4 sites at the end of the 6th growing season. The results are presented for different tree compartments and represent the combined biomass production of the 5 clones at each site. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Sites	Stem (tDM ha^{-1})	Branches (tDM ha^{-1})	Leaves (tDM ha^{-1})	Leafless trees (tDM ha^{-1})	Total (tDM ha^{-1})
Bromptonville	69.89 a	31.22 a	11.70 a	101.1 a	112.8 a
Magog	7.91 c	3.89 c	2.35 c	11.8 c	14.2 c
Roxton Falls	24.24 b	10.57 b	5.53 b	34.8 b	40.4 b
St-Isidore-de-Clifton	29.86 b	13.02 b	6.12 b	42.9 b	49.0 b
SE	2.87	1.58	0.49	4.4	4.8
p <	0.001	0.001	0.001	0.001	0.001

Table 1.6

Mean aboveground biomass yield per tree (kgDM) at the 4 sites at the end of the 6th growing season. Results are presented for different tree compartments and represent a tree-based mean of the combined biomass yield of the 5 clones at each site. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Sites	Stem (kgDM)	Branches (kgDM)	Leaves (kgDM)	Leafless tree (kgDM)	Whole-tree (kgDM)
Bromptonville	36.56 a	16.23 a	6.08 a	52.8 a	58.9 a
Magog	6.87 d	3.36 d	1.98 d	10.2 d	12.2 d
Roxton Falls	12.62 c	5.48 c	2.91 c	18.1 c	21.0 c
St-Isidore-de-Clifton	17.71 b	7.59 b	3.67 b	25.3 b	29.0 b
SE	1.22	0.69	0.18	1.9	2.0
p <	0.001	0.001	0.001	0.001	0.001

The Bromptonville site was by far the most productive site with a total biomass yield of 112.8 tDM ha^{-1} and a mean biomass production of 58.9 kgDM per tree. Compared to Bromptonville, biomass yield per ha was about 8 times lower at the Magog site (14.2 tDM ha^{-1}), while mean biomass production per tree was about 5 times lower (12.2 kgDM). Roxton Falls and St-Isidore-de-Clifton sites were intermediate in rank for total biomass yield per ha and mean biomass per tree. Roxton Falls and St-Isidore-de-Clifton sites were not statistically different for total biomass yield per ha, but mean biomass per tree was significantly higher at St-Isidore-de-Clifton.

The analysis of variance also detected a significant Clone effect for total biomass yield ($p<0.001$) and mean biomass production per tree ($p<0.001$) (Tables 1.7 and 1.8). After 6 years of growth, total biomass yields per ha were comparable for clones 3729 (NxM) and 915311 (MxB) and statistically higher than the three other clones. Clone 3230 (TxD) and clone 915508 (DNxM) occupied an intermediate position. Total biomass yield for clone 3570 (DxN) was significantly lower than all the other clones in this study. The lower biomass yield per ha produced by clone 3570 seems closely related to its low survival rate (Table 1.4), because when comparisons are made on the basis of mean whole-tree biomass (including leaves), clone 3570 does not have a significantly lower yield than clone 3230, or clone 915508. Nevertheless, mean biomass per tree for clone 3570 is still significantly lower than for clones 3729 and 915311, while clone 3729 had a higher mean whole-tree biomass compared to the four other clones. Branch biomass was particularly high for clone 915311, accounting for 33 % of individual tree biomass.

Table 1.7

Total aboveground biomass yield (tDM ha^{-1}) of the 5 hybrid poplar clones at the end of the 6th growing season. The results are presented for different tree compartments and represent the total biomass production of each clone across 4 different sites. Percentage of each tree compartment vs. total biomass is also indicated. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Clones	Stems (tDM ha^{-1})	(%)	Branches (tDM ha^{-1})	(%)	Leaves (tDM ha^{-1})	(%)	Leafless trees (tDM ha^{-1})	(%)	Total (tDM ha^{-1})
3230	32.2 b	67	10.19 c	21	5.61 c	12	42.4 c	88	48.0 b
3570	23.8 c	66	7.95 c	22	4.47 d	12	31.8 d	88	36.3 c
3729	43.2 a	59	20.47 a	28	9.43 a	13	63.6 a	87	73.1 a
915311	34.3 b	55	20.87 a	33	7.61 b	12	55.1 ab	88	62.8 a
915508	31.4 b	62	13.91 b	28	5.01 cd	10	45.3 bc	90	50.3 b
SE	3.2		1.77		0.54		4.9		5.4
$p <$	0.01		0.001		0.001		0.001		0.001

Table 1.8
Mean aboveground biomass production per tree (kgDM) for the 5 hybrid poplar clones at the end of the 6th growing season. The results are presented for different tree compartments and represent the mean biomass production per tree of each clone across 4 different sites. Percentage of each tree compartment vs. total biomass is also indicated. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Clones	Stem (kgDM)	(%)	Branches (kgDM)	(%)	Leaves (kgDM)	(%)	Leafless tree (kgDM)	(%)	Whole-tree (kgDM)
3230	18.5 b	67	5.89 c	21	3.26 c	12	24.4 bc	88	27.7 cd
3570	15.3 c	66	5.11 c	22	2.93 cd	13	20.4 c	87	23.3 d
3729	22.8 a	59	10.86 a	28	5.11 a	13	33.6 a	87	38.8 a
915311	18.3 b	54	11.32 a	33	4.19 b	12	29.7 a	88	33.9 b
915508	17.3 bc	62	7.64 b	28	2.80 d	10	24.9 b	90	27.7 cd
SE	1.4		0.78		0.21		2.1		2.3
$p <$	0.01		0.001		0.001		0.001		0.001

1.3.5 Stem volume after 6 years

A highly significant Site effect ($p<0.001$) was detected for total volume yield per ha and mean volume yield per tree after 6 years of growth (Table 1.9). Moreover, all four sites were statistically different for these two variables. As expected, the ranking of sites in order of decreasing yield was: Bromptonville > St-Isidore-de-Clifton > Roxton Falls > Magog. A volume yield as high as 237.5 m^3/ha was obtained at the Bromptonville site after only 6 years of growth. Interesting yields were also obtained St-Isidore-de-Clifton (98.2 m^3 ha^{-1}) and Roxton Falls (78.4 m^3 ha^{-1}), while the Magog site accumulated only 24.8 m^3 ha^{-1}.

Results of the analysis of variance also indicated a relatively weak but significant clonal effect for total volume yield ($p<0.05$), while no significant effect was detected for mean volume yield per tree. Total volume yield for clone 3729 was statistically higher than for clones 3230, 3570 and 915508. Moreover, clone 915311 showed a statistically higher volume yield than clone 3570.

1.3.6 Annual biomass and volume yields

After 6 years of growth, annual biomass and volume yields at the Bromptonville site were relatively high (16.85 tDM ha^{-1} year^{-1} and 39.58 m^{3} ha^{-1} year^{-1}), while they were very low at the Magog site (1.97 tDM ha^{-1} year^{-1} and 4.14 m^{3} ha^{-1} year^{-1}) (Table 1.10).

Table 1.9

Total stem volume yield (m^{3}/ha) at the end of the 6th growing season and mean volume yield per tree (dm^{3}) by clone and by site. Standard error of the mean (S.E.) was used to determine differences between means; different letters indicate statistically different means.

Clones	Total volume (m^{3}/ha)	Mean volume (dm^{3})	Sites	Total volume (m^{3}/ha)	Mean volume (dm^{3})
3230	105.8 bc	60.7	Bromptonville	237.5 a	124.5 a
3570	85.9 c	54.9	Magog	24.8 d	21.6 d
3729	134.2 a	70.6	Roxton Falls	78.4 c	41.1 c
915311	118.4 ab	63.3	St-Isidore-de-Clifton	98.2 b	58.3 b
915508	104.5 bc	57.4			
SE	10.8	-		9.6	4.2
$p <$	0.05	NS		0.001	0.001

Table 1.10

Annual aboveground biomass and stem volume yield by clone and by site. Total Leafless aboveground biomass was used to calculate annual aboveground biomass yield.

Clones	Annual biomass yield (tDM ha^{-1} yr^{-1})	Annual volume yield (m^{3} ha^{-1} yr^{-1})	Sites	Annual biomass yield (tDM ha^{-1} yr^{-1})	Annual volume yield (m^{3} ha^{-1} yr^{-1})
3230	7.07	17.6	Bromptonville	16.85	39.58
3570	5.30	14.3	Magog	1.97	4.14
3729	10.61	22.4	Roxton Falls	5.80	13.07
915311	9.19	19.7	St-Isidore-de-Clifton	7.15	16.37
915508	7.54	17.4			

1.3.7 Relationship between NO_3 supply rate in soil and biomass and volume yields

A highly significant non linear relationship was observed between NO_3 supply rate in riparian soils and mean volume produced per tree (R^2 0.58, $p<0.001$) (Figure 1.1). A similar relationship was observed between soil NO_3 flux and mean whole-tree biomass per tree (including leaves) (R^2 0.54, $p<0.001$).

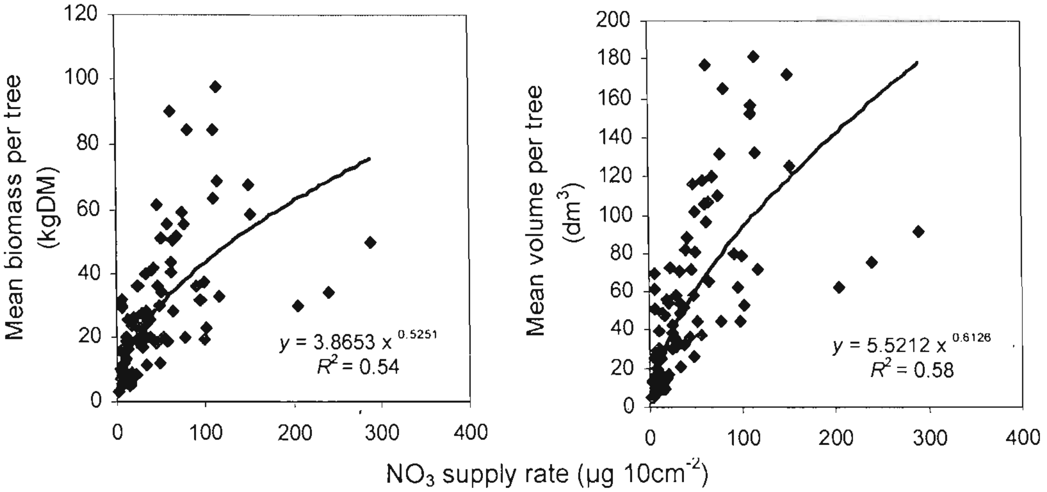

Figure 1.1 Relationship between nitrate (NO_3) supply rate and mean aboveground biomass per tree and mean stem volume per tree (n=80, $p<0.001$). Mean aboveground biomass yield per tree represents the sum of the stem, branches and leaves of a whole hybrid poplar.

1.4 Discussion

1.4.1 Site fertility: an important factor controlling biomass and volume yield in hybrid poplar riparian buffers

Although the four sites are located on agricultural land and have soil pH values ranging between 5.5 and 6.5 (Table 1.3), considered suitable for hybrid poplar cultivation in Eastern Canada (Boysen and Strobl, 1991), very different biomass yields were achieved across the four riparian sites after 6 years of growth. While total aboveground biomass and stem volume reached 112.8 tDM ha^{-1} and 237.5 m^3 ha^{-1} at the Bromptonville site, these values were more than 8 times lower at the Magog site (14.2 tDM ha^{-1} and 24.8 m^3 ha^{-1}) (Tables 1.5 and 1.9).

Site fertility in terms of NO_3 supply rate was the main factor controlling biomass and volume growth in this study (Figure 1.1). Therefore, the high growth rates observed at the Bromptonville and St-Isidore-de-Clifton sites are clearly related to the higher site fertility in terms of NO_3 supply rate (Table 1.1 and 1.5). The source of high NO_3 at both of these pasture sites is probably the result of yearly fertilisation with cow manure, upland of the riparian zone, and the relatively high cattle density (Table 1.1). High yields observed at Bromptonville and St-Isidore-de-Clifton sites are consistent with the fact that hybrid poplar performance is optimal when N availability is high and when small fertilizer doses are frequently applied in plantations (Stanturf *et al.*, 2001; Brown and Driessche, 2002; Coleman *et al.*, 2006).

Other factors may have influenced biomass and volume yields in this study. Relatively high P and K supply rates at the Bromptonville site (Table 1.1) may have played an important role in sustaining high yield. Lower survival rate (Table 1.4), lower soil pH (Boysen and Strobl, 1991; Czapowskyj and Safford, 1993), shorter growing-season or higher elevation (Tabbush and Beaton, 1998), and relatively low K supply rate at St-Isidore-de-Clifton (Table 1.1) are all potential factors that could explain why biomass and volume yields at this site are more than two times lower than what was observed at the Bromptonville site (Table 1.5).

Similar biomass and volume yields per ha were observed at the St-Isidore-de-Clifton and Roxton Falls sites (Table 1.5), although NO_3, P and K supply rates were much lower at the Roxton Falls site. Given that there were no animal or chemical nutrient inputs at this hayfield site, the high soil pH of 6.5, optimal for several hybrid poplar clones (Boysen and Strobl, 1991; Stanturf *et al.*, 2001), probably enhanced nutrient availability at Roxton Falls, otherwise a relatively low fertility site. Moreover, if the St-Isidore-de-Clifton site (elevation: 360 m) had been located at the same elevation as the Roxton Falls site (elevation: 147 m), larger growth differences would have been expected between the two sites (Tabbush and Beaton, 1998). Furthermore, although similar total biomass yields have been observed at St-Isidore-de-Clifton and Roxton Falls, it seems that lower stand density caused by higher mortality resulted in significantly higher mean whole-tree biomass at St-Isidore-de-Clifton (29 kgDM per tree) compared to Roxton Falls (21 kgDM per tree) (Table 1.6).

Although the two least productive sites (Magog and Roxton Falls) share similar values for N and P availability, total biomass was almost three times higher at Roxton Falls (Table 1.1 and 1.5). A low Ca:Mg ratio at the Magog site and high Mn supply rate could explain this result, since a high level of Mg and Mn in soils can be detrimental to crop or broadleaved tree growth (Proctor, 1971; Kitao *et al.*, 1997). Based on the standard of Leech and Kim (Leech and Kim, 1981) for poplar nutrition, foliar nutrient concentration analysis also confirms a nutritional imbalance (low N and P foliar concentrations) and potential Mg toxicity at the Magog site (Fortier *et al.*, 2010). Moreover, some areas of the Magog plantation were often waterlogged. Waterlogged soils are not recommended for hybrid poplar cultivation because they rapidly become oxygen deficient in the root zone (Boysen and Strobl, 1991; Tabbush and Beaton, 1998; Stanturf *et al.*, 2001). The lowest survival rate was also observed at the Magog site, partly because of livestock browsing trees nearest the fence (see Section 1.3.2). Lower stand density due to increased mortality could also have delayed crown closure and therefore enhanced competition from herbaceous species, reducing the early growth of poplars (Boysen and Strobl, 1991; Buhler *et al.*, 1998). It could be argued that lower density generally encourages faster growth of individual trees, however it was not the case at the Magog site probably because the low fertility (and likely Mg toxicity) of this site was inadequate to meet the high nutrient requirements of hybrid poplars (Heilman and

Stettler, 1986). Hence, the combined effect of livestock browsing, low N and P availability, low Ca:Mg ratio, high Mn supply rate and waterlogged soil may explain the very low biomass and volume yield per ha and per tree at the Magog site.

Nevertheless, although the buffer strip at the Magog site produced a relatively small amount of biomass and wood of lower economic interest, hybrid poplars in the buffer have already developed some structural and functional attributes that provide other ecosystem services (stream shading, streambank stability, aesthetic value, wildlife and native plant habitat, etc.).

1.4.2 Clone selection: which clone is better for what product?

Different biomass and volume yields were obtained from the five unrelated clones used in this study (Table 1.7 and 1.9). Aboveground biomass partitioning between stem, branches and leaves was also very different from one poplar clone to the other (Table 1.8). These results have implications for the suitability of the different clones for different products.

For biomass energy and wood chip production, clones 3729 and 915311 would be the more promising clones because they present the highest leafless biomass yields (Table 1.7 and 1.8). These two clones also produced the highest amounts of branches and leaves, which can be used for agricultural land fertilisation and as livestock feed (McWilliam *et al.*, 2004; Singh and Sharma, 2007). The high growth obtained for clone 3729 (synonym: NM6) is consistent with observations reported in southern Quebec and elsewhere (Lo and Abrahamson, 1996; Rivest *et al.*, 2009). The higher growth rate of clone NM6 may be related to its particularly rapid early-growth and its exceptional early-rooting (Brown *et al.*, 1996; Green *et al.*, 2003; Zalesny *et al.*, 2009). Cold resistance and tolerance to low soil fertility could also explain why clones with at least one parent related to the *Tacamahaca* section (balsam poplars, including *P. balsamifera*, *P. maximowiczii* and *P. trichocarpa*) performed better than clone 3570 (DxN), with both of its parental species from the *Aigeiros* section (*P. deltoides* and *P. nigra*) (Zsuffa *et al.*, 1977; Dickmann, 2001; Périnet, 2007) (Table 1.2).

However, if the landowner's goal is to produce sawlogs or peeled products, a particular attention must be taken in order to choose clones that have a lower proportion of branches and a better tree form. Hybrid poplars with a smaller proportion of branches will have fewer and/or smaller knots and will be easier to prune. Consequently, if the goal is to produce sawlogs, veneer and peeled products, clone 915311 is not recommended. Of all five clones, this clone has the highest proportion of branches (Table 1.8), with several low branches of large diameter (>5cm). Furthermore, the stem of clone 915311 tends to develop single or multiple low forks. This particular tree architecture could also enhance its susceptibility to wind damage over the years. Therefore, clone 915311 may not be the ideal candidate for producing large diameter sawlogs on long rotations (20-30 years). Nevertheless, on shorter rotations (5-10 years), this clone can produce a very high amount of biomass.

Clones 3230 (TxD) and 3570 (DxN) were by far the ones with the smallest proportion of branches (Table 1.8). They could be particularly promising for the production of higher value wood products. This is particularly true when mechanical properties of DxN and TxD hybrids are considered. As mentioned by Pliura *et al.* (2007), hybrids that have *P. deltoides* as a parent tend to have a higher wood density, while hybrids with a *P. balsamifera* parent have a lower wood density. In another study, Yu *et al.* (2008), showed that mechanical properties among hybrids could be ranked as follows in order of decreasing strength: DxN > TxD > MxB. For these reasons, landowners must choose carefully their hybrid poplar clones in order to produce the desired end product.

Finally, from an environmental perspective, it could be interesting to choose clones that produce a high amount of leaves in order to rapidly enhance organic matter and carbon input into the soil (Oelbermann, 2002). Clones with the highest aboveground biomass may also have the highest belowground biomass (Heilman *et al.*, 1994), which will also contribute to maintaining or enhancing C levels in riparian soils via fine root turnover (Tufekcioglu *et al.*, 1999; Block *et al.*, 2006). Riparian soils with higher concentrations of organic carbon tend to have a higher denitrification potential, particularly if these soils have a high silt and clay content (Hill *et al.*, 2000; Pinay *et al.*, 2000). Furthermore, terrestrial litter inputs are particularly important in sustaining multiple trophic level food web interactions in headwater streams of Eastern North America (Webster *et al.*, 1995; Wallace *et al.*, 1997).

Still, the use of a diversity of unrelated clones is recommended. This strategy generally improves pest and disease resistance, and provides structural diversity within the buffer since hybrid poplars from different parentages have different tree architectures and rooting patterns (Boysen and Strobl, 1991; Stanturf *et al.*, 2001; Block *et al.*, 2006).

1.4.3 Implications for hybrid poplar culture in Quebec

The annual biomass yield obtained at the Bromptonville site (16.85 tDM ha^{-1} $year^{-1}$) is comparable with the annual biomass yields reported by Labrecque and Teodorescu (Labrecque and Teodorescu, 2005) in short-rotation woody crop plantations (18 000 stems ha^{-1}) established on a marginal agricultural site of southern Quebec. After 4 years of growth, these authors reported annual biomass yields ranging from 16.62 to18.05 tDM ha^{-1} $year^{-1}$ for hybrid poplar clones (NxM hybrids). Our study, at a much lower planting density (2222 stems ha^{-1}), shows that very high yields can also be obtained on fertile agricultural riparian sites such as the Bromptonville site.

In fact, annual volume yield measured at the Bromptonville site was quite exceptional (39.6 m^3 ha^{-1} $year^{-1}$), given the fact that yields above 16 m^3 ha^{-1} $year^{-1}$ have never been reported in hybrid poplar plantations in Quebec (Ménétrier, 2008) (Table 1.10). The volume yield obtained at the Bromptonville site is more comparable to what is observed in very intensive poplar plantations of the North-Central United States, where yields can be as high as 27-45 m^3 ha^{-1} $year^{-1}$ (Riemenschneider *et al.*, 2001). Moreover, higher yields could be expected from all the plantations in this study by simply choosing to use the most productive clone (3729).

Although annual volume yields were much lower at Roxton Falls (13.07 m^3 ha^{-1} $year^{-1}$) and St-Isidore-de-Clifton (16.37 m^3 ha^{-1} $year^{-1}$), these two sites still produced wood volumes that are above average for hybrid poplar plantations growing in normal conditions in Quebec (11.6 m^3 ha^{-1} $year^{-1}$) (Ménétrier, 2008) (Table 1.10).

In the province of Quebec, most plantations are established on abandoned farmland or forest land, and growth rates are generally relatively low (Lteif *et al.*, 2007), while tending costs are the highest in Canada (Yemshanov and McKenney, 2008), mainly because herbicide release treatments are banned on public lands and is no longer subsidized on private lands (Fortier and Messier, 2006). In this study, riparian plantations of hybrid poplars achieved high yields at very low cost given the fact that no site preparation was done prior to planting and only one selective herbicide spraying (1 m^2 per tree) was done following tree planting. Therefore, multifunctional riparian agroforestry systems with hybrid poplars seem to be particularly promising for achieving high yields in a context where the Government of Quebec is trying to adopt a "triad" zoning approach to its forest management (Hunter, 1990; Messier *et al.*, 2003; Gouvernement du Québec, 2008) (i.e. conservation zones, large extensive production zones with ecosystemic management, small intensive production zones with plantation forestry).

Finally, although the harvest of residual biomass (branches, tree crown) in natural temperate and boreal forests is an idea gaining popularity in Quebec (Gouvernement du Québec, 2008), there are indications that this kind of practice is not likely to be sustainable. Residual biomass harvest combined with traditional timber harvest will likely lead to soil impoverishment and carbon loss over a few harvest rotations (Hendrickson *et al.*, 1989; Johnson and Curtis, 2001). Moreover, in Eastern Canada, residual forest biomass is generally located far from the roads, which greatly increases harvest costs and greenhouse gas emissions associated with transportation (Stokes, 1992). In this perspective, producing biomass in agricultural riparian areas appears to be a truly sustainable alternative, because agricultural systems are located very close to roads and transformation centres, and they receive continuous surplus nutrient inputs (fertilisation), that without the buffer strips would otherwise pollute water.

1.5 Conclusion

In this paper, results show that very high yields can be achieved in hybrid poplar riparian buffers planted in extensively managed agricultural landscapes of southern Quebec (pastures and hayfield). Site fertility, particularly in terms of NO_3 supply rate, was an important factor influencing biomass and volume growth of hybrid poplars. On higher fertility sites, establishment of wider riparian buffers could be economically justified if fast-growing poplars are used to produce alternate goods on the farm. As observed in other studies, clone 3729 (NM6) seems particularly promising for achieving high yields in a short time period.

Multifunctional agroforestry systems such as hybrid poplar riparian buffer strips are among the most sustainable ways to produce a high amount of wood and biomass on a relatively short time period, while helping to alleviate environmental problems such as agricultural non-point source pollution (Schultz *et al.*, 2004; Kelly *et al.*, 2007). (Figure 1.2).

Figure 1.2 Hybrid poplar riparian buffer at the Bromptonville site. Top left, view of the buffer at the end of the 2nd growing season (October 2004). Top right, view inside buffer during the 6th growing season (August 2008). Bottom left, view of the buffer during the 4th growing season (July 2006); note stream without planted buffer in foreground. Bottom right, view of the buffer during the 6th growing season (August 2008).

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CHAPITRE II

NUTRIENT ACCUMULATION AND CARBON SEQUESTRATION IN 6-YEAR-OLD-HYBRID POPLARS IN MULTICLONAL AGRICULTURAL RIPARIAN BUFFER STRIPS

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Abstract

Riparian vegetation has a critical role to play in non-point source pollution abatement and water quality protection within watersheds in agricultural areas. In addition to their water quality function, riparian buffers also have the potential to sequester large amounts of carbon (C). In this study, the C and nutrient sequestration by five unrelated clones growing in the riparian zone of four southern Quebec (Canada) agroecosystems is measured aboveground after 6 years of growth and compared to free-growing (unmanaged) herbaceous buffer strips. Very large differences in C sequestration and nutrient accumulation in hybrid poplar buffers were observed across the four agricultural riparian sites. For all variables measured in this study, the largest effect detected by the ANOVA was the Site effect. While C sequestration, N and P accumulation in total aboveground biomass were respectively, 52 t ha^{-1}, 770 kg ha^{-1} and 82 kg ha^{-1} at the Bromptonville site, these values were as low as 6.4 t ha^{-1}, 90 kg ha^{-1} and 10 kg ha^{-1} at the Magog site. Site fertility, in terms of NO_3 supply rate, was the main factor controlling biomass growth, and consequently C sequestration and nutrient accumulation in hybrid poplars. Although Site effect was by far the largest effect in this study, the Clone effect was also important, with clone 3729 (P. nigra L. x P. maximowiczii A. Henry) being the most effective for C and nutrient sequestration. Across the four study sites, total aboveground C sequestration, N and P accumulation at the site level could be respectively enhanced by 31-37%, 29-41% and 30-38% with the sole use of clone 3729. Site x Clone interactions for the variables tested in this study were generally not significant, or significant but small in magnitude compared to main effects (Site and Clone). Important C and nutrient accumulation differences exist after 6 years of growth between hybrid poplar buffers and unmanaged herbaceous buffers. Compared to an unmanaged herbaceous buffer, the distinct advantage of hybrid poplar buffers is that C and nutrient sequestration greatly increase with increasing site fertility, whereas they do so to a much lesser extent in herbaceous buffers.

Keywords

Riparian buffer, hybrid poplar, non-point source pollution, herbaceous buffers agroforestry, site fertility

2.1 Introduction

Worldwide, the intensification of agricultural practices has led to an increase of nutrient, chemical and sediment loads into receiving water bodies. Non-point inputs of nitrogen (N) and phosphorus (P) derived from fertiliser or manure application, soil erosion and high cattle densities are known as major causes of the degradation of aquatic ecosystems (Carpenter *et al.*, 1998). Riparian vegetation has a critical role to play in non-point source pollution abatement and water quality protection within watersheds in agricultural areas (Schlosser and Karr, 1981; Lowrance *et al.*, 1984; Gregory *et al.*, 1991; Osborne and Kovacic, 1993; Lowrance *et al.*, 1997). Therefore, restoration of riparian vegetation has the potential to improve water quality and provide other ecological functions within agroecosystems (habitats, micro-climate, soil stability, etc.) (Naiman *et al.*, 2005).

The presence of riparian vegetated buffers tends to decrease nutrient loads to streams by reducing stream bank and soil erosion, by enhancing sediment deposition, water infiltration, bacterial denitrification, and nutrient accumulation by plant biomass (Lowrance *et al.*, 1997). However, appropriate management of riparian vegetation is essential to maintain some of these functional attributes (Bentrup, 2008), particularly the nutrient accumulation potential (Lowrance *et al.*, 1997; Schultz *et al.*, 2004). Because plant communities will eventually reach a steady-state, a management approach that does not include the harvest of biomass will eventually become less effective in trapping nutrients such as P (Kelly *et al.*, 2007). As described by Vitousek and Reiners (1975), nutrients are retained within an ecosystem as storage pools of nutrients increase in both biomass and soil. However, as biomass increment reaches zero, storage pools of the system reach a steady-state where nutrient outputs equal inputs (Vitousek and Reiners, 1975). A riparian buffer system that reaches this steady-state may be less effective in preventing nutrient leaching to the streams. Moreover, if plants are not harvested, N and P accumulated in biomass will be released back to the soil as riparian vegetation dies and decays (Bedard-Haughn *et al.*, 2005; Dorioz *et al.*, 2006). Thus, periodic harvest of vegetation has been recommended in order to maintain an active nutrient sink (Dosskey, 2001).

In addition to their water quality function, riparian buffers also have the potential to sequester large amounts of carbon dioxide when they are managed as agroforestry systems (Montagnini and Nair, 2004). This is particularly interesting in a context where the agricultural sector accounts for an estimated emission of 10-12% of total global anthropogenic emissions of greenhouse gases (Smith *et al.*, 2007). Thus, multifunctional buffers can be designed to meet both water quality and carbon (C) sequestration objectives on farms, while creating economic opportunities (bioenergy, pulp, solid wood products, carbon credits, etc.) (Rockwood *et al.*, 2004; Licht and Isebrands, 2005).

In temperate ecosystems, hybrid poplars (*Populus* spp.) and other trees from the Salicaceae family where identified as potential species to enhance nutrient capture in the riparian zone (Licht, 1992; O'Neill and Gordon, 1994; Schultz *et al.*, 1995). Because these flood-tolerant pioneer species become established rapidly and grow very fast, they can be an important nutrient sink within a few years (Kelly *et al.*, 2007). In agroforestry systems, fast-growing poplars are also very effective carbon sinks and can be planted to offset agricultural sources of carbon dioxide (Kort and Turnock, 1998; Oelbermann *et al.*, 2004; Peichl *et al.*, 2006).

While a large body of literature exists on hybrid poplar cultivation (Dickmann *et al.*, 2001), few studies have assessed the potential of these species as nutrient and C sinks in the riparian zone of diverse agroecosystems (Haycock and Pinay, 1993; O'Neill and Gordon, 1994; Tufekcioglu *et al.*, 2003). Also, few studies have compared the nutrient and C sequestration potential of hybrid poplar buffer strips with herbaceous buffer systems, unmanaged or planted (Tufekcioglu *et al.*, 2003). The general conclusions of these studies were the following: (1) compared to a grass buffer, a poplar buffer was slightly more efficient for nitrate (NO_3) retention during the winter months with an efficiency of 99%; (2) biomass and N concentration of hybrid poplar roots increased with increasing soil NO_3 concentration, and (3) after 7 years, C accumulation in plant and litter biomass in a poplar and a switchgrass (*Panicum virgatum* L.) buffer averaged 2960 and 820 kg C ha^{-1} $year^{-1}$, respectively, while N immobilization rates averaged 37 and 16 kg N ha^{-1} $year^{-1}$.

In addition, little is known about the nutrient accumulation and C sequestration potential of different hybrid poplar clones across a range of riparian soil fertility conditions. There is also a need to compare these poplar clones to more conventional buffer systems (natural herbaceous vegetation) in the context of Quebec (Canada) agroecosystems, since no study has addressed these issues until now.

In this article, we address three main research questions: (1) how effective can hybrid poplars be at sequestering both C and nutrients in the riparian zone of different agroecosystems? (2) Are some hybrid poplar clones or unmanaged herbaceous vegetation more appropriate to fulfill these ecological services? (3) Is site fertility an important factor in determining hybrid poplar effectiveness for C and nutrient sequestration? The C and nutrient sequestration of five unrelated hybrid poplar clones growing in the riparian zone of four southern Quebec (Canada) agroecosystems is measured after 6 years of growth and compared to free-growing (unmanaged) herbaceous buffer strips.

2.2 Materials and method

2.2.1 Study sites

During May 2003 four hybrid poplar riparian buffer strips where planted along small headwater streams in the Eastern Townships region of southern Québec, Canada. The buffers had accumulated 6 years (seasons) of growth in the year of the study (2008). Three of the four buffers (Magog, Bromptonville, and St-Isidore-de-Clifton) are located in pastures with different cattle densities and different surrounding landscapes. The other buffer (Roxton Falls) is in the riparian zone of a hayfield. The natural vegetation of the region is dominated by hardwood species, mainly sugar maple (*Acer saccharum* Marsh.).

Three study sites (Bromptonville, Magog and Roxton Falls) are located in the hilly regional landscape unit of Sherbrooke, with gentle slopes and a continental subhumid moderate climate (Robitaille and Saucier, 1998). This landscape unit has 71 % of its area in natural and managed forest (mostly privately owned), 28 % in agricultural land use and in 1 % urban areas. The St-Isidore-de-Clifton site is located in the Mont Mégantic landscape unit, with subhumid-subpolar climate, higher elevation, steeper hillside slopes and a lower area in agricultural use (9 % of land use) (Robitaille and Saucier, 1998). Both landscape units share a similar annual precipitation regime (1000-1100 mm).

Cattle densities at the three pasture sites are 0.6 cow ha^{-1} at Bromptonville, 0.2 cow ha^{-1} at Magog, and 0.5 cow ha^{-1} at St-Isidore-de-Clifton. Bromptonville and St-Isidore-de-Clifton sites are fertilized each year with cow manure, while Magog and Roxton Falls sites are not. Every 5 years, 0.8 t ha^{-1} of lime is also applied at the St-Isidore-de-Clifton site. A summary of site characteristics is presented in Table 2.1.

At each study site, riparian buffers where planted on both sides of the streams for a total length of 90 m and a width of 5.5 m on each stream bank. A row of silver maple (*Acer saccharinum* L.) was planted directly on the stream bank, as recommended by Schultz *et al.* (1995). One meter away from the silver maple row, 3 hybrid poplar rows where planted, with a spacing of 1.5 m between rows and 3 m between trees within a row (4.5 m^2 per hybrid poplar or ~ 2222 hybrid poplars per ha). Bare root cuttings (2 m-long) were planted manually at 30-40 cm depth. Rooted cuttings were chosen in order to improve initial survival (Zsuffa *et al.*, 1977). Planting stock was provided by the Berthierville nursery of the Ministère des Ressources Naturelles et de la Faune (MRNF) of Québec.

Table 2.1

Site characteristics of the four riparian buffer strip sites.

Sites	Land use	Yearly fertilization	Cattle density (cow ha^{-1})	Elevation (m)	Growing season (d)	Topography
Bromptonville	Pasture	Cow manure	0.6	140	180-190	Hilly - gentle slopes
Magog	Pasture	none	0.2	208	180-190	Hilly - gentle slopes
Roxton Falls	Hayfield	none	-	147	180-190	Hilly - gentle slopes
St-Isidore-de-Clifton	Pasture	Cow manure	0.5	360	170	Hilly - moderate slopes

There was no site preparation prior to planting. Fencing was installed one meter away from the third hybrid poplar row in pasture sites to exclude livestock. One month after planting, in June 2003, glyphosate (4 L ha^{-1}) was applied locally at the base of each hybrid poplar (1m^2 per tree) using a backpack sprayer and a cardboard tube to protect trees from drift. Herbicide was applied only once on approximately 25% of the buffer area. This minimal weed control strategy, and fencing, led to the rapid recolonisation of the buffer by natural herbaceous and shrubby vegetation. At some sites, indigenous trees have also begun to colonise the planted buffer: *Larix laricina* (Du Roi) K. Koch, *Pinus strobus* L., *Acer saccharum*, *Alnus rugosa* (Du Roi) J. Clausen, etc.

Five unrelated hybrid poplar clones where used in this study (synonyms, abbreviation of hybrid type and clone number are given in parentheses): (1) *P. trichocarpa* Torr. & Gray x *P. deltoides* cv. Boelare (*P.* x *generosa*, TxD, 3230), (2) *P. deltoides* Bartr. ex Marsh. x *P. nigra* L. (*P.* x *canadensis* Moench, DxN, 3570), (3) *P.* x *canadensis* x *P. maximowiczii* (DNxM, 915508), (4) *P. nigra* L. x *P. maximowiczii* A. Henry (NM6, NxM, 3729) and (5) *P.*

maximowiczii x *P. balsamifera* L. (MxB, 915311). The five poplar clones were chosen because they have different growth patterns, physiological characteristics, and because they had been selected for superior disease resistance/tolerance and growth characteristics in trials in southern Quebec (Périnet *et al.*, 2001).

2.2.2 Experimental design

A randomized block design was used at each of the 4 sites, with 4 blocks (replicates) and 5 hybrid poplar clones (treatments) for a total of 80 experimental plots. Each block contains 5 experimental plots (one clone per plot). Plots are 4.5 m wide and 9 m long (40.5 m^2). Each plot contains 9 trees from a single clone (3 rows; 3 trees per row). Trees are spaced 3 m apart on the row, and the rows are 1.5 m apart. A total of 180 hybrid poplars were planted at each site (36 trees of each clone) for a total of 720 hybrid poplars. This design allowed us to test 5 poplar clones in 4 different riparian environments simultaneously, a common procedure in crop cultivar trials (Steel and Torrie, 1980).

Outside of the randomized block design that contains the hybrid poplar plots, two unmanaged herbaceous buffer plots are present at each site (one on each side of the stream, at the end of planted strips). These unmanaged plots consisted of free-growing herbaceous vegetation that was never harvested since the establishment of hybrid poplar buffers (2003). As in the case of the hybrid poplar buffers, the unmanaged vegetated buffers were protected by a fence at the three pasture sites to prevent livestock grazing. These unmanaged plots are located near the hybrid poplar buffer but far enough to prevent shading by poplars. At each site, the size of unmanaged plots is 6 m (buffer width) x 3 m (18 m^2).

2.2.3 Soil characteristics

Soil samples were taken at 15 cm depth in each plot in 2007 at the Bromptonville and Magog sites, and in 2008 at the St-Isidore-de-Clifton and Roxton Falls sites (total of 80 samples). All samples where analysed for pH. A composite sample was made by pooling samples from 5 plots in order to determine soil texture and organic matter content at the block level. Soil samples where air dried prior to analysis. The determination of soil pH was made using a 2:1 ratio of water to soil. The Bouyoucos (Bouyoucos, 1962) method was used to determine soil particle size distribution, and textural class was determined in accordance with the Canadian Soil Classification Committee (Comité d'experts sur la prospection pédologique d'Agriculture Canada, 1987). Soil organic matter content was determined by loss on ignition at 550°C.

The soil of the Bromptonville site developed on glacial outwash, deposited over lacustrine clay (Cann and Lajoie, 1943). It is well drained and named "Sheldon sandy loam" (Cann and Lajoie, 1943). The soils of the Magog, Roxton Falls and St-Isidore-de-Clifton sites are developed on glacial till. Their respective drainage class and soil name are as follows: Magog (imperfectly drained, "Magog stony loam"), Roxton Falls (well to excessively drained, "St-François sandy loam"), and St-Isidore-de-Clifton (well drained, "Greensboro loam") (Cann and Lajoie, 1943; Cann *et al.*, 1948). Based on the height of stream bank taluses (1 to 2 m grade over 5.5 m buffer strip width, from stream edge to field edge), and the soil surveys cited above, soil depths within the riparian buffers exceed 1m, and no cemented or dense layers are present to restrict rooting depth. Soil characteristics are presented in Table 2.2

Table 2.2

Soil characteristics (0-15 cm) of the study sites: pH, organic matter content (OM), textural class and drainage. Drainage classes were obtained from soil surveys of the Ministry of Agriculture of Canada (Cann and Lajoie, 1943; Cann *et al.* 1948).

Sites	pH	OM (%)	Textural class	Drainage
Bromptonville	6.36	6.21	Silty clay	Good
Magog	5.81	7.47	Clay	Imperfect
Roxton Falls	6.54	4.69	Clay	Good to excessive
St-Isidore-de-Clifton	5.52	7.46	Silty clay	Good
SE	0.04	-		
$p <$	0.001	NS		

2.2.4 Soil nutrient availability

Nutrient availability in the hybrid poplar buffers was determined using Plant Root Simulator (PRS^{TM}-Probes) technology from Western Ag Innovations Inc. Saskatoon, Canada. The PRS-probes consist of an ion exchange membrane encapsulated in a thin plastic probe, which is inserted into the ground with little disturbance of soil structure. The membrane exhibits surface and sorption characteristics similar to those of a plant root. The PRS-probes are an ideal tool to assess nutrient supply rates (ions fluxes) by continuously adsorbing ions over the burial period. Nutrient availability predicted with this method is generally significantly correlated with conventional soil extraction methods over a wide range of soil types (Qian *et al.*, 1992). This technology has also been previously used in agronomic, forestry and environmental studies (Adderley *et al.*, 2006; Coll *et al.*, 2007; Nelson *et al.*, 2007).

Three pairs of probes (an anion and a cation probe in each pair) were buried along the first row of poplars (stream side) and three other pairs were buried along the third row of poplars (field side), for a total of six pairs of probes in each experimental plot (80 plots). For the Magog and Bromptonville sites, probes were buried on August 11 and removed on August 26, 2008. For the Roxton Falls and St-Isidore-de-Clifton sites, probes were buried from August 12 to August 27, 2008. Burial duration was 15 days at all sites. After removal, probes were washed in the field with deionised water and returned to Western Ag Labs for analysis (NO_3, P, K, Ca, Mg). Composites were made by combining the six pairs of probes in each experimental plot. Probe supply rates are reported as µg of nutrient per 10 cm^2.

2.2.5 Riparian vegetation sampling procedures

Near the end of the 6th growing season (from August 30 to September 17, 2008), we selected one representative hybrid poplar in each experimental plot, for a total 80 trees (each tree represents 4.5 m^2 of plot area). In each plot, this representative tree was selected because it was the closest to the average diameter at breast height of all hybrid poplars in the plot. Trees were cut and aboveground components (leaves, branches and stem) were separated and weighed fresh with a tripod scale. Subsamples from stem, branches and leaves were immediately weighed in the field and taken to the lab to determine dry weight. Following dry weight determination, subsamples from stem (n=80), branches (n=80) and leaves (n=80) were ground in a Wiley mill (1-mm screen) and stored in sealed plastic jars for chemical analysis.

The herbaceous layer under poplars was also harvested in order to determine its nutrient and C content. In early August 2008, 1m^2 samples of herbaceous vegetation were harvested (aerial parts clipped down to soil level) at different positions under two representative clones (3570 and 915311). At each site, 8 samples were collected under each of the 3 poplar rows for a total of 24 samples per site. Samples were taken to the lab to determine dry weight. The procedure used to prepare subsamples for chemical analysis was the same as for the poplars.

Herbaceous vegetation located in the unmanaged plots outside of the hybrid poplar buffers was also harvested. In early August, 1m^2 samples of herbaceous vegetation were harvested at the same positions (distance to stream) where the poplar understory vegetation was harvested. At each site, 3 samples per plot where harvested for a total 6 samples per site (3 samples on each side of the stream). Samples were taken to the lab to determine dry weight. The procedure used to prepare subsamples for chemical analysis was the same as for the poplars.

2.2.6 Chemical analysis of plant tissues

Nutrient concentrations (P, K, Ca and Mg) in poplar tissues and herbaceous vegetation were determined by the calcination method (AOAC, 1999) at the Agri-Direct Laboratory, Longeuil (Qc, Canada). Carbon and N concentrations were determined by the combustion method at high temperature (960°C) followed by thermal conductivity detection. Carbon and N analyses were conducted by the Centre for Forest Research laboratory at the University of Sherbrooke (Qc, Canada).

2.2.7 Nutrient accumulation and carbon sequestration potential

Harvested poplars were used to establish allometric relationships between aboveground biomass (stem, branches, and leaves) and diameter at breast height (1.3 m above the soil surface). These allometric relationships were developed for each of the five clones and were used to calculate the biomass of stems, branches and leaves for the entire experimental design (Fortier *et al.*, 2010). These biomass data were then multiplied with nutrient and C concentrations obtained by chemical analysis, in order to estimate the nutrient accumulation and C sequestration of five hybrid poplar clones in four agricultural riparian environments.

For poplar understory vegetation and herbaceous vegetation in the unmanaged buffers, nutrient and C concentrations were multiplied by biomass measurements in $1 m^2$ samples. All nutrient accumulation and C sequestration data were scaled up to one ha area for purposes of comparison with other studies.

2.2.8 Statistical analysis

For data analysis related to hybrid poplars, ANOVA tables were constructed in accordance with Peterson (1985), and degrees of freedom, sum of squares, mean squares and F-values were computed. When a factor was declared statistically significant (Site, Clone and Site x Clone interaction), the standard error of the mean (SE) was used to evaluate differences between means for three levels of significance ($p<0.05$, $p<0.01$ and $p<0.001$). All of the ANOVAs were run with the complete set of data (4 sites, 5 clones, 4 blocks = 80 experimental plots). Site effects reported in this study are on means of all 5 clones at each site, while Clone effects reported are on means of each separate clone across the 4 study sites. Simple regression models were developed with data from all the poplar plots (n=80). For the presentation of results in figures, abbreviations of the names of plantation sites are used (Bromptonville = BRO, Magog = MAG, Roxton Falls = ROX, St-Isidore-de-Clifton = STI).

Because the unmanaged buffer plots were located outside the randomized block design and only two of these plots are present at each site, we performed a *t*-test at the site level in order to compare hybrid poplar riparian buffer compartments and unmanaged buffers (means with different sample sizes). All statistical analyses were done with JMP 6 from SAS Institute (Cary, NC).

2.3 Results

2.3.1 Relationships between nutrient supply rate in riparian soils and nutrient concentrations in poplar aboveground compartments

There was a clear link between the nutrient supply rate measured in riparian soils at each site and the nutrient concentrations in different poplar aboveground compartments (Figure 2.1). This was reflected by highly significant relationships between nutrient supply rate and nutrient concentrations in different poplar compartments as shown in Figure 2.2. Except for Ca, the strongest relationships were obtained when the supply rate of a particular nutrient was related to its foliar content (NO_3 supply rate vs. N foliar content, $R^2=0.47$, $p<0.001$; K supply rate vs. K foliar content, $R^2=0.68$, $p<0.001$; Mg supply rate vs. Mg foliar content, $R^2=0.61$, $p<0.001$). This was also true for the relationship between P supply rate and P concentration in leaves ($R^2=0.22$, $p<0.001$), whereas no significant relationship was observed when P supply rate was related to P content in branches or in stems. The weakest relationship was obtained for NO_3 supply rate and N content in stems ($R^2=0.13$, $p<0.01$).

Consequently, high supply rates of NO_3 and P at Bromptonville and St-Isidore-de-Clifton are associated with higher N and P concentrations in poplar leaves and branches at both of these sites. Elevated K supply rate observed at Bromptonville resulted in a higher K concentration in all aboveground poplar components (stems, branches, and leaves) at this site. A similar pattern was observed for Ca at St-Isidore-de-Clifton and Roxton Falls sites, and for Mg at the Magog site.

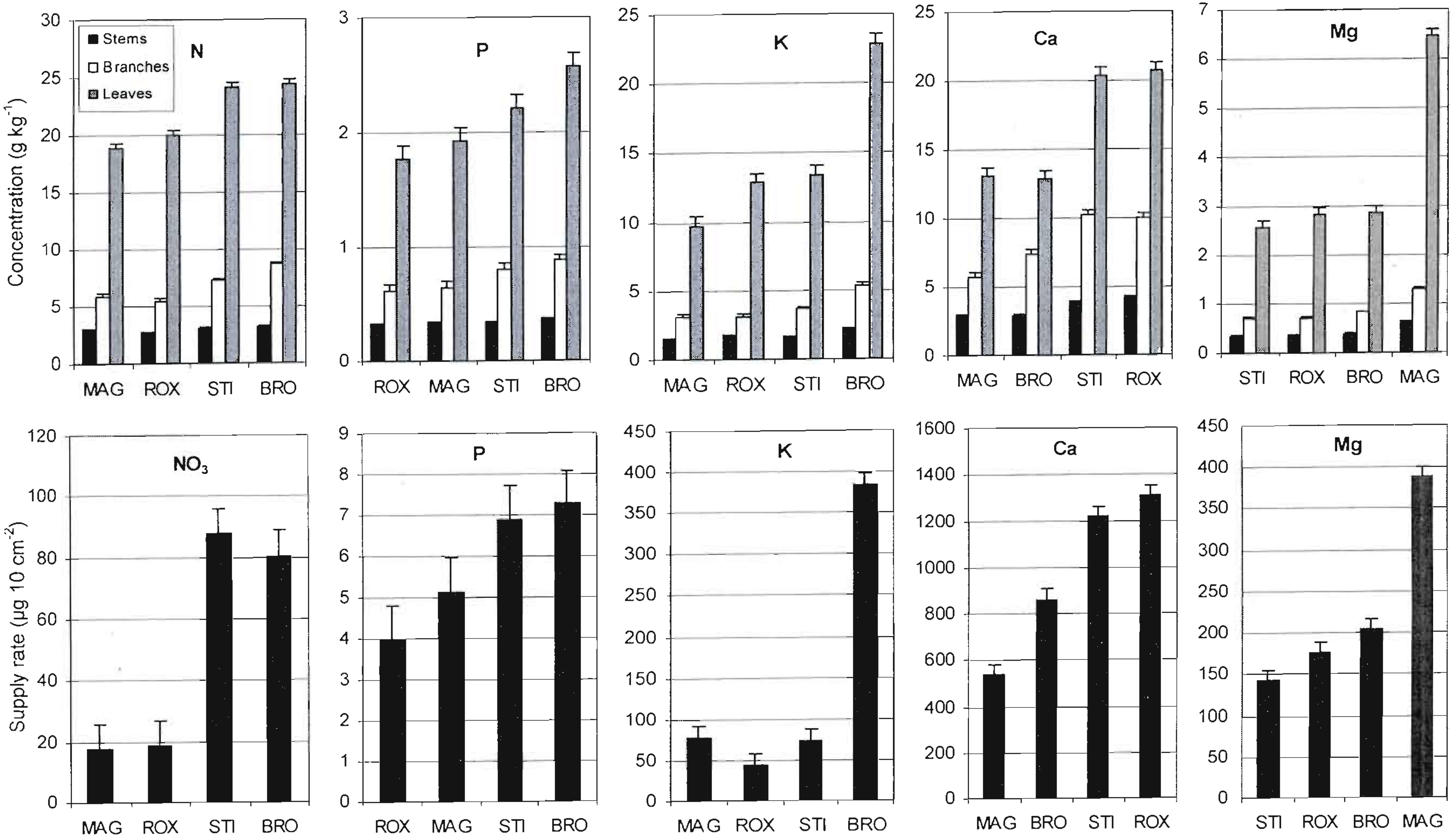

Figure 2.1 Concentration (g kg^{-1} of plant tissue) of nutrients (N, P, K, Ca, Mg) in aboveground hybrid poplar compartments (top diagrams) at the four riparian sites at the end of the 6th growing season, and nutrient supply rate (µg 10 cm^{-2}) measured in riparian soils of the same sites (bottom diagrams). PRS-Probes were buried during a 15 day period in late August 2008. For each variable, site effect is significant at $p<0.001$, except for P supply rate ($p<0.05$) and P concentration in stems (not significant). Vertical bars represent standard errors (SE).

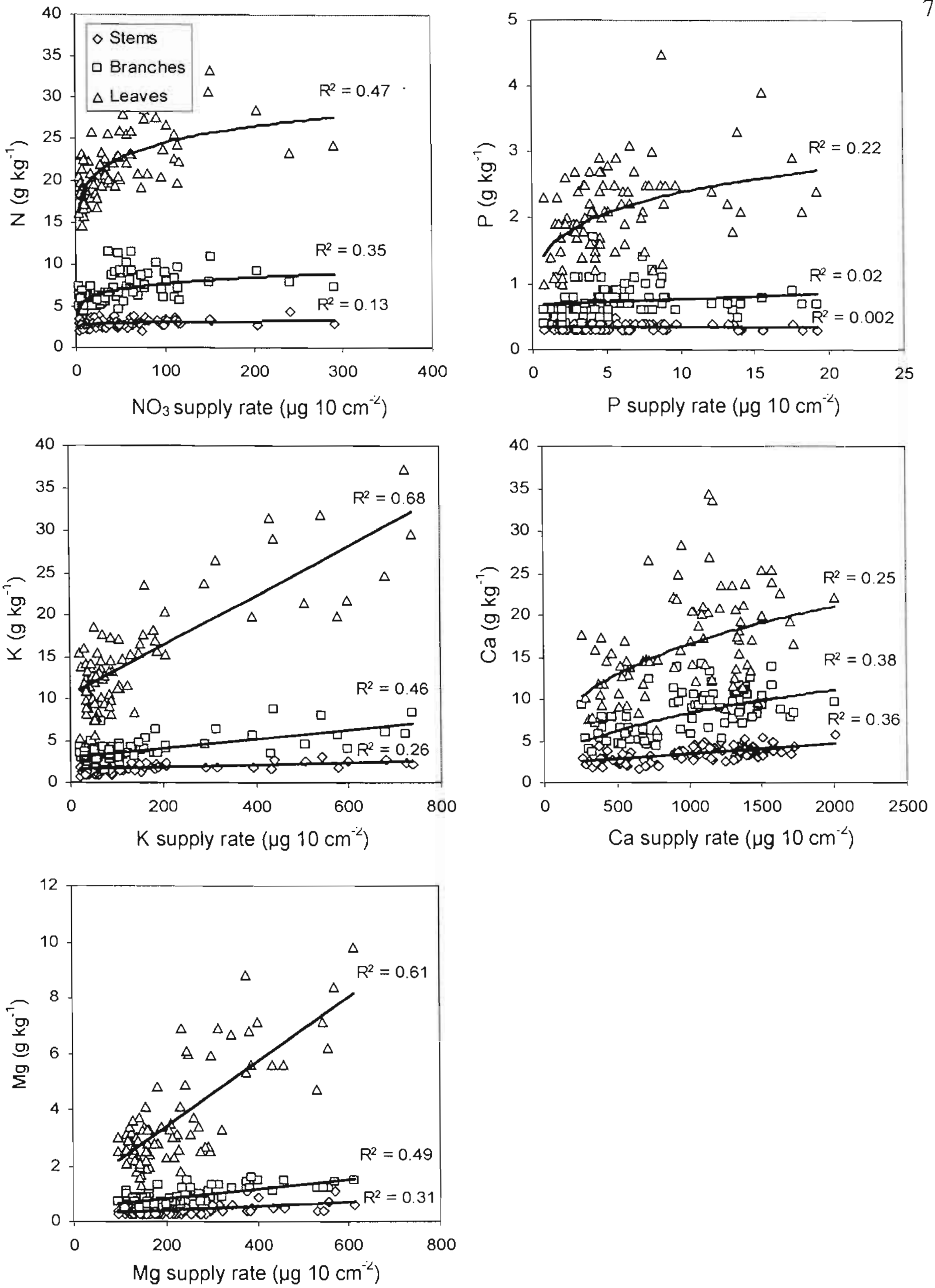

Figure 2.2 Relationship between supply rate (µg 10 cm^{-2}) of nutrient (NO_3, P, K, Ca, Mg) and nutrient concentration (g kg^{-1} of plant tissue) in hybrid poplar compartments. For each relationship, n=80 and $p<0.001$, except for NO_3 supply rate vs. N concentration in stem ($p<0.01$) and P supply rate vs. P concentration in branches and stem (not significant).

Finally, there were significant Clone effects for most nutrient and C concentrations measured in different poplar compartments (C, N, Ca, K and Mg in stem, C, N, K, Mg in branches, and C, N, Ca, Mg in leaves). Weak but significant ($p<0.05$) Site x Clone interactions were also observed (N, Ca, K, Mg in stems, and C, N, Ca, Mg in leaves). However, in all cases, Site effect was by far the largest effect, followed by the Clone effect. No Clone effect and Site x Clone interaction was observed for nutrient supply rates.

2.3.2 Carbon sequestration and nutrient accumulation by hybrid poplars after 6 years

In this section and the following, as well as in tables and figures, the term « total C and nutrient accumulation or sequestration » reflects what is accumulated in all aboveground tree biomass (stems + branches + leaves), while the term « woody biomass » refers to the aboveground woody parts of the trees (stems + branches).

For C and nutrient sequestration in hybrid poplars, few weak ($p<0.05$) Site x Clone interactions were observed in this study (total biomass and woody biomass K accumulation, and woody biomass N accumulation). In all cases, Site effect was by far the largest effect, followed by the Clone effect. Therefore, only Site and Clone effects are reported in the results section.

After 6 years of growth, total aboveground C sequestration and nutrient accumulation (N, P, K, Ca and Mg) were significantly higher in hybrid poplars at the Bromptonville buffer compared to the three other sites. Significantly lower amounts of C and nutrients were accumulated at the Magog site compared to the three other sites (Figure 2.3, Table 2.3). Roxton Falls and St-Isidore-de-Clifton sites occupied an intermediate position. These two sites were not statistically different for total aboveground C sequestration and Ca, Mg and K accumulation, while significantly higher values were observed at St-Isidore-de-Clifton for N and P accumulation (Figure 2.3, Table 2.3). A similar pattern was observed when sites were compared for C sequestration and nutrient accumulation in woody biomass.

Large differences exist in C sequestration and nutrient accumulation among different tree components (Figure 2.3, Table 2.3). Depending on the site, 84-90% of C was sequestered in woody biomass, while only 52-64% of N, 53-64% of P, 50-55% of K, 57-74% of Ca and 38-60% of Mg were accumulated in poplar woody biomass. Therefore, a large proportion of nutrients and a relatively small amount of C were accumulated in leaves.

On a per tree basis, total aboveground C sequestration and N accumulation were significantly higher in clone 3729 compared to the four other clones. Total P accumulation for clone 3729 was not statistically different from clone 915311, but it was significantly higher than in clones 3230, 3570 and 915508. Clone 3570 shows a significantly lower C sequestration value when compared to the four other clones. However, total N and P accumulation for this clone were not statistically different than what was observed for clone 3230.

When C, N and P accumulation are compared on a per tree basis in poplar woody biomass, different patterns of significance are observed. Clone 3729 and 915311 are not statistically different for C sequestration. Nevertheless, these two clones show significantly higher C sequestration in woody biomass when compared to the three other clones. Woody biomass N accumulation for clone 3729 was the highest, while P accumulation was not significantly different from what was observed for clones 915311 and 915508, although it was higher than for clones 3230 and 3570. Finally, clone 3570 did not show lower C, N or P accumulation than clone 3230, when woody biomass is considered.

For comparison purposes, Table 2.4 shows the potential increase in C sequestration, N and P accumulation associated with the exclusive use of clone 3729 in each riparian buffer site. Depending on the site, C sequestration can be enhanced by 29-35% in woody biomass and by 31-37% in total aboveground biomass, while N accumulation can be enhanced by 19-40% in woody biomass and by 29-41% in total aboveground biomass. Moreover, P accumulation in woody biomass could be enhanced by 17-29% and by 30-38% when total aboveground biomass is considered.

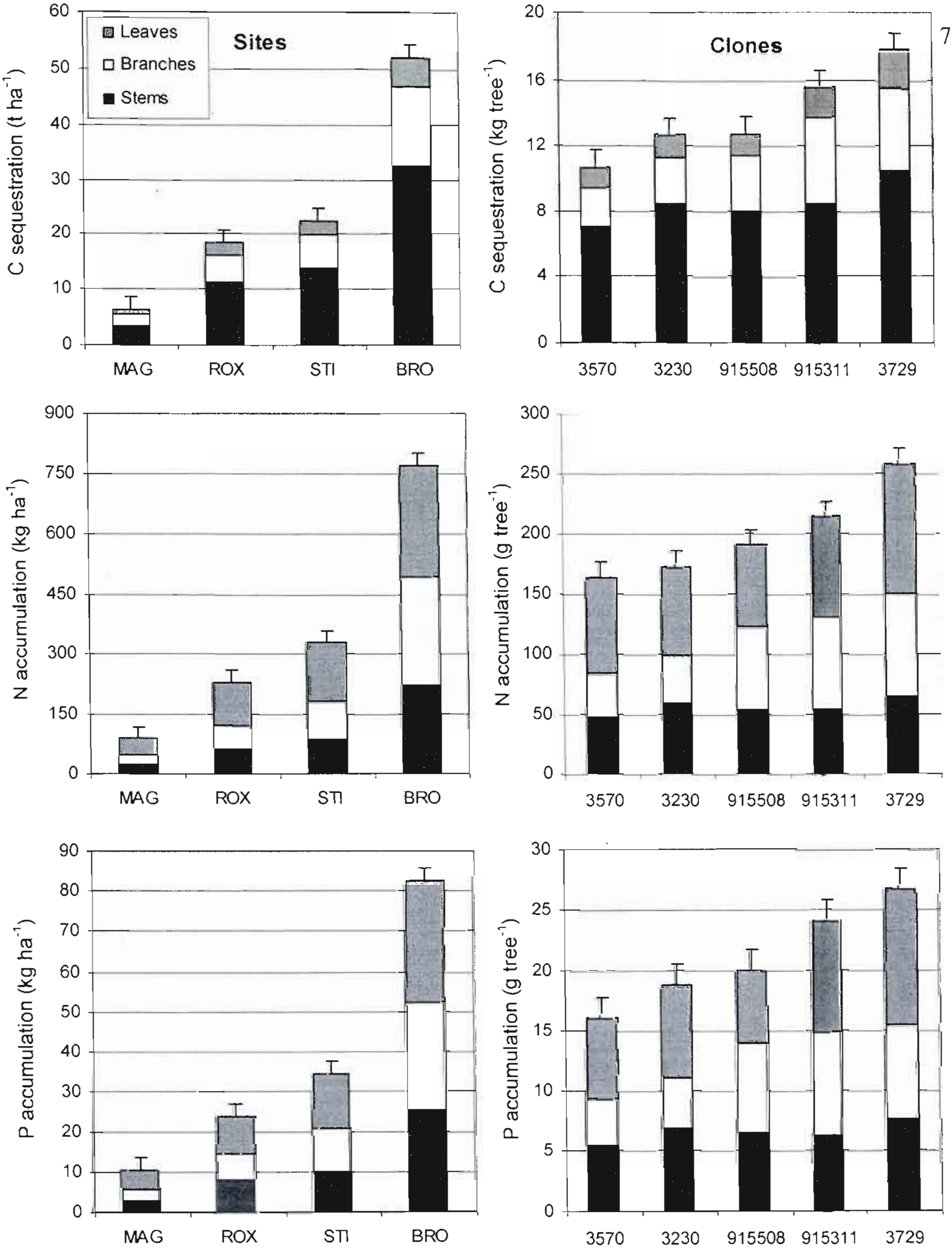

Figure 2.3 Aboveground C sequestration, N and P accumulation at the four hybrid poplar riparian buffer sites (t ha^{-1} or kg ha^{-1}) and for the five clones (kg tree^{-1} or g tree^{-1}) at the end of the 6th growing season. The results are presented for different poplar compartments and S.E. is indicated only for total sequestration or accumulation values. For each variable, site and clone effects are significant at $p<0.001$. Vertical bars represent standard errors (SE).

Table 2.3

Aboveground C sequestration (t ha^{-1}), and N, P, Ca, Mg and K accumulation (kg ha^{-1}) in total biomass (stems + branches + leaves) and in woody biomass (stems + branches) of hybrid poplars at the four riparian buffer sites at the end of the 6th growing season. The percentage of C and nutrients accumulated in hybrid poplar woody biomass is also indicated (% Woody). For each variable, site effect is significant at $p<0.001$.

		Sites				S.E.
		Bromptonville	Magog	Roxton Falls	St-Isidore-de-Clifton	
C (t ha^{-1})	Total biomass	52.01	6.40	18.51	22.44	2.22
	Woody biomass	46.74	5.35	16.06	19.70	2.01
	% Woody	90%	84%	87%	88%	
N (kg ha^{-1})	Total biomass	770.3	90.6	231.4	328.3	29.1
	Woody biomass	490.1	47.0	121.7	184.3	18.1
	% Woody	64%	52%	53%	56%	
P (kg ha^{-1})	Total biomass	82.4	10.3	23.8	34.5	3.3
	Woody biomass	52.42	5.45	14.23	20.70	2.28
	% Woody	64%	53%	60%	60%	
K (kg ha^{-1})	Total biomass	581.8	47.0	143.3	177.9	19.3
	Woody biomass	317.9	24.0	71.5	95.0	13.0
	% Woody	55%	51%	50%	53%	
Ca (kg ha^{-1})	Total biomass	580.4	76.7	327.6	385.6	38.8
	Woody biomass	427.3	43.7	204.8	249.2	27.2
	% Woody	74%	57%	63%	65%	
Mg (kg ha^{-1})	Total biomass	81.8	24.8	30.6	33.6	3.2
	Woody biomass	49.45	9.43	15.43	18.66	1.98
	% Woody	60%	38%	50%	55%	

Table 2.4

Comparison between the most efficient hybrid poplar clone for aboveground C sequestration, N and P accumulation (clone 3729) and the mean for all 5 clones at each site. The potential increase (%) for C sequestration, N and P accumulation associated with the exclusive use of clone 3729 is also indicated in both total biomass (stems + branches + leaves) and woody biomass (stems + branches).

Sites	C ($t\ ha^{-1}$) Woody biomass	C ($t\ ha^{-1}$) Total biomass	N ($kg\ ha^{-1}$) Woody biomass	N ($kg\ ha^{-1}$) Total biomass	P ($kg\ ha^{-1}$) Woody biomass	P ($kg\ ha^{-1}$) Total biomass
Magog - 3729	7.0	8.5	56	117	6.4	14.3
Magog - 5 clones	5.4	6.4	47	91	5.5	10.3
Increase	31%	32%	19%	29%	17%	38%
Roxton Falls - 3729	20.7	24.3	161	319	18.4	31.6
Roxton Falls - 5 clones	16.1	18.5	122	231	14.2	23.8
Increase	29%	31%	33%	38%	29%	33%
St-Isidore-de-Clifton - 3729	26.4	30.3	243	429	25.3	45.0
St-Isidore-de-Clifton - 5 clones	19.7	22.4	184	328	20.7	34.5
Increase	34%	35%	32%	31%	22%	30%
Bromptonville - 3729	63.2	71.1	686	1088	66.9	110.5
Bromptonville - 5 clones	46.7	52.0	490	770	52.4	82.4
Increase	35%	37%	40%	41%	28%	34%

2.3.3 Relationships between nutrient supply rate in riparian soils and nutrient accumulation by hybrid poplars

On a per tree basis, there were positive relationships between NO_3 supply rate in riparian soils and total C sequestration (R^2=0.54, p<0.001), N accumulation (R^2=0.59, p<0.001) and P accumulation (R^2=0.56, p<0.001) in hybrid poplars (Figure 2.4). Weaker relationships were observed between P supply rate and P accumulation (R^2=0.21, p<0.001), N accumulation (R^2=0.16, p<0.01, data not shown) and C accumulation (R^2=0.15, p<0.01, data not shown) in hybrid poplars. Positive relationships were also observed between K supply rate and C sequestration (R^2=0.34, p<0.001, data not shown), N accumulation (R^2=0.39, p<0.001, data not shown) and P accumulation (R^2=0.38, p<0.001, data not shown) in hybrid poplars. A positive relationship was also observed between K supply rate and K accumulation (R^2=0.49, p<0.001; data not shown).

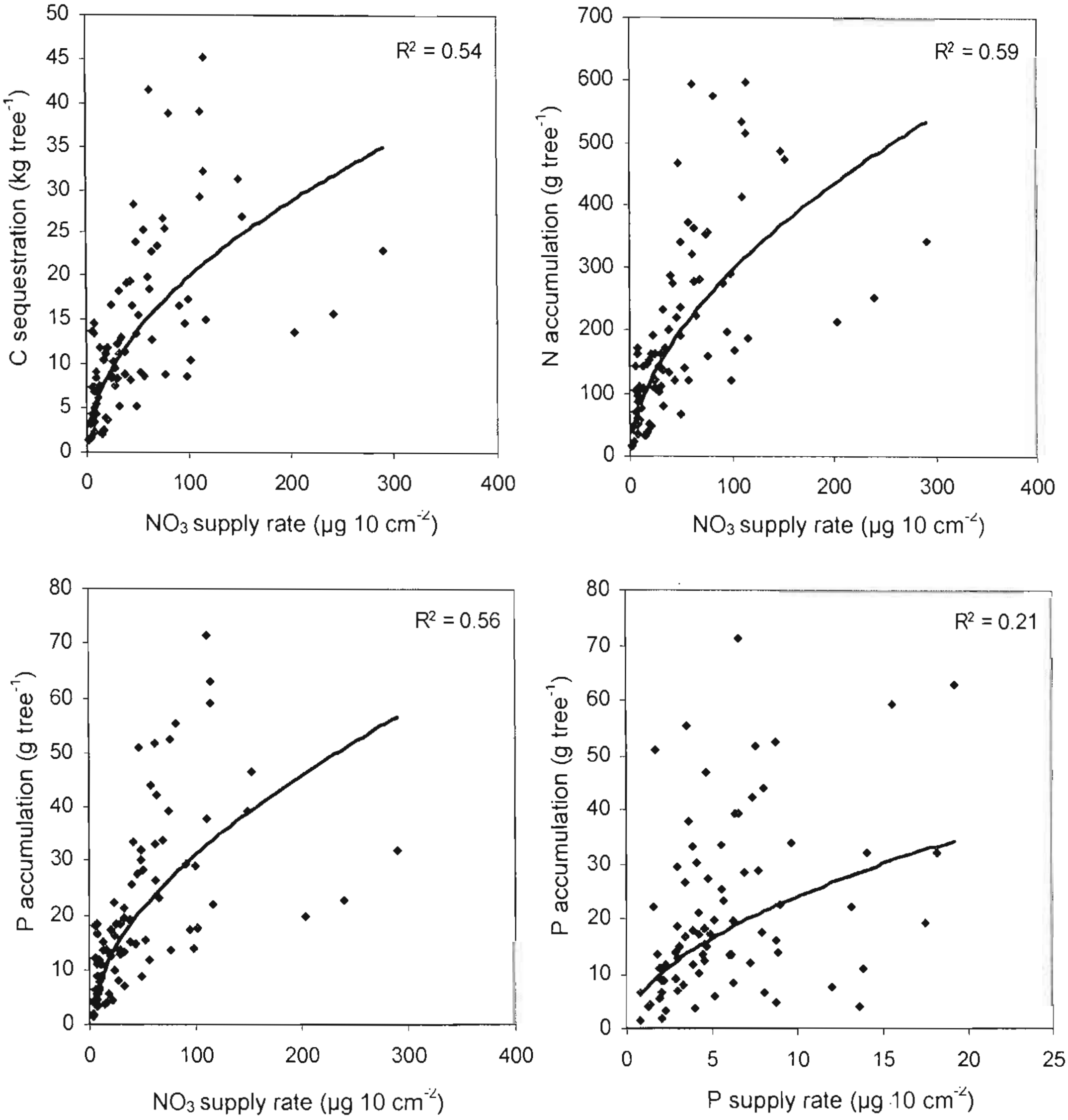

Figure 2.4 Relationships between NO_3 and P supply rate (µg 10cm^{-2}) and C, N and P accumulation (g or kg tree^{-1}) in aboveground biomass (sum of stem, branches and leaves) of hybrid poplars at the end of the 6th growing season. For each relationship, n=80 and p<0.001.

2.3.4 Comparison between different hybrid poplar buffer components and free-growing vegetated buffers after 6 years of growth

At the four sites, aboveground biomass and C sequestration in whole hybrid poplars, woody parts of hybrid poplars, poplar understory herbaceous vegetation, and free-growing vegetated buffer (unmanaged buffer) follow a similar pattern of significance (Figure 2.5). Aboveground biomass and C sequestration in whole poplars and woody biomass were statistically higher than in poplar understory vegetation and the unmanaged buffer. No significant difference was observed when poplar understory vegetation was compared to the unmanaged buffer.

Nitrogen accumulation by hybrid poplars (whole trees or woody parts only) at the Magog site was not statistically different from what was observed in the unmanaged buffer. Nitrogen accumulation was not statistically different when poplar understory vegetation was compared to the unmanaged buffer of this site. The same conclusions can be drawn for P accumulation at the Magog site.

At the Roxton Falls site, N accumulation by whole hybrid poplars was significantly higher when compared to N accumulation by poplar woody biomass, poplar understory or the unmanaged buffer. No significant difference was observed when the unmanaged buffer was compared to poplar woody biomass or poplar understory vegetation.

In the case of P accumulation, Bromptonville, Roxton Falls and St-Isidore-de-Clifton sites had the same pattern. Whole poplars had a significantly higher P accumulation than poplar woody biomass, while poplar woody biomass had a greater P accumulation than poplar understory or unmanaged buffer. Phosphorus accumulation by poplar understory vegetation was not statistically different from P accumulation by the unmanaged buffer. This pattern was also observed for N accumulation at Bromptonville and St-Isidore-de-Clifton.

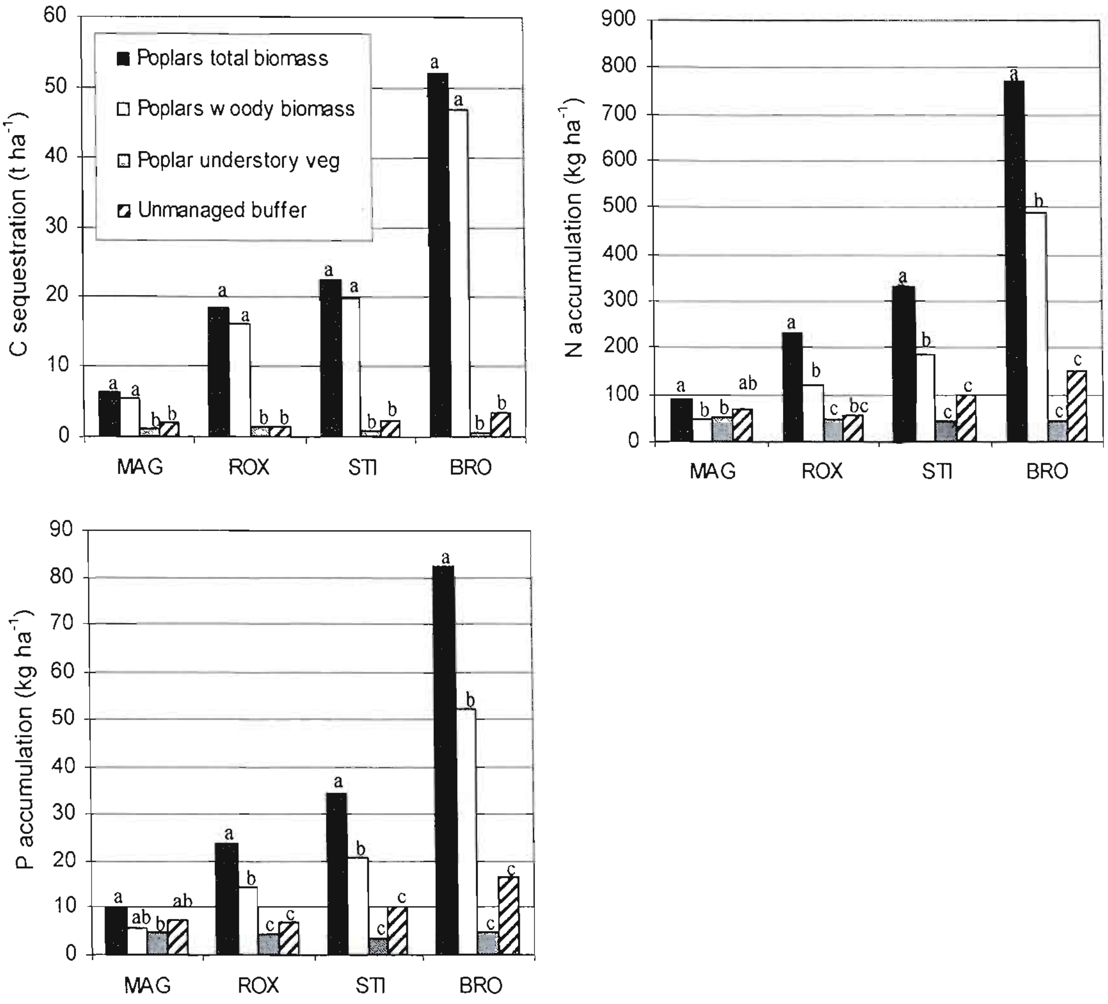

Figure 2.5 Carbon (C) sequestration (t ha^{-1}), N and P accumulation (kg ha^{-1}) for different hybrid poplar riparian buffer compartments after 6 growing seasons (Poplar understory veg = Poplar understory herbaceous vegetation). For comparison purposes, values for adjacent free-growing vegetated buffers (unmanaged buffer) are also presented. For each site, columns with the same letter are not significantly different at $p<0.05$.

2.4 Discussion

2.4.1 The effect of site fertility on C sequestration and nutrient accumulation in hybrid poplar riparian buffers

After 6 years of growth, very large differences in C sequestration and nutrient accumulation in hybrid poplar buffers were observed across the four agricultural riparian sites (Figure 2.3 and Table 2.3). For all variables measured in this study, the largest effect detected by the ANOVA was the Site effect. While C sequestration, N and P accumulation in total aboveground biomass were respectively, 52 t ha^{-1}, 770 kg ha^{-1} and 82 kg ha^{-1} at the Bromptonville site, these values were as low as 6.4 t ha^{-1}, 90 kg ha^{-1} and 10 kg ha^{-1} at the Magog site. Therefore, the effectiveness of hybrid poplars as nutrient and carbon sinks in the agricultural riparian zone depends largely on site variables such as soil fertility.

Site fertility in terms of NO_3 supply rate was the main factor controlling biomass growth (Fortier *et al.*, 2010), and consequently C sequestration and nutrient accumulation in hybrid poplars (Figure 2.4). Bromptonville and St-Isidore-de-Clifton sites are clearly the most fertile, and good soil drainage at both sites seems particularly favourable to sustain vigorous tree growth (Figure 2.1, Tables 2.1 and 2.2) (Cann and Lajoie, 1943; Boysen and Strobl, 1991; Stanturf *et al.*, 2001). The source of high NO_3 at both of these pasture sites is most probably the consequence of annual fertilization with cow manure and a relatively high cow density (Table 2.1). It is well known that higher yields in hybrid poplar plantations are sustained when N amendments are relatively high and applied frequently (Stanturf *et al.*, 2001; Brown and van den Driessche, 2002; Coleman *et al.*, 2006). Moreover, according to the leaf nutrient concentration (N, P and K) of hybrid poplars (Figure 2.1), it is clear that a more balanced nutritional status, in terms of nutrient requirements, was reached at Bromptonville and St-Isidore-de-Clifton (Hanson, 1994).

Relatively high P and K supply rates at the Bromptonville site (Figure 2.1) may also have played an important role in sustaining vigorous tree growth, and therefore high C sequestration and nutrient capture. Lower survival rate (Fortier *et al.*, 2010), lower soil pH (Boysen and Strobl, 1991), shorter growing season (Tabbush and Beaton, 1998) and relatively low K supply rate at St-Isidore-de-Clifton are all potential factors that could explain why C and nutrient sequestration at this site are more than two times lower than what was observed at the Bromptonville site (Figure 2.1, Table 2.1 and 2.2). Compared to the St-Isidore-de-Clifton site, only slightly lower C and nutrient sequestration were observed at Roxton Falls, although NO_3, P and K supply rates where much lower at this site. Since there were no animal or chemical nutrient inputs at this hayfield site, a soil pH value of 6.5, which is optimal for several hybrid poplar clones (Boysen and Strobl, 1991; Stanturf *et al.*, 2001), may have enhanced nutrient availability at Roxton Falls, a relatively low fertility site (Figure 2.1 and Table 2.2).

We also observed synergism between the high growth rates and the relatively high N, P and K concentrations in different poplar compartments at the Bromptonville site, which resulted in an increased N, P and K accumulation (Jarrell and Beverly, 1981). For example, although total aboveground biomass was 2.8 times higher at Bromptonville when compared to Roxton Falls (Fortier *et al.*, 2010), N, P and K accumulation were, respectively 3.3, 3.5 and 4.1 times greater at the Bromptonville site. This synergism between biomass production and nutrient concentration also positively affected N and P accumulation at St-Isidore-de-Clifton. Moreover, relatively high P concentrations in poplar branches and leaves at Bromptonville and St-Isidore-de-Clifton may be attributable to the relatively high P supply rates at both of these sites, but also to the effect of N fertilization (cow manure and cow dejections), which is known to increase P assimilation and P concentrations in plant tissues (Grunes, 1959).

The adverse effect of an elevated Mg supply rate on poplar growth and, consequently, on poor C, N and P accumulation at the Magog site (Figure 2.1 and 2.3, Table 2.3) is consistent with the general assumption that high Mg concentration in soils tends to reduce crop yield (Proctor, 1971). It seems obvious that there was a nutritional imbalance related to the « concentration effect » for Mg at the Magog site since total Mg accumulation was disproportionately high compared to biomass accumulation (Jarrell and Beverly, 1981). Hence, although biomass yield was 8 times lower at Magog when compared to Bromptonville, Mg accumulation was only 3.3 times lower. Very high levels of Mg in poplar leaves combined with relatively low foliar N, P and K concentrations at the Magog site is also a sign of nutritional imbalance (Leech and Kim, 1981; Hanson, 1994).

Furthermore, the Magog site was imperfectly drained, which contrasted with the three other sites (well drained) (Cann and Lajoie, 1943; Cann *et al.*, 1948) (Table 2.2), and some parts of the Magog plantation where frequently waterlogged (J. Fortier, field observations). Waterlogged soils favour microbial mobilization of Mg in soils (Silverman and Munoz, 1980). This could explain the relatively high Mg supply rate and high Mg concentration in poplar tissues at this site. Imperfect drainage is also associated with reduced growth in hybrid poplar stands (Tabbush and Beaton, 1998; Stanturf *et al.*, 2001). Finally, survival rate at the Magog site was about 20-35% lower than at the three other sites (Fortier *et al.*, 2010). The combination of all these factors could explain the low C sequestration, N and P accumulation at this site.

2.4.2 Clone selection: an important determinant for C sequestration and nutrient accumulation

Although Site effect was by far the largest effect in this study, the Clone effect was also important (Figure 2.3). In a previous study on biomass yields after 6 years in the same experimental design, we observed important growth differences among the five hybrid poplars clones, with clones 3729 and 915311 having the highest yields (Fortier *et al.*, 2010). In this study, these higher growth rates are translated into higher C and nutrient sequestration for clone 915311 and, particularly for clone 3729, compared to the three other clones (Figure 2.3). Across the four study sites, total aboveground C sequestration, N and P accumulation at the site level could be, respectively enhanced by 31-37%, 29-41% and 30-38% with the sole use of clone 3729 (Table 2.4).

It is well known that clone 3729 (also known as NM6) has a higher early growth rate compared to other poplar clones (Brown *et al.*, 1996). This may be related to its exceptional early rooting compared to other hybrid types (Green *et al.*, 2003; Zalesny *et al.*, 2009). Early rooting ability of clone 3729 may be an important factor in rapidly acquiring high amounts of nutrients and water to sustain high yields. Longer term studies also suggest that clone 3729 maintains its high growth rate throughout the years. After 9 years of growth, clone 3729 had the highest basal area in comparison with 54 other poplar clones of various parentage (Lo and Abrahamson, 1996). Other factors such as nutrient requirements (Heilman and Norby, 1998), nutrient-use efficiency (Lodhiyal and Lodhiyal, 1997), water-use efficiency (Blake *et al.*, 1984), light-use efficiency (Cannell *et al.*, 1988) and phenotypic plasticity, in response to differential N availability (Cooke *et al.*, 2005) could also explain differences in C and nutrient sequestration observed between the five clones studied here.

Although several Site x Clone interactions were observed for nutrient concentrations in different poplar compartments (see section 2.3.1), few weak Site x Clone interactions were observed in terms of nutrient sequestration (see section 2.3.2), with the Site effect always remaining the largest effect, followed by the Clone effect. This trend may be related to the fact that no significant Site x Clone interactions were seen for biomass growth (Fortier *et al.*, 2010). Therefore, biomass growth appears to be the main determinant for C and nutrient accumulation.

2.4.3 Comparison of hybrid poplar buffers with unmanaged buffers

As shown in Figure 2.5, important C and nutrient accumulation differences exist after 6 years of growth between hybrid poplar buffers and unmanaged herbaceous buffers. Compared to an unmanaged herbaceous buffer, the distinct advantage of hybrid poplar buffers is that C and nutrient sequestration greatly increase with increasing site fertility (Figure 2.5), whereas they do so to a much lesser extent in herbaceous buffers.

Nevertheless, results comparing unmanaged buffer and hybrid poplar buffer have to be interpreted with caution since nutrients and C accumulated in the herbaceous layer only represent what was accumulated in a single year. Much higher nutrient exportation would be expected from the unmanaged buffer if herbaceous vegetation had been harvested each year.

Higher nutrient exportation from the poplar buffers would also have occurred if poplar understory vegetation had been harvested each year (Figure 2.5).

2.4.4 Hybrid poplar buffer design and management implications

In this study, site fertility, especially in terms of NO_3 supply rate, is the most important factor in determining how effective hybrid poplars can be at sequestering both C and nutrients. Therefore, hybrid poplars would be a very appropriate choice to effectively respond to high non-point inputs of N originating from fertilized crops or pastures. Since riparian buffer NO_3 removal efficiency is negatively correlated with NO_3 inputs (Sabater *et al.*, 2003), there is a need to design buffers with nutrient demanding trees such as hybrid poplar in areas where N leaching is more problematic. As pointed out by Bradshaw *et al.* (2000), because riparian ecosystems receive nutrient inputs episodically, poplars may have developed the ability to store high amounts of N in the form of protein for subsequent use. High N availability in soil may also enhance P concentration and accumulation in vegetation (Grunes, 1959).

However, if hybrid poplars remain unharvested, the P and N assimilation function of the buffer could eventually be compromised (Lowrance *et al.*, 1997; Dosskey, 2001). As trees reach a steady-state in their growth, the buffer could become nutrient-saturated and decaying vegetation would also contribute to soil N and P pools (Kelly *et al.*, 2007). Consequently, an unmanaged buffer may potentially become a nutrient source rather than a sink over the years (Dorioz *et al.*, 2006).

For these reasons, it is recommended to harvest whole hybrid poplars in late summer when they still have all their leaves. This strategy will ensure a maximum N and P exportation from the buffer zone, given the fact that N and P contained in leaves, respectively accounted for 36-48% and 36-47% of total aboveground N and P content of 6-year-old hybrid poplars (Table 2.3). However, whole-tree harvest in alluvial poplar stands may lead to soil depletion in N, P and K and eventually limit tree growth potential (White, 1974). In this context, there is a need to evaluate the tradeoffs between a maximal nutrient removal objective and a maximal growth rate objective. It was also argued by Kelly *et al.* (2007) that a growing season harvest would limit the ability of poplars to regenerate through vegetative means, in comparison with a non-growing season harvest. Therefore, these authors propose a complete harvest of poplars during the dormant season in order to insure stand regeneration over multiple cutting cycles of 7-10 years.

Clone selection is also an important factor to consider if maximal C and nutrient sequestration is needed. However, although important clonal differences exist in terms of C and nutrient sequestration (Figure 2.3, Table 2.4), we would recommend the use of a diversity of unrelated clones in order to enhance buffer resilience to insect pests and pathogens (Stanturf *et al.*, 2001). We also believe that planting and managing a clonal diversity is a safer strategy on the long term.

Furthermore, clonal diversity will also improve structural diversity within the buffer because hybrid poplars from different parentages have different tree architectures and rooting patterns (Boysen and Strobl, 1991; Block *et al.*, 2006). Because of these differences in rooting patterns, a multiclonal buffer may have a greater capacity to remove nutrients and pollutants from different soil depths within the buffer.

2.5 Conclusion

This study shows that substantial amounts of C and nutrients can be accumulated in hybrid poplar riparian buffer systems. However, the effectiveness of hybrid poplars in sequestering both C and nutrients seems to largely depend on site fertility, particularly in terms of NO_3 supply rate. Important differences in C and nutrient sequestration also exist between clones, with clone 3729 being the best performing clone across the four study sites. Finally, compared to unmanaged herbaceous buffer systems, ecological services generated by multiclonal hybrid poplar buffers, in terms of C and nutrient sequestration, greatly increased as site fertility increased.

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CHAPITRE III

UNDERSTORY PLANT SPECIES DIVERSITY AND BIOMASS IN HYBRID POPLAR RIPARIAN BUFFER STRIPS IN PASTURES

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Abstract

Apart from their water quality functions, riparian habitats are known to be unique components of agricultural landscapes because they support plant communities and animals that are not found in other farmland habitats. However, little is known about the influence of planted agroforestry systems on riparian plant diversity. In this study, understory plant biomass and species richness were measured in 6-year old hybrid poplar riparian buffer strips, in the understory of two unrelated clones, planted on three pasture sites of southern Quebec. Canopy openness was the most important factor controlling understory biomass in hybrid poplar buffers. Large differences in canopy openness were observed between sites and between poplar clones, with lower understory biomass observed on sites with lowest canopy openness, and under clone 915311 which produces more shade. Higher total species richness was observed at the low soil fertility site of Magog, where poplar growth is low and light availability is high (high canopy openness). Nevertheless, the lower species richness observed at the Bromptonville and St-Isidore-de-Clifton sites was mainly related to a lower richness of introduced and upland species, with mean native and mean wetland species richness being similar across the three study sites. Total understory plant diversity (Simpson's index) was similar across the three study sites. Decrease in light availability was also closely related to a decrease in the cover and richness of upland and introduced species, without having a significant effect on native and wetland species cover and richness. The largest differences between hybrid poplar buffer understory vegetation and adjacent free-growing herbaceous buffer vegetation were observed for plant biomass, and not species richness. Finally, hybrid poplar clone selection in the buffer design appears to be very important because clone 915311 dramatically reduced understory vegetation growth and lowered the cover of all species groups, including native and wetland species, compared to clone 3570. We suggest that hybrid poplar riparian buffers could be a very promising tool to restore connectivity between forest fragments in agriculture-dominated landscapes, because they can create a forest cover within 6 years on fertile sites, while lowering introduced species richness and cover without significantly compromising native species and native wetland species richness and diversity.

Keywords

Plant species richness, canopy openness, native species, wetland species, introduced species, herbaceous buffer.

3.1 Introduction

Riparian ecosystems have a central role to play in non point source pollution abatement and water quality protection within agricultural watersheds (Schlosser and Karr, 1981; Lowrance *et al.*, 1984; Gregory *et al.*, 1991; Osborne and Kovacic, 1993; Lowrance *et al.*, 1997; Décamps *et al.*, 2004). Besides their water quality functions, riparian ecosystems are known to be unique habitats of agricultural landscapes because they support plant communities and animals not found in other farmland habitats (Boutin *et al.*, 2003; Jobin *et al.*, 2004). However, little is known about the influence of planted agroforestry systems on riparian floral diversity since most designs have included establishment of vigorous perennial herbaceous crops, such as cool and warm season grasses (*Agrostis alba* L, *Bromus inermis* Leyss., *Festuca rubra* L., *Lolium perenne* L., *Medicago sativa* L.and *Panicum virgatum* L..) (Tufekcioglu *et al.*, 2003; Schultz *et al.*, 2004; Kelly *et al.*, 2007; Duchemin and Hogue, 2009). Inclusion of such perennial crops is generally intended for impeding water runoff across the riparian zone and enhancing sediment deposition and nutrient capture by the buffer, but also for producing harvestable grasses for forage or bioenergy.

Multifunctional plantations such as riparian buffer strips are among the more sustainable options to produce wood and biomass (Rockwood *et al.*, 2004; Licht and Isebrands, 2005; Fortier *et al.*, 2010a, b; Paquette and Messier, 2010). Nevertheless, tree plantations are negatively perceived by some of the public and some environmentalists mainly because they have lower biodiversity compared to natural forests (Potton, 1994; Stephens and Wagner, 2007). It is even argued that exotic monospecific plantations are «biological deserts»

(Rosoman, 1994). However, tree plantations, even those composed of exotic species, can support more biodiversity than the agricultural systems (pasture and row crops) they replace (O'Loughlin, 1995). These opposing views illustrate the need and the high interest of obtaining empirical data on the effect of planted riparian tree buffers on plant diversity.

There is also a need to document the potential effects of planted riparian buffer strips on understory plant biomass and diversity because the understory component of the buffer has a large influence on many ecosystem services within agroecosystems (runoff control, soil stabilisation and formation, nutrient cycling, habitat for crop pollinators and natural enemies of insect pests, etc.) (Marquez *et al.*, 1999; Zaimes *et al.*, 2004; Altieri *et al.*, 2005; Mankin *et al.*, 2007; Fortier *et al.*, 2010b). Furthermore, agronomic concerns exist regarding the potential role of riparian buffers (natural or planted) systems as sources of weeds, or as corridors for the movement of weedy species within agricultural landscapes. In the agricultural landscape of southern Quebec, Canada, this information exists for different natural riparian habitats (herbaceous, shrubby and naturally wooded strips) (Boutin *et al.*, 2003), but not for planted hybrid poplar riparian buffers strips.

There are few studies that assess understory biomass and diversity in poplar plantations. In Sweden, it as been shown that small-scale afforestation with poplar stands increases plant diversity in agriculture-dominated landscapes (Weih *et al.*, 2003). In the rangelands of Argentina, little evidence of local extinctions or invasions following poplar afforestation was observed (Clavijo *et al.*, 2005). These authors found that afforested poplar stands had a higher proportion of C3 grasses, lower species diversity, but similar species richness (number of species) when compared to adjacent native grassland. Spontaneous establishment of several woody species have also been observed in poplar plantations in Flanders, Belgium (Lust *et al.*, 2001).

Several factors can affect understory biomass and biodiversity in poplar plantations. Tending operations seem to be an important factor affecting species richness in very low density poplar plantations on alluvial soils in France (200 stem ha^{-1}). Understory species richness tends to increase with increasing frequency and intensity of disking operations, while understory plant biomass tends to decrease (Laquerbe, 1999; Laquerbe, 2000). However, most species that contributed to this diversity were annual or biennial species, since perennial species are highly affected by tending disturbances. In these hybrid poplar plantations, understory plant biomass generally ranges between 250-1000 g m^{-2}, although values as high as 2000 g m^{-2} were observed in the oldest and least maintained plantations (Laquerbe, 1999). This is similar to values reported in the United States, where eastern cottonwood (*Populus deltoides*) plantations on alluvial soils produce understory biomasses exceeding 1200 g m^{-2} (Wesley *et al.*, 1981).

Site, plantation age and position in the landscape (alluvial vs. upland) are also known to affect herbaceous species richness in hybrid poplar stands. Berthelot *et al.* (2005) observed that herbaceous species richness was higher in younger plantations (7-15 yrs) than in mature plantations (24-30 yrs), with particularly low species richness in mature upland plantations. However, in overmature and unexploited plantations (40-45 yrs) species richness tends to increase when compared to mature plantations (Berthelot *et al.*, 2005). Generally, as poplar plantations aged, the canopy closed and tending operations decreased. During these changes in stand structure and disturbance level, understory communities exhibited different successional stages; from annual pioneer species to meadow perennial species, and finally to forest woody species similar to post-pioneer stages of natural riparian forests (Laquerbe, 1999; Laquerbe, 2000).

Other factors that may affect understory biomass growth and diversity in hybrid poplar buffer strips have not been widely studied. Hybrid poplar clone selection can have an important effect on understory biomass growth and diversity because different clones have different growth rates and tree architecture, which in turn, could affect light availability (Eckenwalder, 2001; Paquette *et al.*, 2008; Fortier *et al.*, 2010a).

Understory plant biomass and species richness were measured in 6-year old hybrid poplar riparian buffer strips, in the understory of two unrelated clones, planted on three pastures sites of southern Quebec. The objectives of this study are (1) to determine the effects of different sites and clones on understory plant biomass and species richness, (2) to determine if hybrid poplar riparian buffers can contribute to the establishment of native plants vs. introduced species, (3) to determine if hybrid poplar riparian buffers can contribute to the establishment of native riparian (wetland) species, (4) to compare hybrid poplar understory biomass and species richness with conventional free-growing herbaceous strips near streams in pastures.

3.2 Material and methods

3.2.1 Study sites

During May 2003 three hybrid poplar riparian buffer strips were planted on pastures along small headwater streams in the Eastern Townships region of southern Québec, Canada. The buffers had cumulated 6 years (seasons) of growth in the year of the study (2008). The natural vegetation of the region is dominated by hardwood species, mainly sugar maple (*Acer saccharum* Marsh.).

Two study sites (Bromptonville and Magog) are located in the Sherbrooke regional landscape unit, characterized by gentle slopes (Robitaille and Saucier, 1998). Natural and managed forests (most privately owned) occur over 71 % of this landscape, and 28 % is in agricultural land use. The St-Isidore-de-Clifton site is located in the Mont Mégantic landscape unit, characterized by higher elevation, steeper hillside slopes and a lower area in agricultural use (9 % of land use) (Robitaille and Saucier, 1998). Both landscape units share similar annual precipitation (1000-1100 mm).

Cattle densities at the sites are 0.6 cow ha^{-1} at Bromptonville, 0.5 cow ha^{-1} at St-Isidore-de-Clifton, and 0.2 cow ha^{-1} at Magog. Cow manure is spread each year at the Bromptonville and St-Isidore-de-Clifton pastures, but not at the Magog pasture. Lime is also applied (0.8 t ha^{-1}) at 5 year intervals the St-Isidore-de-Clifton site.

At each study site, riparian buffers where planted on both sides of the stream for a total length of 90 m and a width of 5.5 m on each stream bank. A row of silver maple (*Acer* *saccharinum* L.) was planted directly on the stream bank, as recommended by Schultz *et al.* (1995). One meter away from the silver maple row, 3 hybrid poplar rows were planted, with a spacing of 1.5 m between rows and 3 m between trees within a row (4.5 m^2 per hybrid poplar or ~ 2222 hybrid poplars per ha). Bare root cuttings (2 m-long) were planted manually at 30-40 cm depth. Rooted cuttings were chosen in order to improve initial survival (Zsuffa *et al.*, 1977). Planting stock was provided by the Berthierville nursery of the Ministère des Ressources Naturelles et de la Faune (MRNF) of Québec.

There was no site preparation prior to planting. Fencing was installed one meter away from the third hybrid poplar row to exclude livestock. One month after planting, in June 2003, glyphosate (4 L ha^{-1}) was applied locally at the base of each hybrid poplar (1m^2 per tree) using a backpack sprayer and a cardboard tube to protect trees from drift. Herbicide was applied only once on approximately 25% of the buffer area. This minimal weed control strategy, and fencing, led to the rapid recolonisation of the buffer by natural herbaceous and shrubby vegetation. At some sites, indigenous trees have also begun to colonise the planted buffer: *Larix laricina* (Du Roi) K. Koch, *Pinus strobus* L., *Acer saccharum*, *Alnus rugosa* (Du Roi) J. Clausen, etc.

Two unrelated hybrid poplar clones were used in this study (synonyms, abbreviation of hybrid type and clone number are given in parentheses): (1) *Populus deltoides* Bartr. ex Marsh. x *Populus nigra* L. (*P.* x *canadensis* Moench, DxN, 3570) and (2) *Populus maximowiczii* x *Populus balsamifera* L. (MxB, 915311). These clones were chosen because they have different growth patterns and branching habits (Fortier *et al.*, 2010a).

Soil characteristics and nutrient availability within the hybrid poplar buffers strips were measured in previous studies (Fortier *et al.*, 2010a, b) and are presented in Table 3.1 along with other site characteristics. Based on the results of our previous study (Fortier *et al.*, 2010a), mean aboveground biomass per tree (stem+branches+leaves) is also shown for clones 3570 and 915311 at each site.

Table 3.1
Site and soil characteristics of the three riparian buffer strips. Nutrient supply rate (μg 10 cm^{-2}) measured with PRS-probes in the soil of the three riparian hybrid poplar buffer strips are also presented, as well as mean aboveground biomass per tree (stem+branches+leaves) for clones 915311 and 3570 (see additional details in Fortier *et al.* 2010 a,b).

Site and soil characteristics	Sites		
	Bromptonville	Magog	St-Isidore-de-Clifton
Land use	Pasture	Pasture	Pasture
Elevation (m)	140	208	360
Soil texture (0-15 cm)	Silty clay	Clay	Silty clay
Organic matter (%)	6.21	7.47	7.46
pH	6.36	5.81	5.52
NO_3	80.5	17.4	87.9
NH_4	5.52	9.09	14.07
P	7.28	5.14	6.90
K	383.6	77.6	74.3
Ca	860	540	1220
Mg	204	388	142
915311 (kg tree^{-1})	67	14	31
3570 (kg tree^{-1})	46	7	23

3.2.2 Experimental design

A randomized block design was used at each of the 3 sites, with 4 blocks (replicates) and 5 hybrid poplar clones (treatments) for a total of 60 experimental plots. Each block contains five experimental plots (one clone per plot). Plots are 4.5 m wide and 9 m long (40.5 m^2). Each plot contains 9 trees from a single clone (3 rows; 3 trees per row). Trees are spaced 3 m apart on the row, and the rows are 1.5 m apart. However, only two of the five clones were used to study the understory, and thus the total number of experimental plots in this study is 24 (3 sites x 4 blocks x 2 clones).

Outside of the randomized block design that contains the hybrid poplar plots, two unmanaged herbaceous buffer plots are present at each site (one on each side of the stream, at the end of planted strips). These unmanaged plots consisted of free-growing herbaceous vegetation that was never harvested since the establishment of the hybrid poplar buffers (2003). As in the case of the hybrid poplar buffers, the free-growing vegetated buffers were protected by a fence to prevent livestock grazing. These unmanaged plots are located near the hybrid poplar buffers, but far enough to prevent shading. At each site, the size of unmanaged plots is 5.5 m (buffer width) by 3 m (16.5 m^2).

3.2.3 Vegetation sampling

Vegetation sampling was done in the first week of August 2008 at all three sites. In each hybrid poplar experimental plot, 1 m^2 microplots were placed at three different positions within each plot: (1) under the hybrid poplar row on the field side; (2) under the hybrid poplar row in the middle of the plot and (3) under the poplar row on the streamside. Within each microplot, the percent cover of each vascular plant species was recorded by cover class (1, 0-1%; 2, 1-5%, 3, 5-25%; 4, 25-50%; 5, 50-75%; 6, 75-100%; 7, 100%), and then harvested (aerial parts clipped down to soil level) for total biomass determination. Harvested understory samples were placed in large paper bags and taken to the lab to determine dry weight. A total of 72 microplots were sampled in hybrid poplar plots (3 sites x 2 clones x 4 blocks x 3 microplots per plot = 72). Voucher specimens were taken and pressed to confirm or determine the species of grasses, *Carex*, *Juncus*, *Scirpus* and *Aster*, and to identify a few unknown species.

Recorded species (Table 3.2) were divided into three types of categories: (1) native or introduced, (2) wetland affinity or non wetland (upland), and (3) weed or non weed. Introduced species are those that did not occur in the study area prior to European settlement, and that have colonised the sites as a result of human activity. Species and status (native or introduced) designation follow the nomenclature and information found in Marie-Victorin *et al.* (2002). Wetland affinity designation is based on a species' obligate or facultative association with wetland habitat, or the absence of such an association (upland species). The list of wetland species was taken from Gauthier (1997). Because only two species recorded were listed as wetland obligate species, we pooled them with wetland facultative species to produce a single wetland species category. Weed status was assigned based on two provincial lists (Gouvernement du Québec, 1981; MAPAQ, 2009). From these lists, we removed the following species: *Bromus inermis* Leyss., *Phalaris arundinacea* L, *Phleum pratense* L. and *Trifolium pratense* L. because they are pasture forage species that are often planted, and therefore cannot be considered weed species in the context of the present study (hybrid poplar buffers located in pastures).

Herbaceous vegetation located in the unmanaged (free-growing) plots outside of the hybrid poplar buffers was also sampled in microplots, at the same positions (distance relative to stream) where the hybrid poplar understory vegetation was sampled for percent cover by species and total biomass. At each site, 3 microplots were sampled per unmanaged plot, for a total 6 microplots per site (3 on each side of the stream). Sampling was identical to that of hybrid poplar understory microplots.

3.2.4 Simpson's diversity index

Simpson's Index (D) was used to characterize understory diversity in hybrid poplar buffers strips at the site level:

$$D = \Sigma(n / N)^2$$

Where n is the plant cover of a particular species and N is the total plant cover at each site. Following calculation of D, Simpson's diversity index (1-D) and Simpson's reciprocal index (1/D) were calculated at the site level. Simpson's diversity index (1-D) gives the probability (between 0 and 1) that two individuals randomly selected will belong to different species. For Simpson's reciprocal index, the lowest value (1) would represent a community with only 1 species, while the highest value would be equal to the number of species in a community where all species have the same plant cover. For both Simpson's diversity index (1-D) and Simpson's reciprocal index (1/D), the higher the value the higher is the diversity.

Table 3.2 :
Frequency and relative cover of understory plant species in the three hybrid poplar riparian buffers

				Bromptonville (n=8)		Magog (n=8)		St-Isidore-de-Clifton (n=8)	
Species	Status	Wetland affinity[1]	Weed vs. non weed[2]	Freq. (%)	Rel. cover (%)	Freq. (%)	Rel. cover (%)	Freq. (%)	Rel. cover (%)
Agrimonia gryposepala	N	Upl	Nw	-	-	25	0.4	-	-
Alnus rugosa	N	Fac	Nw	-	-	12.5	1.2	-	-
Ambrosia artemisiifolia	N	Upl	W	50	0.4	-	-	-	-
Asclepias syriaca	N	Upl	W	12.5	1.9	-	-	-	-
Aster puniceus	N	Fac	Nw	-	-	-	-	12.5	0.3
Aster simplex	N	Fac	Nw	12.5	6.6	37.5	0.6	-	-
Carex crinita	N	Fac	Nw	-	-	25	1.9	-	-
Carex gracillima	N	Upl	Nw	-	-	12.5	+	-	-
Carex pallescens	N	Upl	Nw	-	-	25	0.3	-	-
Carex scoparia	N	Fac	Nw	-	-	25	0.1	-	-
Carex sp.	N	-	Nw	50	1.6	-	-	25	0.3
Carex stipata	N	Fac	Nw	-	-	-	-	12.5	0.7
Carex vulpinoidea	N	Fac	Nw	12.5	1.1	12.5	0.3	25	0.6
Cornus stolonifera	N	Fac	Nw	25	0.2	-	-	-	-
Danthonia compressa	N	Upl	Nw	-	-	87.5	6.7	-	-
Epilobium glandulosum	N	Upl	Nw	-	-	-	-	12.5	0.1
Equisetum arvense	N	Upl	W	62.5	8.1	75	1.8	75	4.6
Erigeron strigosus	N	Upl	Nw	12.5	1.1	-	-	-	-
Fragaria virginiana	N	Upl	Nw	-	-	50	3.1	12.5	0.3
Galium palustre	N	Fac	Nw	37.5	1.7	100	7.2	87.5	4.1
Geum allepicum	N	Upl	Nw	12.5	0.5	-	-	-	-
Impatiens capensis	N	Fac	Nw	100	16.0	37.5	0.2	37.5	1.1
Juncus effusus	N	Fac	Nw	-	-	12.5	0.1	25	0.1
Juncus tenuis	N	Fac	Nw	-	-	12.5	0.1	-	-
Larix laricina	N	Fac	Nw	-	-	12.5	0.3	-	-
Mentha piperita	N	Fac	Nw	-	-	37.5	2.6	-	-
Myosotis laxa	N	Fac	Nw	-	-	-	-	25	1.8
Onoclea sensibilis	N	Fac	Nw	25	0.5	25	0.3	37.5	1.3
Parthenosissus quinquefolia	N	Upl	Nw	12.5	0.1	-	-	-	-
Phalaris arundinacea	N	Fac	Nw	62.5	8.0	12.5	1.2	-	-
Pilea pumila	N	Fac	Nw	12.5	+	-	-	-	-
Poa palustris	N	Fac	Nw	12.5	0.9	-	-	-	-
Polygonum persicaria	N	Fac	W	50	1.5	-	-	-	-
Polygonum sagittatum	N	Obl	Nw	62.5	3.5	37.5	0.1	50	0.2

Prunella vulgaris	N	Upl	Nw	-	-	37.5	0.4	25	0.3
Prunus virginiana	N	Upl	Nw	-	-	12.5	0.3	-	-
Rhus typhina	N	Upl	Nw	12.5	0.5	-	-	-	-
Rubus idaeus	N	Upl	Nw	12.5	1.1	-	-	12.5	0.1
Rumex crispus	N	Upl	Nw	-	-	12.5	+	-	-
Salix sp.	N	-	Nw	-	-	-	-	12.5	0.3
Scirpus atrovirens	N	Fac	Nw	-	-	75	1.9	-	-
Scirpus rubrotinctus	N	Obl	Nw	-	-	-	-	12.5	1.2
Solidago canadensis	N	Upl	W	50	6.7	100	3.4	62.5	2.8
Solidago graminifolia	N	Upl	W	12.5	1.0	12.5	0.3	37.5	2.2
Solidago rugosa	N	Upl	Nw	-	-	50	1.7	25	0.3
Verbena hastata	N	Fac	Nw	25	0.5	25	0.1	-	-
Achillea millefolium	I	Upl	W	12.5	+	12.5	0.3	-	-
Agropyron repens	I	Upl	W	37.5	5.0	62.5	1.4	50	5.5
Agrostis alba	I	Fac	Nw	62.5	3.5	75	3.4	100	12.5
Agrostis rubra	I	Upl	Nw	-	-	100	22.9	-	-
Arctium minus	I	Upl	W	12.5	0.5	-	-	-	-
Bromus inermis	I	Upl	Nw	-	-	-	-	12.5	0.7
Chenopodium album	I	Upl	W	12.5	0.1	-	-	-	-
Chrysanthemum leucanthemum	I	Upl	W	-	-	12.5	0.3	12.5	0.1
Cirsium arvense	I	Upl	W	62.5	1.6	-	-	62.5	1.6
Cirsium vulgare	I	Upl	W	12.5	0.1	-	-	-	-
Festuca elatior	I	Upl	Nw	-	-	37.5	1.5	-	-
Galeopsis tetrahit	I	Upl	W	-	-	25	0.3	-	-
Glecoma hederacea	I	Upl	Nw	12.5	5.0	-	-	-	-
Hieracium pilosella	I	Upl	W	-	-	25	0.6	-	-
Hieracium pratense	I	Upl	W	-	-	-	-	25	0.3
Hypericum perforatum	I	Upl	W	-	-	25	0.6	25	1.5
Leontodon autumnalis	I	Upl	Nw	-	-	62.5	1.4	50	2.7
Malva moschata	I	Upl	Nw	-	-	-	-	12.5	0.1
Malva neglecta	I	Upl	Nw	-	-	-	-	12.5	0.1
Melilotus alba	I	Upl	W	-	-	12.5	0.3	-	-
Oxalis stricta	I	Upl	W	37.5	0.3	62.5	1.3	50	0.5
Phleum pratense	I	Upl	Nw	87.5	7.5	100	10.2	100	17.6
Plantago lanceolata	I	Upl	Nw	-	-	75	5.6	-	-
Plantago major	I	Upl	W	12.5	0.5	12.5	0.1	50	0.4
Potentilla anserina	I	Fac	Nw	-	-	-	-	12.5	0.7
Potentilla reptans	I	Upl	Nw	-	-	37.5	0.6	-	-
Ranunculus acris	I	Upl	W	75	1.1	87.5	2.2	100	6.1
Rhamnus catharticus	I	Upl	Nw	-	-	12.5	0.3	-	-
Rhamnus frangula	I	Upl	Nw	37.5	0.2	12.5	+	-	-

Rhinantus crista-galli	I	Upl	Nw	-	-	12.5	+	-	-
Solanum dulcamara	I	Upl	Nw	12.5	0.1	-	-	-	-
Stellaria graminea	I	Upl	W	50	0.7	75	1.2	87.5	3.0
Stellaria media	I	Upl	W	12.5	0.1	25	0.1	37.5	0.8
Taraxacum officinale	I	Upl	W	100	3.4	87.5	1.4	100	13.4
Thlaspi arvense	I	Upl	W	-	-	37.5	1.0	-	-
Tragopogon pratensis	I	Upl	W	-	-	12.5	0.7	-	-
Trifolium pratense	I	Upl	Nw	37.5	0.6	62.5	2.1	37.5	1.6
Veronica serpyllifolia	I	Upl	Nw	-	-	50	0.8	25	0.3
Vicia cracca	I	Upl	W	75	4.8	100	3.2	100	7.8
Poaceae sp.	-	-	-	37.5	1.4	-	-	-	-

I: introduced species, N: native species, W: weed, Nw: non weed [1], Fac: facultative wetland species [2], Obl: obligate wetland species[2], Upl: upland species, +: species with a cover lower than 0.05%. Pasture forage species are underlined.

[1] Gauthier (1997)

[2] Gouvernement du Québec (1981) and MAPAQ (2009)

3.2.5 Canopy openness measurements

Canopy openness measurements at each site where made during the first week of July 2008. Hemispherical photographs were taken 1 m above the ground level at the same positions where microplots were placed in both hybrid poplar plots and unmanaged plots. Canopy openness measurements were obtained from hemispherical photographs using the software Gap Light Analyser V 2.0 (University Simon Fraser, British Columbia, Canada).

3.2.6 Statistical analysis

The data from the three microplots were combined to produce data per plot. Species richness in a plot was determined by cumulating all species encountered in the three microplots. Species percent cover in a plot is the average of that measured in three microplots. Understory plant biomass in a plot is the average of that measured in three microplots. Percent data for canopy openness were arcsin transformed prior to analysis.

For hybrid poplar understory data analyses, ANOVA tables were constructed in accordance with Peterson (1985), and degrees of freedom, sum of squares, mean squares and *F*-values were computed. When a factor was declared statistically significant (Site, Clone and Site x Clone interaction), the standard error of the mean (SE) was used to evaluate differences between means for three levels of significance ($p<0.05$, $p<0.01$ and $p<0.001$). All of the ANOVAs were run with the complete set of data (3 sites, 2 clones, 4 blocks = 24 experimental plots). Site effects reported in this study are on means of both clones at each site, while Clone effects reported are on means of each separate clone across the 3 study sites. Simple regression models were developed with data from all the hybrid poplar plots (n=24). For the presentation of results in figures, abbreviations of the names of plantation sites are used (Bromptonville = BRO, St-Isidore-de-Clifton = STI, Magog = MAG,).

Because the unmanaged herbaceous buffer plots were located outside of the randomized block design, and only two of these plots are present at each site, we performed a *t*-test at the site level in order to compare hybrid poplar riparian buffer understory and unmanaged herbaceous buffers (means with different sample sizes). All statistical analyses were done with JMP 6 from SAS Institute (Cary, NC).

3.3 Results

3.3.1 Relationship between understory biomass and plant cover

A significant relationship ($R^2=0.75$, $p<0.001$) was obtained between the total percent plant cover per plot and the understory biomass per plot in hybrid poplar riparian buffer strips (Figure 3.1). Total percent plant cover is therefore a good estimator of plant biomass in this study.

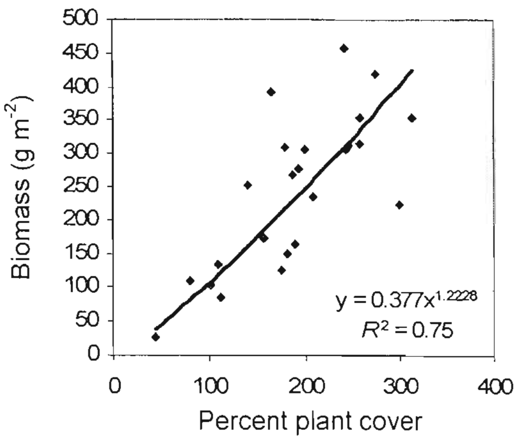

Figure 3.1 Relationship between mean understory percent plant cover per plot and mean understory biomass per plot (g m^{-2}) (n=24, p<0.001).

3.3.2 Canopy openness in hybrid poplar buffers

A highly significant Site effect (p<0.001) was detected by the ANOVA for canopy openness measured 1 m above the ground level, with the Bromptonville site having the lowest canopy openness (mean of both clones) and the Magog site having the highest (Figure 3.2). A highly significant Clone effect was also observed (p<0.001), with clone 915311 having the lowest canopy openness across the three study sites (Figure 3.2). Canopy openness values under 8% were measured above a few microplots in clone 915311 at both the Bromptonville and St-Isidore-de-Clifton sites, while canopy openness was never lower than 13% in clone 3570.

3.3.3 Understory biomass in hybrid poplar buffers

A highly significant Site effect (p<0.001) was detected by the ANOVA for understory biomass, with Bromptonville and St-Isidore-de-Clifton sites having the lowest understory biomass (mean of both clones) and Magog the highest (Figure 3.2). A highly significant Clone effect was also observed (p<0.001), with clone 915311 having the lowest understory biomass across the three study sites (Figure 3.2). Understory biomass values as low as 3.6 g m^{-2} were measured in microplots in clone 915311 at the Bromptonville site, while understory biomass was never lower than 76.9 g m^{-2} in microplots of clone 3570 (Figure 3.3).

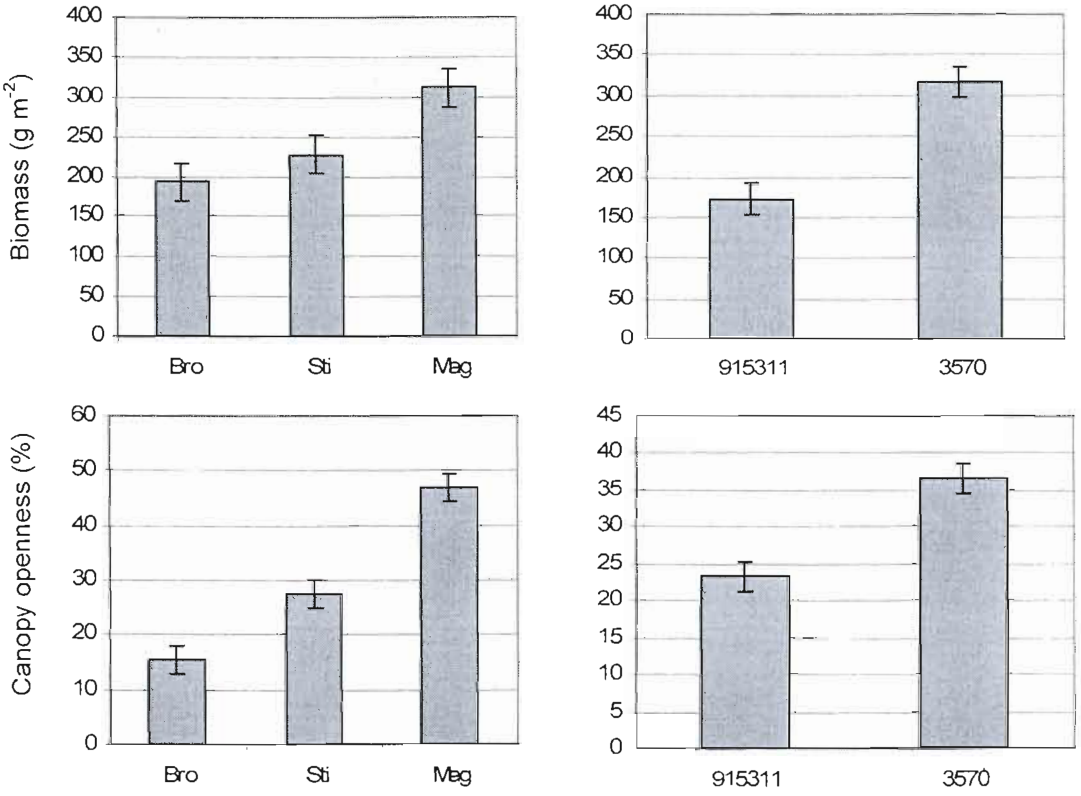

Figure 3.2 Top diagrams, understory biomass (g m^{-2}) at the three hybrid poplar buffer sites and under the two hybrid poplar clones; Site effect is significant at $p<0.05$ and Clone effect is significant at $p<0.001$. Bottom diagrams, canopy openness (%) measured 1 m above the ground level at the three hybrid poplar buffer sites and under the two hybrid poplar clones; Site and Clone effects are significant at $p<0.001$. Vertical bars represent SE.

Figure 3.3 On the left, understory vegetation under clone 3570. On the right, understory vegetation under clone 915311. Both photographs were taken the 4th of August 2008 in block 2 at the Bromptonville site (6th growing season). The lowest biomass values were observed in these specific plots for each clone within the entire experimental design.

3.3.4 Relationship between canopy openness and understory plant biomass

For each study site, highly significant relationships ($p<0.001$) were obtained between canopy openness above each microplot and understory biomass in each microplot in hybrid poplar buffers ($R^2=0.81$ at Bromptonville; $R^2=0.64$ at St-Isidore-de-Clifton; $R^2=0.51$ at Magog) (Figure 3.4). Understory biomass increase is very high as canopy openness increases at the Bromptonville site, while a slower rate of increase is observed at the St-Isidore site, and an even slower rate of increase is observed at the Magog site.

3.3.5 Plant species richness and cover in hybrid poplar buffers

At the site level, total species richness was highest at Magog (56 species), compared to Bromptonville (43 species) and St-Isidore-de-Clifton (41 species) (Table 3.3). This trend was also observed for native, introduced, wetland and upland species. However, the

Bromptonville site had a higher Native / Introduced species ratio. Furthermore, the relative cover of native (64%) and wetland (44%) species was particularly high at the Bromptonville site. All three sites contained a similar number of weed species, but the relative cover of weedy species was particularly low at the Magog site (20%). Simpson's Index of diversity was relatively high at the three sites (Table 3.3). Simpson's reciprocal index shows that the Bromptonville site may have slightly more species diversity although its recorded species richness is lower than the Magog site.

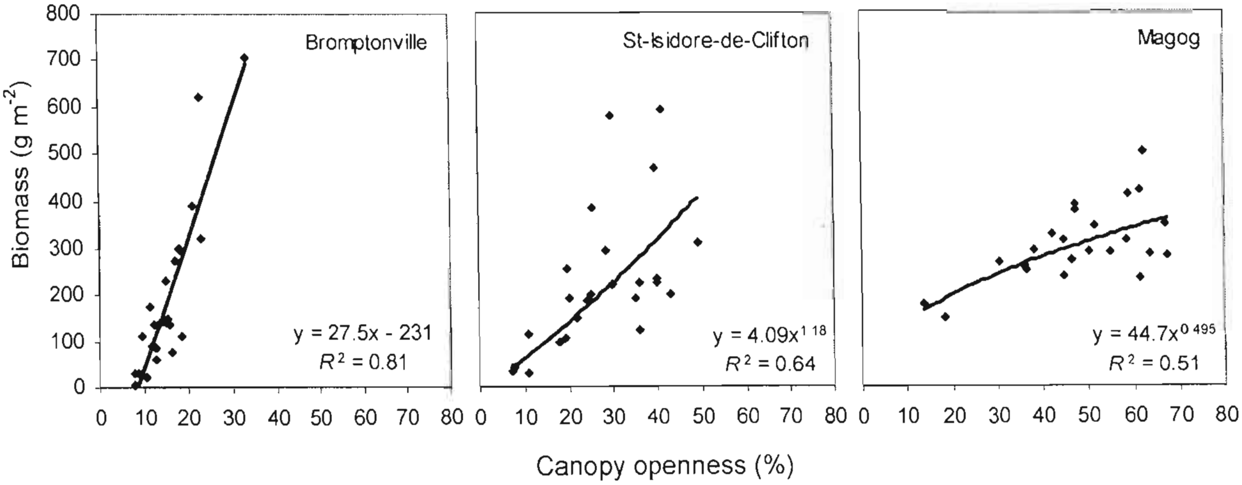

Figure 3.4 Relationships between canopy openness (%) at 1 m above the ground level and understory vegetation biomass (g m^{-2}) at the three hybrid poplar buffer sites in all microplots (n=24 per site). All relationships are significant at p<0.001.

Table 3.3
Total number of species, relative cover of species groups (%) and Simpson's diversity index (1-D) and reciprocal index (1/D) at the three hybrid poplar riparian buffer sites.

	Bromptonville	Magog	St-Isidore-de-Clifton	All sites
Total species	43	56	41	86
Native species	23	28	20	46
Introduced species	19	28	21	39
Native / introduced ratio	1.21	1	0.95	1.18
Wetland species	13	17	12	26
Upland species	28	39	27	57
Wetland / upland ratio	0.46	0.43	0.44	0.45
Non weed species	23	37	26	58
Weed species	19	19	15	27
Non weed / weed ratio	1.21	1.95	1.73	2.15
Relative Native cover (%)	64	36	23	-
Relative Introduced cover (%)	35	64	77	-
Relative Weed cover (%)	38	20	51	-
Relative Non weed cover (%)	61	80	49	-
Relative Wetland cover (%)	44	21	25	-
Relative Upland cover (%)	53	79	75	-
Simpson's diversity index (1-D)	0.93	0.92	0.91	-
Simpson's reciprocal index (1/ D)	15.0	11.8	11.7	-

A significant Site effect was observed for mean number of species per plot (total, $p<0.05$; introduced, $p<0.01$ and upland species, $p<0.05$), with the Magog site always having the highest species richness (Table 3.4). The mean number of introduced species per plot was particularly low at the Bromptonville site (7.6 species). No significant Site effect was observed for the mean number of native and wetland species, and no Clone effect was observed for mean number of species in all species groups.

Significant Site x Clone interactions were observed for mean percent plant cover for introduced ($p<0.05$) and upland ($p<0.05$) species in hybrid poplar buffers (Figure 3.5). Site x Clone interaction for mean percent plant cover for total species was significant at a slightly higher p value ($p=0.057$). These interactions are related to the fact that no clone effect was observed at the Magog site for these variables, while a clone effect was observed at the

Bomptonville and St-Isidore-de-Clifton sites, with clone 3570 having the highest mean percent plant cover. A significant Clone effect (3 sites mean) for mean percent plant cover for native ($p<0.05$) and wetland ($p<0.05$) species was also observed in hybrid poplar buffers (Figure 3.5), with clone 3570 always having the highest mean percent plant cover. Site effects and Site x Clone interactions for both of these variables were not significant.

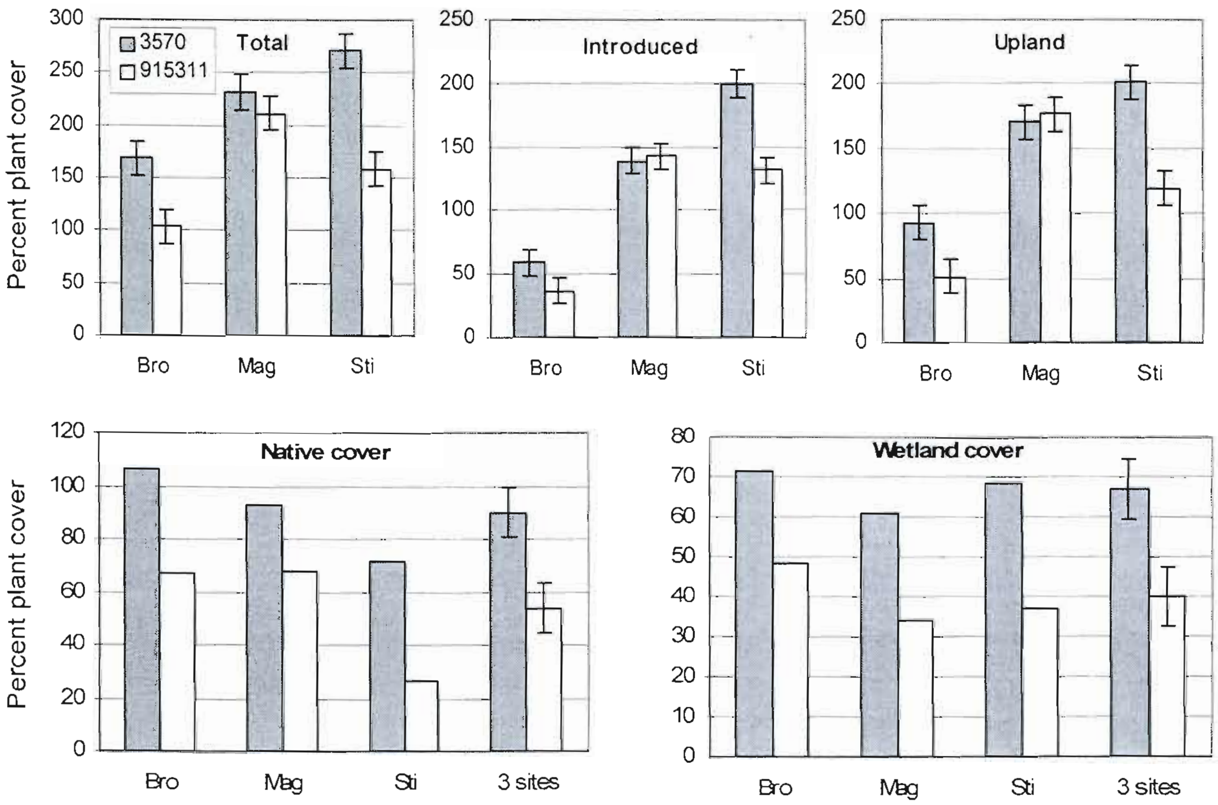

Figure 3.5 Top diagrams, Site x Clone interactions for mean percent plant cover for total ($p=0.057$), introduced ($p<0.05$) and upland ($p<0.05$) species in hybrid poplar buffers. Bottom diagrams, Clone effect (3 sites mean) for mean percent plant cover for native ($p<0.05$) and wetland ($p<0.05$) species in hybrid poplar buffers; Site effects and Site x Clone interactions for both of these variables were not significant. Vertical bars represent standard errors (SE).

Table 3.4
Mean number of species (total, native, introduced, wetland and upland) in the understory of the three hybrid poplar riparian buffers strips.

Sites	Total species	Native species	Introduced species	Wetland species	Upland species
Bromptonville	15.4	7.4	7.63	5.00	9.50
Magog	23.1	10.0	13.13	5.75	17.38
St-Isidore-de-Clifton	16.9	6.3	10.63	4.38	12.13
SE	1.9	-	0.94	-	1.58
$p<$	0.05	NS	0.01	NS	0.05

3.3.6 Relationship between canopy openness, understory species richness and plant cover

Highly significant relationships ($p<0.001$) were observed between canopy openness and the mean number of introduced ($R^2=0.46$) and upland ($R^2=0.43$) species, while no significant relationship exists between canopy openness and the mean number of native and wetland species (Figures 3.6 and 3.7) in hybrid poplar buffer strips. Highly significant relationships ($p<0.001$) were also observed between canopy openness and the mean percent plant cover for introduced ($R^2=0.51$) and upland ($R^2=0.65$) species, while no significant relationship exists between canopy openness and the mean percent plant cover for native and wetland species (Figures 3.6 and 3.7).

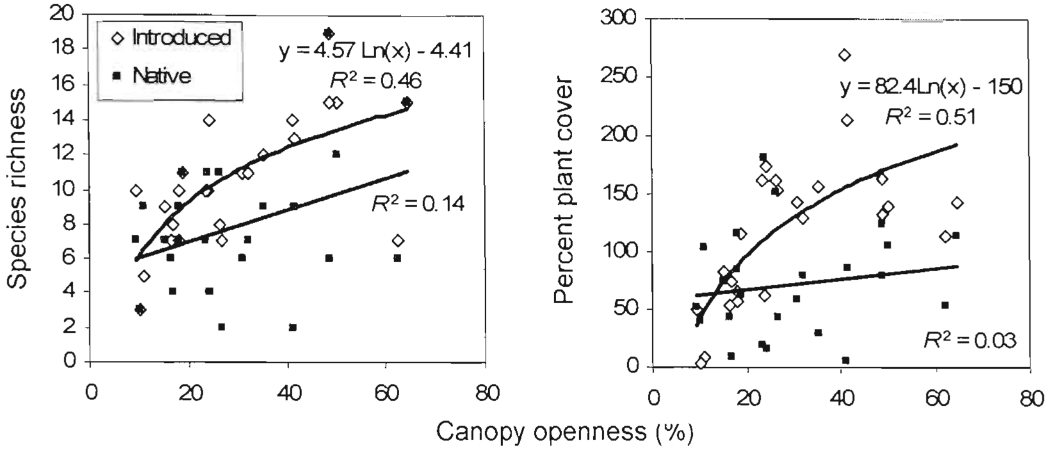

Figure 3.6 On the left, relationship between canopy openness (%) and species richness of introduced (R^2=0.46, p<0.001) or native (R^2=0.14, NS) species in hybrid poplar buffer understory. On the right, relationship between canopy openness (%) and the mean percent plant cover of introduced (R^2=0.51, p<0.001) or native (R^2=0.03, NS) species in hybrid poplar buffer understory.

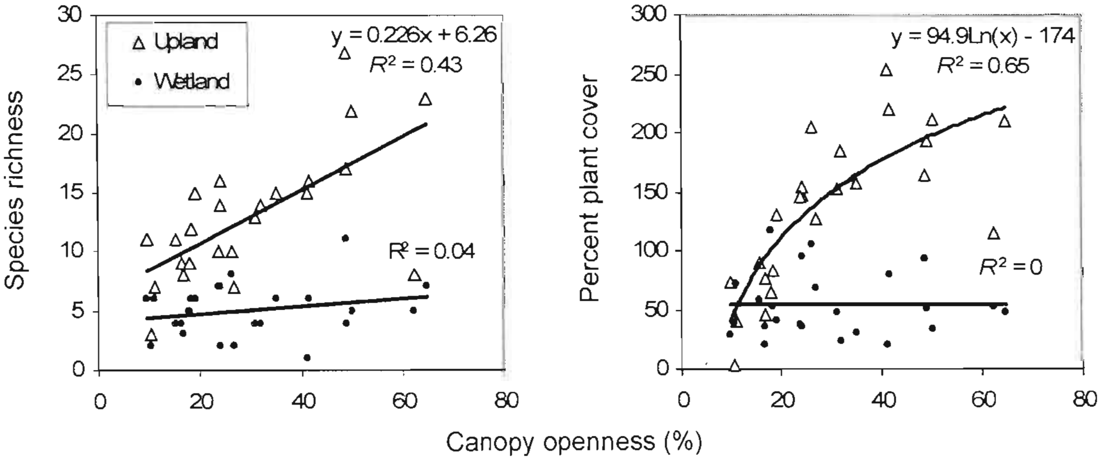

Figure 3.7 On the left, relationship between canopy openness (%) and species richness of upland (R^2=0.43, p<0.001) or wetland (R^2=0.04, NS) species in hybrid poplar buffer understory. On the right, relationship between canopy openness (%) and the mean percent plant cover of upland (R^2=0.65, p<0.001) or wetland (R^2=0, NS) species in hybrid poplar buffer understory.

3.3.7 Comparison between hybrid poplar buffers and free-growing herbaceous buffers

At the site level, significant differences exist between free-growing herbaceous buffers and hybrid poplars buffers, but only for a limited number of variables (Figure 3.8). At each site, understory biomass and canopy openness was lower in the hybrid poplar buffer compared to the free-growing herbaceous buffer, with the largest differences observed at the Bromptonville site. Mean percent plant cover for introduced species was significantly lower in hybrid poplar buffers compared to the free-growing herbaceous buffers, but only at the Bromptonville site. Species richness (mean number of total species) was not significantly different at each site between hybrid poplar buffer understory and herbaceous buffers. Lower richness in native species was found at the Bromptonville site when the understory vegetation of clone 915311 was compared to the free-growing buffers, while no significant difference was observed when the comparison was made with clone 3570 (data not shown). However, percent plant cover for native species was not significantly different at the Bromptonville site between poplar buffer understory and free-growing buffers (Figure 3.8). At the St-Isidore-de-Clifton and Magog sites, no significant differences were observed for species richness and mean percent plant cover for introduced species between the hybrid poplar buffer understory and the free-growing buffers. Moreover, at the three sites, no significant differences were observed for species richness and mean percent plant cover for wetland species between the hybrid poplar buffer understory and the free-growing buffer. Finally, weed cover was only statistically lower under clone 915311 compared to adjacent herbaceous buffers, but only at Bromptonville and St-Isidore-de-Clifton sites (data not shown).

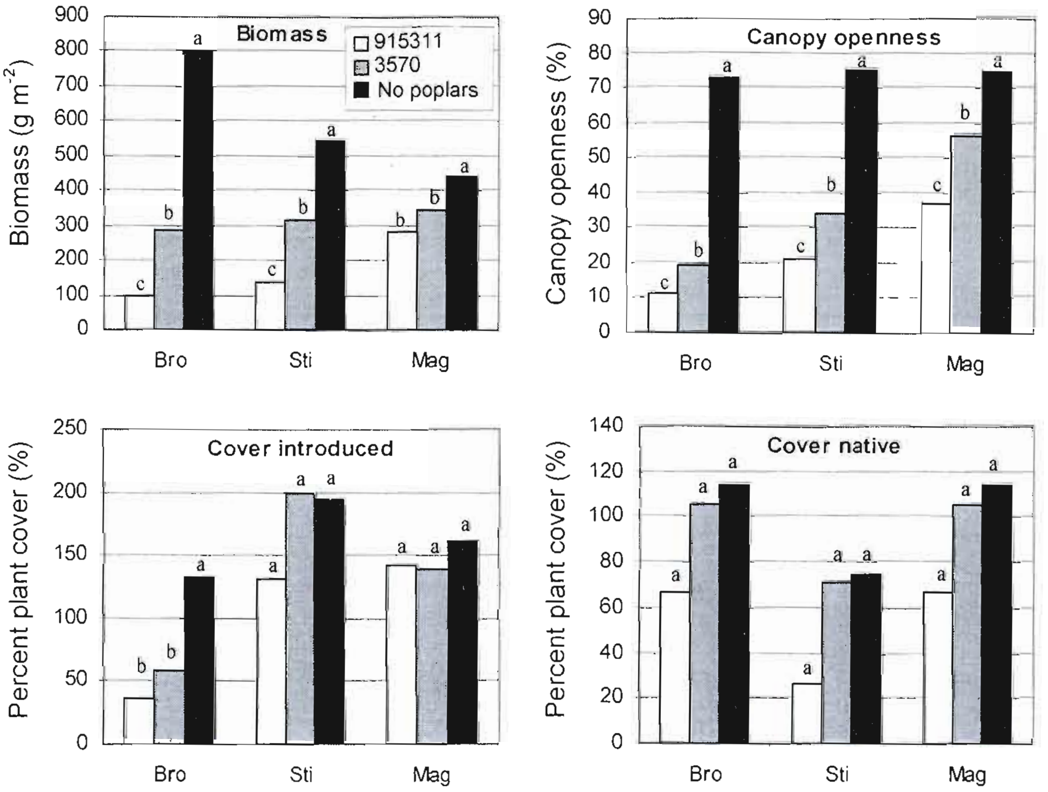

Figure 3.8 Plant biomass (g m^{-2}), canopy openness (%) and plant cover of introduced and native species for the two hybrid poplar clones (915311; 3570) and the adjacent free-growing herbaceous (no poplars) buffer at each site. Comparisons are made at the site level and columns with the same letter are not statistically different at $p<0.05$. For plant biomass and canopy openness calculation, observations from all microplots where used (n=12 for each clone at each site; n=6 for herbaceous buffer at each site). For plant cover calculation, observations from all plots where used (n=4 for each clone at each site; n=2 for herbaceous buffer at each site).

3.4 Discussion

3.4.1 Light availability: an important factor affecting understory biomass

In this study, canopy openness was an important factor affecting understory biomass in 6 year-old hybrid poplar buffers located in the riparian zone of pastures (Figures 3.2, 3.3 and 3.4). Large differences in canopy openness were observed between sites and between poplar clones, and were reflected by lower understory biomass observed on sites and under the clone with lower canopy openness (Figure 3.2). This is probably the consequence of the large differences in hybrid poplar total aboveground biomass (stems, branches and leaves) previously reported across the three study sites and for the two poplar clones after 6 years (Fortier *et al.*, 2010a) (Table 3.1).

Clone 915311 also had a much larger proportion of its biomass allocated to branches and leaves (45%) compared to clone 3570 (35%) (Fortier *et al.*, 2010a). This could explain why canopy openness values under 8% were measured above a few microplots in clone 915311 (Bromptonville and St-Isidore-de-Clifton sites), with canopy openness never being lower than 13% in clone 3570, although mean aboveground biomass for clone 3570 at Bromptonville (46 kg tree^{-1}) is much larger than for clone 915311 at St-Isidore-de-Clifton (31 kg tree^{-1}).

Very low canopy openness under clone 915311 at the Bromptonville and St-Isidore sites led to the almost complete inhibition of understory biomass growth in some microplots, a situation that was never observed under clone 3570 (Figure 3.3). Other factors than light availability under clone 915311 could also have affected understory biomass growth. Clone 915311 is a *P. maximoviczii* x *P. balsamifera* hybrid, and *P. balsamifera* has secondary chemicals in its leaves that are also known to reduce N availability in soils receiving its litter (Schimel *et al.*, 1998), and this may have inhibited understory plant growth under this particular clone.

At the site level, other factors than canopy openness could have affected understory biomass growth in hybrid poplar buffers. Although light availability at the Magog site was 2.5 times higher than at the Bromptonville site, understory biomass is only 60% higher (Figure 3.2). Moreover, no significant understory biomass differences are observed between the Bromptonville and the St-Isidore-de-Clifton sites, although canopy openness is significantly higher by 44% at the St-Isidore-de-Clifton site (Figure 3.2). Site factors such as soil fertility and elevation probably affected understory biomass growth. At Bromptonville, a fertile site located at low elevation (Table 3.1), small increases in canopy openness are reflected by very high increases in understory biomass, while this trend is observed to a much lesser extent at St-Isidore-de-Clifton (high soil fertility, but high elevation), and even less so at Magog (low soil fertility) (Figure 3.4, Table 3.1). As they dramatically affected hybrid poplar growth (Fortier *et al.*, 2010a), these site factors could also explain the large differences in herbaceous vegetation growth measured in the free-growing buffers (804 g m^{-2} at Bromptonville; 546 g m^{-2} at St-Isidore-de-Clifton; 440 g m^{-2} at Magog), althought light availability was almost identical at the three sites (73-75% of canopy openness) (Figure 3.8).

3.4.2 Effect of hybrid poplar riparian buffer on understory species richness and plant cover

Higher total species richness was observed at the low soil fertility site of Magog, where poplar growth is low, light availability is high, as well as understory biomass (Table 3.1, 3.3 and 3.4, Figure 3.2). This is consistent with the hypothesis that species richness is expected to be highest in relatively resource poor habitats (Tilman, 1982). Furthermore, exclusion of understory species through competition for light may not have yet occurred at the Magog site (Tilman, 1982). Berthelot *et al.* (2005) also reported that species richness tends to decrease as poplar plantations grow.

Nevertheless, species diversity was similar in the three hybrid poplar buffers (Table 3.3). In addition, the lower species richness observed at the Bromptonville and St-Isidore-de-Clifton site was mainly related to a lower number of introduced and upland species, with the mean richness of native and wetland species not being statistically different across the three study sites (Table 3.4). As hybrid poplar buffers grow, their canopies close and the richness and the cover of introduced and upland species decline; a trend that was not observed for native and wetland species (Figures 3.6 and 3.7). This also explains why no Site effect on native and wetland species cover was detected by the ANOVA (Figure 3.5).

Reduction in richness and cover of introduced and upland species with canopy closure may be related to the fact that most introduced upland species recorded in this study are shade-intolerant species, that colonise open, disturbed habitats (ex. *Achillea millefolium* L., *Hypericum perforatum* L., *Ranunculus acris* L., *Taraxacum officinale* Weber) (Humbert *et al.*, 2007). Conversely, no apparent effect of canopy closure on native and wetland species richness and cover was observed (Figures 3.6 and 3.7), probably because several of those species are more shade tolerant (*Aster puniceus* L., *Equisetum arvense* L., *Impatiens capensis* Meerb., *Onoclea sensibilis* L., etc.) than the introduced upland species (Humbert *et al.*, 2007). A much higher relative cover for native and wetland species was also observed at the Bromptonville site, where light availability is the lowest (Table 3.3, Figure 3.2).

No Clone effect was observed for understory species richness in this study. Nevertheless, as seen for understory biomass, plant cover for total, introduced, upland, native and wetland species was generally lower under clone 915311, compared to clone 3570, except for total, introduced and upland species plant cover at the Magog site, which were similar (Figure 3.5). Therefore, low light availability under clone 915311 did not significantly affect species richness, but it is partly responsible for the low plant cover for all species groups, compared to clone 3570.

It is important to mention that most species found in hybrid poplar buffers are common species, and no species were of high conservation value, an observation that was also reported in various types of natural riparian buffers (herbaceous, shrub covered and wooded strips) in agricultural landscapes of southern Quebec (Boutin *et al.*, 2003). However, this is hardly surprising because 6 years ago the riparian vegetation at the buffer plantation sites consisted mostly of forage species that were repeatedly grazed and trampled by livestock. The cover offorage pasture species is still high at the three sites (Table 3.2).

Nevertheless, 6 years after the hybrid poplar buffers were established (including fencing to prevent livestock grazing), a total of 86 species were recorded in microplots across the three study sites, with 46 species being native (Table 3.2 and 3.3). Higher species richness would undoubtedly have been observed if the complete area of the hybrid poplar buffer had been surveyed or if wider buffers had been established (Forman and Baudry, 1984; Ma *et al.*, 2002). A total of 26 wetland species were recorded, with only two being non native: *Agrotis alba* (a pasture grass) and *Potentilla anserina*. The wetland species *Phalaris arundinacea* (also a pasture grass) has probably been sown at the Bromptonville and Magog pastures, although it is native in the region (White *et al.*, 1993). Richness and cover of weed species were relatively high, but most weed species found in the hybrid poplar buffers were introduced species of upland open habitats (Tables 3.2 and 3.3).

Although no species with high conservation value were found in the hybrid poplar buffers, some species are still important for conservation. Although it is classified as an agricultural weed species in Quebec, *Asclepias syriaca* (found at the Bromptonville site) is the obligate host species for the reproduction and the caterpillar life stage of the monarch butterfly (*Danaus plexippus*), a native migratory butterfly listed as a species of concern in Canada (Gouvernement du Québec, 1981; MAPAQ, 2009; COSEPAC, 2010). This illustrates the paradox that can exist between the agronomic concerns and the ecological concerns for particular plant species.

3.4.3 Comparison between hybrid poplar riparian buffer strip understories and free-growing herbaceous strips

The greatest differences between hybrid poplar buffer understories and free-growing herbaceous buffers were observed for biomass, but not for species richness. Compared to free-growing herbaceous buffers, understory biomass in hybrid poplar buffers was lower at all sites, particularly under clone 915311 (Figure 3.8). Larger differences in understory biomass were observed at richer sites, where poplar growth is high and canopy openness is low (Table 3.1). Site soil richness may also have favoured biomass growth in the free-growing herbaceous buffers of Bromptonville and St-Isidore-de-Clifton, although high elevation may have negatively affected biomass growth at St-Isidore-de-Clifton (Table 3.1). Nonetheless, as reported in other studies, riparian buffer established with perennial herbaceous species (swithchgrass, smooth brome, alfalfa, etc.) generally have plant biomasses ranging from 1000-2000 g m^{-2} (Tufekcioglu *et al.*, 2003; Kelly *et al.*, 2007), while much lower values where observed in the free-growing herbaceous buffers (440-804 g m^{-2}). Therefore, free-growing herbaceous buffers may not be as efficient as perennial crop buffers for runoff control, particularly if they are not colonized by stiff-stemmed species such as switchgrass (Schultz *et al.*, 2004).

Species richness for all species groups was comparable between hybrid polar buffer understories and herbaceous buffers at the three sites, despite a lower richness in native species observed under clone 915311 at the Bromptonville site (data not shown). Introduced species cover was also lower under both clones at the Bromptonville site, while native species cover was not statistically lower, although it tended to be relatively low under clone 915311. No significant difference in wetland species richness and cover were observed between the two types of buffers.

Based on these observations, it cannot be argued that the establishment of hybrid poplar buffers will reduce farmland diversity if they become an alternative to conventional free-growing herbaceous buffers. This is particularly true if poplar clones with an open narrow crown are selected over clones with a wide and dense crown, such as clone 915311 (Fortier *et al.*, 2010a). In addition, as light becomes a limiting factor for introduced (upland) shade-intolerant species, a shift in the relative cover of species groups may occur, with native (wetland) species becoming dominant (Figures 3.6 and 3.7). This phenomenon is not likely to happen in free-growing herbaceous buffers, unless they are colonised by woody species.

Finally, weed cover was only statistically lower in clone 915311 understories when compared to adjacent herbaceous buffers, but only at Bromptonville and St-Isidore-de-Clifton sites (data not shown). Hence, poplar buffers will probably continue to contain weed species in agricultural landscapes, as it is was equally observed in many types of natural riparian habitats in agricultural landscapes (Boutin *et al.*, 2003).

3.4.4 Hybrid poplar buffer design and management implications

Six years after their establishment, hybrid poplar buffers have caused an important shift in structure and function of the riparian ecosystems of pastures (Fortier *et al.*, 2010a, b), evolving from a livestock-disturbed herbaceous system to a tree-dominated system in which livestock have been excluded. The large modification of the light regime observed at the Bromptonville and St-Isidore-de-Clifton sites has considerably reduced understory biomass compared to adjacent free-growing herbaceous buffers, with mean understory biomasses as low as 97 g m^{-2} in clone 915311 at Bromptonville (Figures 3.3 and 3.8). This inhibition of understory plant growth could compromise important buffer functions, such as runoff control and surface soil stabilisation.

To enhance these buffer functions, it has been proposed to establish a dense cover of perennial crops, in the understory of the poplars or between the tree buffer and the cultivated field (Lowrance *et al.*, 1997; Schultz *et al.*, 2004; Kelly *et al.*, 2007; Duchemin and Hogue, 2009). These strategies should be implemented in areas prone to significant runoff (slopes, row crops, slow water infiltration, high precipitation regime, etc.). Heavy periodic pruning of hybrid poplar branches, periodic selective harvest of poplars, or more intensive management practices, such as complete harvest of trees are all interesting strategies (particularly in high density stands) that could be used, whether or not in combination with perennial grass establishment (Sheridan *et al.*, 1999; Dosskey, 2001; Schultz *et al.*, 2004; Kelly *et al.*, 2007). As seen in this study, higher light penetration in the buffer can strongly stimulate understory plant growth, particularly on fertile sites (Figure 3.4).

However, if non point source pollution control is not a major concern, but restoration of native and wetland plant communities is an important objective, landowners should avoid complete harvest of poplars and try to maintain a relatively high shade level within the buffers, in order to promote the establishment of native wetland species over introduced (upland) species (Figure 3.7). Maintaining canopy openness near 15-20 %, with pruning and selective harvests, will have a large negative impact on introduced and upland species, as they are mostly shade-intolerant (Humbert *et al.*, 2007), without compromising wetland and native species cover and richness (Figures 3.6 and 3.7).

Clone 915311 is a large biomass producer and can be a very interesting clone if the objective is to produce biomass for bioenergy or whole-tree chips in the riparian zone (Fortier *et al.*, 2010a). However, *P. balsamifera* related clones, that have a large and dense crown such as clone 915311, are not recommended in the buffer design, whether the objective is to maintain vigorous understory growth for runoff control or to promote native and wetland species cover (Figures 3.2, 3.3 and 3.5). With understory biomass and canopy openness values being as low as 3.6 g m^{-2} and 7.6 % in 1 m^2 microplots after only 6 years, it is clear that this clone can negatively affect richness and cover of species of ecological interest, as well as runoff interception by the buffer. Futhermore, management practices that cause the inhibition of understory plant growth should be avoided since understory vegetation is one of the most important elements of biodiversity within plantations, and often is the single best predictor of animal diversity (Lopez and Moro, 1997; Humphrey *et al.*, 1999; Hartley, 2002).

Very low understory plant cover in more widely spaced upland poplar plantations (625 stem ha-^{1} vs 2222 stem ha-^{1} in this study) was also observed under clone 915311 when it was compared to a *P. deltoides* x *P. nigra* clone (Boothroyd-Roberts *et al.*, in preparation). However, little canopy openness differences were observed between clones (Boothroyd-Roberts *et al.*, in preparation). Consequently, further investigation is required to evaluate if secondary chemicals contained in leaves of *P. balsamifera* related clones have an inhibitory effect on soil processes and understory plant growth (Schimel *et al.*, 1998). In other words, it is not certain that pruning the branches of clone 915311 will necessarily cause an important increase in understory plant cover or biomass, although it will certainly enhance light availability.

Underplanting of native hardwoods and shade tolerant shrubs can also be done to gradually convert the hybrid polar buffer in a more natural riparian system (Truax *et al.*, 2000; Gardiner *et al.*, 2004). This has been done the year following this study with red oak (*Quercus rubra* L.), bur oak (*Q. macrocarpa* Michx.) and beaked hazel (*Corylus cornuta* Marsh.), but it may not be necessary if the buffer is located near a forest patch. The Magog buffer, which is almost connected to an adjacent forest, is a good example since it has already been colonised by larch and speckled alder (Table 3.2), but also by white pine and sugar maple (not recorded in the microplots, but observed in the buffers).

If a higher level of restoration is intended, artificial reintroduction of high conservation value species, such as ant dispersed forest herbs, typical of mature undisturbed deciduous forests, is recommended, but only once structural and functional attributes are restored in the understory (Aubin *et al.*, 2008). The colonisation of broadleaf tree plantations by species of high conservation value with low dispersal ability is generally low even after 50 years, although these types of plantations had long developed structural, functional and compositional understory attributes that were similar to those of natural forests.

Standing dead poplars are also important structural attributes to maintain in the buffer in order to promote bird diversity (Hartley, 2002; Boesch *et al.*, 2007). For example, a pileated woodpecker (*Dryocopus pileatus* L.) has been observed feeding, on several occasions, on 6-year-old dead poplars at the Bromptonville buffer, although the buffer is a very small wooded area (90 m long x 5.5 m wide on each side of the stream) that is relatively isolated from the nearby forests.

Finally, we suggest that hybrid poplar riparian buffers could be a very promising tool to restore connectivity between forest fragments in agriculture-dominated landscapes, since they can create a forest cover within 6 years on fertile sites. Although connectivity restoration provided by artificial corridors may benefit introduced and invasive species more than the native species they were intended to help (Panetta, 1991), results presented in this study suggest that adequately designed artificial buffer strips can contribute to lower introduced species richness and abundance without significantly compromising native species and native wetland species diversity.

3.5 Conclusion

In this study, canopy openness was an important factor affecting understory biomass in 6 year-old hybrid poplar buffers located in the riparian zone of pastures. Large differences in canopy openness were observed between sites and between poplar clones, and were reflected by lower understory biomass observed on sites with lower canopy openness, and under clone 915311 which produces more shade. Higher total species richness was observed at the low soil fertility site of Magog, where poplar growth is low and light availability is high. Nevertheless, the lower species richness observed at the Bromptonville and St-Isidore-de-Clifton sites was mainly related to a lower richness of introduced and upland species, with mean native and wetland species richness being similar across the three study sites. In addition, total understory plant diversity was similar across the three study sites.

Decrease in light availability was also closely related to a decrease in the cover and richness of upland and introduced species, without having a significant effect on native and wetland species cover and richness. The largest differences between hybrid poplar buffer understory vegetation and free-growing herbaceous buffer vegetation were observed for plant biomass, and not species richness. Finally, hybrid poplar clone selection in the buffer design appears to be very important since clone 915311 dramatically inhibited understory growth and lowered the cover of all species groups, including native and wetland species, compared to clone 3570.

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CHAPITRE IV

HYBRID POPLARS WITH PARENTS FROM DIFFERENT *POPULUS* SECTIONS DIFFER IN NITRATE REDUCTASE ACTIVITY

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Sera soumis à Botany

Abstract

Leaf nitrate reductase activity (NRA) of five unrelated hybrid poplar clones (3230, *Populus trichocarpa* Torr. & Gray x *P. deltoides* cv. Boelare; 3570, *P. deltoides* Bartr. ex Marsh. x *P. nigra* L.; 3729, *P. nigra* x *P. maximowiczii* A. Henry; 915508, *P.* x *canadensis* Moench x *P. maximowiczii*; 915311, *P. maximowiczii* x *P. balsamifera* L.) was measured in this study. Nitrate reductase activity was also used to compare the response of these hybrid poplar clones in two different riparian plantation environments. At any leaf age, clone 3570 had a higher NRA than any other clone studied. Nitrate reductase activity patterns in relation to leaf age were also different from one clone to another. Site effect on leaf NRA was also observed, but not for all clones, which resulted in a Site x Clone interaction. Although NO_3 availability was far higher at the Bromptonville site, the NRA of four clones (3230, 3729, 915311 and 915508) out of five was lower or equivalent to the NRA values measured at the Magog site. Only clone 3570 had a large NRA increase at the nitrate-rich Bromptonville site, although tree size (aerial biomass) was 6.5 times greater at this site. This may be related to the fact that both of the parental species of clone 3570 are from the *Aigeiros* section of the *Populus* genus (*P. deltoides* and *P. nigra*) compared to the four other clones, which all had at least one parental species from the *Tacamahaca* section. Nitrate reductase activity differences of more than one order of magnitude were measured between the hybrid poplar clones used in this study. We suggest these important NRA differences reflect the genetic assemblage (parentage) of the five unrelated clones, and possibly that this influences soil N-form preferences.

Keywords

Populus deltoides x *Populus nigra*, unrelated clones, *Aigeiros, Tacamahaca*, riparian environment

4.1 Introduction

Poplars (*Populus* spp.) are commonly planted for production and restoration purposes in different types of plantation systems and environments (agricultural, abandoned farmlands, clear-cut forest, contaminated sites, riparian buffers, intercropping systems, etc.) (Stanturf *et al.*, 2001; Laureysens *et al.*, 2004; Licht and Isebrands, 2005; Lteif *et al.*, 2007; Rivest *et al.*, 2009; Fortier *et al.*, 2010a). A large number of poplar hybrids exist throughout the world and there are large variations in structure and physiological functions, based on genetics, between these hybrids (Bradshaw *et al.*, 2000; Eckenwalder, 2001).

Because they can be clonally propagated with ease, poplars from the *Tacamahaca* section (including *P. balsamifera* L., *P. trichocarpa* Torr. & Gray, *P. maximoviczii* L.) and the *Aigeiros* section (including *P. deltoides* Bartr. ex Marsh. and *P. nigra* L.) and their hybrids form the basis of most poplar breeding programs worldwide (Riemenschneider *et al.*, 2001). Poplars from those two sections differ widely in their natural distributions, as they are adapted to different soil and climatic conditions, with poplars from the *Tacamahaca* section being better adapted to cool climates and relatively poor soils, and poplars from the *Aigeiros* section being better adapted to rich alluvial soils of temperate bottomlands (Zsuffa *et al.*, 1977; Dickmann, 2001; Cooke and Rood, 2007). For example, balsam poplar (*P. balsamifera*), growing in the Alaskan Taïga, is able to assimilate both NH_4 and amino-acids, with no apparent preference (Kielland *et al.*, 2006). Moreover, during fertilisation trials, *P. balsamifera* and other hybrids with one parental species related to the *Tacamahaca* section, tended to prefer NH_4 fertilisation over NO_3 fertilisation (Desrochers *et al.*, 2007). Conversely, high NO_3:NH_4 ratio in the soil solution highly stimulates root development in Eastern cottonwood (*P. deltoides*) (Woolfolk and Friend, 2003). These N-form preferences could partly explain spatial and temporal distribution, or ecological niches of different poplar species, and they may be closely linked to the ability of poplar species to reduce nitrate from the soil solution (Min *et al.*, 1998; Min *et al.*, 1999). Therefore, different physiological responses for N assimilation are expected if poplars from the *Tacamahaca* and the *Aigeiros* sections are hybridized, because they have adapted to different types of environments, with different soil N-form availabilities.

Nitrate reductase (NR) is the first key enzyme of the nitrate assimilation pathway. It reduces nitrate to nitrite, which is further reduced to ammonium and then incorporated to amino acids. Because NR is a substrate-induced enzyme (Campbell, 1988), *in vivo* nitrate reductase activity (NRA) in the leaves and in roots has been a useful method for detecting new patterns and generating hypotheses concerning N assimilation in a wide range of species, management practices and environmental conditions: NO_3 reduction occurrence and differences in leaves of various field, forest edge and woody species (Al Gharbi and Hipkin, 1984; Smirnoff *et al.*, 1984); partitioning of NO_3 assimilation between root and shoot of higher plants (Andrews, 1986); relationship between NO_3 reduction localisation in ferns in relation to environment and physiological characteristics (Stewart *et al.*, 1986); red oak (*Quercus rubra* L.) and red ash (*Fraxinus pennsylvanica* Marsh.) responses to clearcut, forest and field environment (Truax *et al.*, 1994a); butternut (*Juglans cinerea* L.), white ash (*Fraxinus americana* L.) and bur oak (*Q. macrocarpa* Michx.) response to different vegetation management strategies (Lambert *et al.*, 1994); species succession and NO_3 availability changes after clearcut (Truax *et al.*, 1994b; Högbom *et al.*, 2002); effect of N deposition on NO_3 use by sugar maple (*Acer saccharum* Marsh.) (Eddy *et al.*, 2008); black walnut (*J. nigra* L.) seedling growth and physiology in response to N-form availability (Nicodemus *et al.*, 2008), etc.

In poplars, Dykstra (1974) showed important differences in leaf NRA between hybrid poplar clones *P. tristis* x *balsamifera* and *P. deltoides* x *nigra*. In free-growing populations, similar observations were reported by Al Gharbi and Hipkins (1984) when *P. alba*, *P. deltoides* x *nigra* and *P. tremula* where compared. In trembling aspen (*P. tremuloides*), Min *et al.* (1998) showed that NRA in roots and in leaves is rapidly induced following nitrate exposure, with leaves having the greatest activity. More recently, Black *et al.* (2002) reported that NRA in *P. tremula* x *alba* was at least 10-fold greater in leaves than in stems, or in roots, at all nitrate availabilities. These authors concluded that most nitrate assimilation occurs in poplar leaves, a finding that was later corroborated by Rosenstiel *et al.* (2004) in cottonwood (*P. deltoides*).

To our knowledge, no field study has evaluated if contrasted riparian site conditions can affect NRA in different, unrelated hybrid poplar clones, with parental species from the *Tacamahaca* and the *Aigeiros* section. The first objective of this paper is to evaluate if there are differences in leaf NRA between hybrid poplar clones of different parentages. The second objective is to evaluate if NRA of different clones is influenced to the same extent by different levels of NO_3 availability across two riparian sites.

4.2 Materials and methods

4.2.1 Study sites

In May 2003, two multiclonal hybrid poplar riparian buffers were planted along headwater streams in the Eastern Townships region of southern Quebec, Canada. The buffer had cumulated 5 years of growth in 2007, the year of the study. The two riparian buffer study sites (Bromptonville: 45°29 N; 71°59 W; Magog: 45°14 N; 72°07 W) are located in pastures of the regional landscape unit of Sherbrooke (Robitaille and Saucier, 1998). This landscape unit is characterised by gentle slopes, a continental sub-humid moderate climate, a growing season of 180-190 days and a precipitation regime of 1000-1100 mm/year. Cattle densities at the two pasture sites are 0.6 cow ha^{-1} at Bromptonville and 0.2 cow ha^{-1} at Magog. The Bromptonville site is fertilized each year with cow manure, while the Magog site receives no fertilisation. Site characteristics are presented in Table 4.1.

Five unrelated hybrid poplar clones where used in this study (synonyms, abbreviation of hybrid type and clone number are given in parentheses): (1) *Populus trichocarpa* Torr. & Gray x *P. deltoides* cv. Boelare (*P.* x *generosa*, TxD, 3230), (2) *P. deltoides* Bartr. ex Marsh. x *P. nigra* L. (*P.* x *canadensis* Moench, DxN, 3570), (3) *P.* x *canadensis* x *P. maximowiczii* (DNxM, 915508), (4) *P. nigra* L. x *P. maximowiczii* A. Henry (NM6, NxM, 3729) and (5) *P. maximowiczii* x *P. balsamifera* L. (MxB, 915311) (Table 4.2). The five poplar clones were chosen because they have different growth patterns, physiological characteristics, and because they had been selected for superior disease resistance/tolerance and growth characteristics in trials in southern Quebec (Périnet *et al.*, 2001).

Table 4.1
Site and soil characteristics of the two riparian sites.

Sites	Elev. (m)	Land use	Cattle density (cow/ha)	Yearly fertilisation	Drainage[1]	Textural class	pH	Organic matter (%)
Bromptonville	140	Pasture	0.6	Cow manure	Good	Silty clay	6.36	6.21
Magog	208	Pasture	0.2	None	Imperfect	Clay	5.81	7.47
SE	-	-	-	-	-	-	0.03	-
$p<$	-	-	-	-	-	-	0.001	NS

[1] Drainage classes from Cann and Lajoie (1943)

Table 4.2:
Name, parentage and origin of planted hybrid poplar clones.

Clone number	Scientific name (common name)	Parentage	Origin
3570	*P.* x *canadensis* Moench	D x N	Belgium
3230	*P.* x *generosa* A. Henry (Boelare)	T x D	Belgium
3729	*P. nigra* x *P. maximowiczii* (NM6)	N x M	Germany
915311	*P. maximowiczii* x *P. balsamifera*	M x B	Québec
915508	*P.* x *canadensis* x *P. maximowiczii*	DN x M	Québec

4.2.2 Experimental design

A randomized block design was used at each of the two sites, with 4 blocks (replicates) and 5 hybrid poplar clones (treatments) for a total of 40 experimental plots. Each block contains 5 experimental plots (one clone per plot). Plots are 4.5 m wide and 9 m long (40.5 m^2). Each plot contains 9 trees from a single clone (3 rows, 3 trees / row). Each tree is spaced 3 m on the row and the rows are 1.5 m apart. Tree rows were planted parallel to stream bank. A total of 180 hybrid poplars where planted at each site (36 trees of each clone) for a total of

360 hybrid poplars, two blocks on each side of the stream. This design allowed us to test 5 poplar clones in two different riparian environments simultaneously, a common procedure in crop cultivar trials (Steel and Torrie, 1980).

4.2.3 Soil characteristics

At both sites, soil samples were taken at 15 cm depth in each plot in July 2007 (total of 40 samples). All samples where analysed for pH. A composite sample was made by pooling samples from 5 plots in order to determine soil texture and organic matter content at the block level. Soil samples where air dried prior to analysis. The determination of soil pH was made using a 2:1 ratio of water to soil. The Bouyoucos (Bouyoucos, 1962) method was used to determine soil particle size distribution, and textural class was determined in accordance with the Canadian Soil Classification Committee (Comité d'experts sur la prospection pédologique d'Agriculture Canada, 1987). Soil organic matter content was determined by loss on ignition at 550°C.

The soil of the Bromptonville site developed on glacial outwash, deposited over lacustrine clay (Cann and Lajoie, 1943). It is well-drained and named "Sheldon sandy loam" (Cann and Lajoie, 1943). The soil of the Magog site developed on glacial till. It is imperfectly drained and named "Magog stony loam" (Cann and Lajoie, 1943). Soil characteristics are presented in Table 4.1.

4.2.4 Soil nutrient availability

Nutrient availability in the hybrid poplar buffers was determined using Plant Root Simulator (PRS^{TM}-Probes) technology from Western Ag Innovations Inc. Saskatoon, Canada. The PRS-probes consist of an ion exchange membrane encapsulated in a thin plastic probe, which is inserted into the ground with little disturbance of soil structure. The membrane exhibits surface and sorption characteristics similar to those of a plant root. The PRS-probes are an ideal tool to assess nutrient supply rates (ions fluxes) by continuously adsorbing ions over the burial period. Nutrient availability predicted with this method is generally significantly correlated with conventional soil extraction methods over a wide range of soil types (Qian *et al.*, 1992). This technology has also been previously used in agronomic, forestry and environmental studies (Adderley *et al.*, 2006; Coll *et al.*, 2007; Nelson *et al.*, 2007).

Three pairs of probes (an anion and a cation probe in each pair) were buried along the middle row (of 3 rows parallel to stream bank) of poplars in each experimental plot (40 plots). For the Bromptonville site, probes were buried on August 16 and removed on August 30, 2007. For the Magog site, probes were buried from August 17 to August 31, 2007. Burial duration was 15 days at both sites. After removal, probes were washed in the field with deionised water and returned to Western Ag Labs for analysis (NO_3^-, NH_4^+, P, K, Ca, Mg and Mn). Composites were made by combining the three pairs of probes in each experimental plot. Probe supply rates are reported as µmol of nutrient 10 cm^{-2} 15 day period^{-1} and are presented in Table 4.3.

Table 4.3
Nutrient supply rate (µmol 10 cm^{-2} 15 day period^{-1}) measured at the two riparian sites. The NO_3:NH_4 nutrient supply rate molar ratio is also indicated.

Sites	NO_3	NH_4	NO_3:NH_4	P	Ca	K	Mg	Mn
Bromptonville	1.12	0.634	1.8	0.0862	32.2	12.9	10.4	0.051
Magog	0.40	0.927	0.4	0.0437	17.7	2.6	20.3	0.324
SE	0.16	0.057	-	0.0119	1.4	0.5	0.9	-
$p<$	0.01	0.01	-	0.05	0.001	0.001	0.001	NS

4.2.5 Nitrogen mineralization rate

A sequential coring technique was used to measure nitrification and ammonification rates at the two riparian sites (Raison *et al.*, 1987). In each experimental plot, two pairs of hard PVC tubes (20 cm in length and 5.5 cm in diameter) were inserted 15 cm vertically into the soil. The first pair of tubes and their soil content were immediately removed and placed in a portable ice box and transported to the lab for extraction with 2 M KCl (Keeney and Nelson, 1982) within 24 h. The content of each pair of tubes was mixed thoroughly and duplicate extractions were made for each composite. During the following days, the concentration of NO_3 and NH_4 were determined using a Tecator FIAstar continuous flow analyzer.

The second pair of tubes remained in the soil for a 24 day period (from 17 July to 9 August 2007). They were capped with tape to prevent N loss from leaching by rain. A small hole was pierced laterally on each tube (1 cm from the top) to allow aeration. After 24 days, tubes were removed from the soil and the same procedure (as for initial tubes) was used in order to determine concentrations of N-forms. Nitrification was calculated as the NO_3 concentration of the soil at the end of the incubation period minus the NO_3 concentration at the beginning. Ammonification was obtained the same way.

4.2.6 Nitrate reductase activity assay

In order to verify that the substrate (KNO_3) concentration that would be used in further NRA experiments was not limiting, we evaluated the effect of different substrate concentrations (0, 1, 5, 10, 15, 20, 40, 100, 150 and 200 mM) on NRA of two representative hybrid poplar clones (3570 and 915311).

Measurement of the *in vivo* NRA in poplar leaves was done according to the method developed by Jaworski (1971) and optimized for broadleaf tree species (Truax *et al.*, 1994a). In early summer (June 29, 2007), leaves from the upper shoots were taken at noon at the

Bromptonville site. For each of the two clones, a composite sample was made by combining two leaves from two different trees. The plastochron index was used to select fully expanded leaves at the same developmental stage (Larson and Isebrands, 1971). Leaf plastochron index 7 (LPI 7) was selected for all samples. Samples were put in a plastic bag and immediately placed in a portable icebox (4°C). The sampling operations were always done within 1 h and plant material was brought back to the lab within 30 min after sampling.

At the lab, the leaves from each sample were cut into small pieces (2 x 2 mm) and 0.1 g of fresh tissue, in duplicate for each composite sample, was placed in a test tube containing 5 ml of incubating solution (pH 7.5), containing 100 mM phosphate buffer, 1.5 % 1-propanol and the different KNO_3 concentrations. Tissues samples and solutions were vortexed for 2 min to enhance infiltration of the assay medium. Each test tube was sealed and incubated in the dark for 1 h at 30°C. A blank was done for each composite sample. The enzymatic reaction was stopped by immersing the tubes in boiling water during 5 min. The colorimetric determination of the reaction was achieved by mixing 1 ml of incubation solution with 1 ml of 0.02 % NED and 1 ml of sulphanilamide. After 30 min, the samples were centrifuged at 2000 x *g* for 5 min and the supernatant was read in a spectrophotometer at 540 nm. Nitrate reductase activity is expressed as the amount of NO_2 measured in the test tube after the 1 h incubation period, calculated for 1 g of dry leaf tissue.

The effect of leaf age on NRA was assessed for the five hybrid poplar clones. The same procedure as the one described above was employed, except that leaf samples from LPI 3 to LPI 9 were collected from the five clones at the Bromptonville site (2-3 July, 2007). Based on the enzymatic kinetics assay, we used a substrate (KNO_3) concentration of 40 mM.

In mid July (10 and 11 July, 2007) and late August (28 and 29 August, 2007), NRA assays were performed with plant material from the two riparian buffer sites (Bromptonville and Magog). In each experimental plot (n of plots = 40), a composite sample was made by combining two leaves from two different trees of a single clone (one clone per plot). Leaf samples were collected in the same manner as in the previous assays and the same procedure was used for NRA determination. Based on the observations concerning the effect of leaf age on NRA, plant material corresponding to LPI 6 was used for all clones in this assay.

In order to facilitate discussion on NRA results, characteristics of hybrid poplar clones at each site are also presented in Table 4.5: mean whole-tree aerial biomass (including leaves), mean leaf biomass, leaf N concentration, leaf N accumulation, mean leaf nitrate reductase activity, and total leaf NRA per tree. Biomass, N concentration and N accumulation data were taken from Fortier *et al.* (2010a; 2010b).

4.2.7 Statistical analysis

ANOVA tables were constructed in accordance with Peterson (1985), and degrees of freedom, sum of squares, mean squares and *F*-values were computed. When a factor was declared statistically significant (Sites, Clones and Sites x Clones interaction), the standard error of the mean (SE) was used to evaluate differences between means for three levels of significance ($p<0.05$, $p<0.01$ and $p<0.001$). All of the ANOVAs were run with the complete set of data (2 sites, 5 clones, 4 blocks = 40 experimental plots). Results of enzymatic kinetics and effect of leaf age on NRA are presented as means with standard deviations (SD).

4.3 Results

4.3.1 Nitrogen supply rate, soil N concentration and N mineralization

Nitrate supply rate was approximately three times higher at the Bromptonville site compared to the Magog site, while NH_4 supply rate was approximately 50 % higher at the Magog site (Table 4.3). This resulted in very contrasting molar ratios of NO_3:NH_4 availability (1.8 at Bromptonville vs. 0.4 at Magog). Initial NO_3^- concentration measured at the beginning of the mineralization study was approximately 60 % higher at the Bromptonville site, while initial NH_4^+ concentration was more than twice higher at the Magog site (Table 4.4). After the incubation period (24 days), a three-fold increase in NO_3 concentration occurred at

Bromptonville, while only a two-fold increase was observed at Magog. This resulted in a higher nitrification rate at Bromptonville. At both sites, NH_4 concentration in soil showed a decrease after the incubation period because of high nitrification rates. Because nitrification rate was higher at Bromtptonville, the decrease in NH_4 concentration was also higher, although ammonification rates were not statistically different between the two sites.

Table 4.4

Nitrification and ammonification rates (mmol N kg of soil^{-1} 24 day period^{-1}) measured at the two riparian sites (17 July – 9 August, 2007). Nitrate and ammonium concentrations at the beginning (initial) and at the end (final) of the *in situ* incubation period are also presented.

Sites	NO_3 initial	NO_3 final	Nitrification rate	NH_4 initial	NH_4 final	Ammonification rate
Bromptonville	0.082	0.273	0.191	0.068	0.016	-0.0519
Magog	0.051	0.101	0.051	0.162	0.151	-0.0116
SE	0.006	0.028	0.025	0.015	0.017	-
$p<$	0.01	0.001	0.001	0.001	0.001	NS

4.3.2 Nitrate reductase activity

The effect of leaf age or developmental stage on NRA was different from one clone to another (Figure 4.1). At all developmental stages, leaf NRA of clone 3570 was higher than any other clones and showed a rapid decrease with leaf age. Clone 3729 had a higher leaf NRA value than clones 3230, 915311 and 915508, at all developmental stages, except for LPI 8. For the three other clones (3230, 915311 and 915508), leaf NRA was relatively low, with a maximum value observed at LPI 3. At almost all leaf developmental stages, clone 915508 had the lowest NRA. The pattern of NRA decrease with leaf age observed for clone 3570 cannot be generalized to the other clones because most of them had similar NRA at LPI 9, when compared to LPI4, LPI 5 or LPI 6.

For the two NRA assays at the two riparian sites (10-11 July and 28-29 August 2009), a significant Site x Clone interaction was detected by the ANOVA (Figure 4.2). During the

July assay, NRA of clone 3570 was statistically higher than any other clones at both sites. However, during the August assay, only NRA of clone 3570 at the Bromptonville site was statistically higher than any other clones at both sites. During both assays, clone 3570 had a significantly higher NRA at the Bromptonville site than at the Magog site, while NRA of the four other clones was generally higher at the Magog site or equivalent to what was observed at the Bromptonville site. The NRA of clone 3570 at Bromptonville was almost twice as high in the August assay than in the July assay, while little difference in NRA was observed at the Magog site between the two assay dates. In fact, at the Bromptonville site, NRA of all clones was generally higher in the August assay compared to the July assay. This trend was not observed at the Magog site.

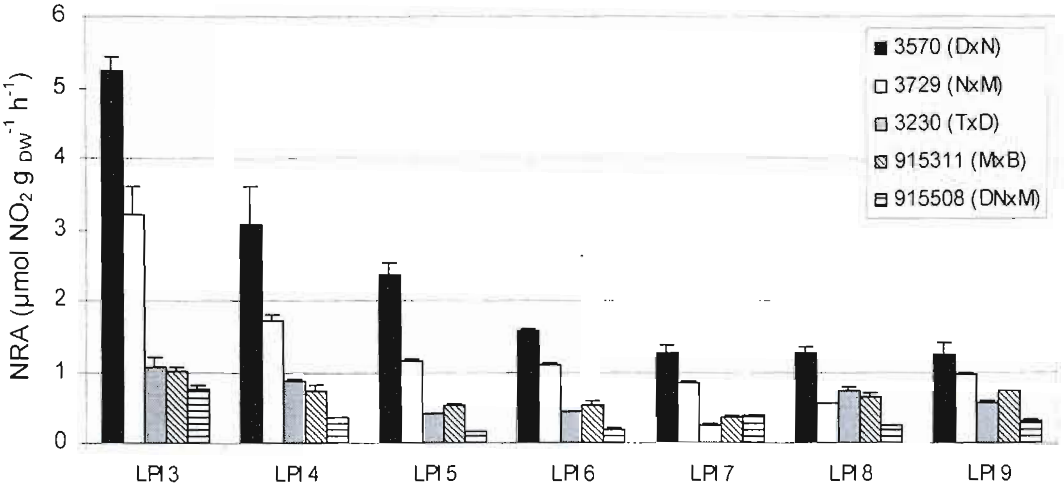

Figure 4.1 Effect of leaf age (developmental stage) on nitrate reductase activity (NRA) of five hybrid poplar clones. Leaf plastochron index (LPI) is used as an indicator of leaf age. All data points are means of duplicate samples analysis and vertical bars represent SD of the means.

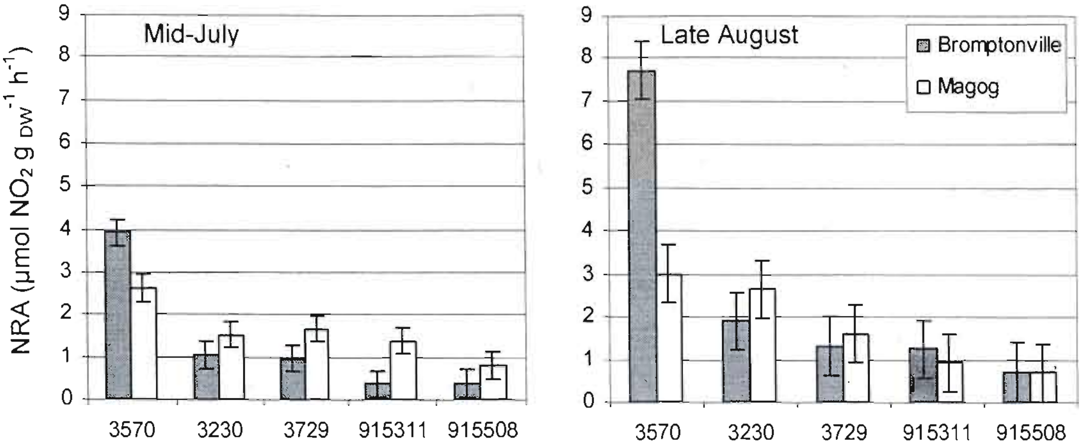

Figure 4.2 Nitrate reductase activity (NRA) of five hybrid poplar clones at the two riparian buffer sites. On the left, the NRA assay was done in mid-July (10 and 11 July, 2007) and Site x Clone interaction is significant at $p<0.05$. On the right, NRA assay was done in late August (28 and 29 August, 2007) and Site x Clone interaction is significant at $p<0.01$. Vertical bars represent SE of the means.

Table 4.5

Characteristics of hybrid poplar clones at each site: mean whole-tree biomass including leaves (kg tree^{-1}), mean leaf biomass (kg tree^{-1}), Leaf N concentration (g kg^{-1}), Leaf N accumulation (g tree^{-1}), leaf nitrate reductase activity (NRA) (µmol NO_2 g $_{DW}^{-1}$ h^{-1} and total leaf NRA) and total leaf NRA (mmol NO_2 tree^{-1} h^{-1})*.

Sites and clones	Whole-tree biomass[1] (kg tree^{-1})	Leaf biomass[1] (kg tree^{-1})	Leaf N concent.[2] (g kg^{-1})	Leaf N accumul.[2] (g tree^{-1})	Leaf NRA[3] (µmol NO_2 g $_{DW}^{-1}$ h^{-1})	Total leaf NRA[4] (mmol NO_2 tree^{-1} h^{-1})
Bromptonville						
3570	46	5.1	28	144	5.7	29.0
3230	52	5.3	25	134	1.4	7.6
3729	76	8.6	23	197	1.1	9.6
915311	69	6.9	21	142	0.8	5.4
915508	51	4.5	25	116	0.5	2.4
Magog						
3570	7	1.2	19	23	2.9	3.4
3230	10	1.5	20	29	2.1	3.2
3729	17	3.0	18	55	1.7	5.0
915311	14	2.6	17	47	1.2	3.1
915508	13	1.6	19	31	0.7	1.2

[1] See additional details in Fortier et al. 2010a

[2] See additional details in Fortier et al. 2010b

[3] Leaf NRA was calculated by taking the mean value of the two assays presented in Figure 4.2

[4] Total leaf NRA was calculated by multiplying leaf NRA with mean leaf biomass per tree

4.4 Discussion

4.4.1 Effect of leaf age on NRA

At any leaf age, clone 3570 had a higher NRA than any other clones studied here (Figure 4.1). The pattern of NRA in relation to leaf age was also different from one clone to another. The pattern of NRA decrease with leaf age observed for clone 3570 is consistent with the observations of Black *et al.* (2002) in *P.tremula* x *alba* and with those of Pokhriyal and Raturi (1985) in Eastern cottonwood (*P. deltoides*). This pattern was not clear for all the other hybrid poplar clones in this study, because most of them (3230, 915311 and 915508) had similar NRA at LPI 8 and LPI9 when compared to LPI3, LPI4 or LPI 5. This indicates that for some clones the physiological process of nitrate reduction is almost equivalent in activity in both sink (young) and source (old) leaves. Therefore, the physiological importance of mature leaves in providing carbohydrates and amino acids to expanding leaves may be different from one hybrid poplar clone to another (Giaquinta, 1978; Huber *et al.*, 1992). However, in all five clones LPI 3 had the highest NRA. Localization of high NRA in younger leaves may indicate that newly acquired NO_3^- is rapidly translocated to the upper parts of the tree in order to stimulate shoot growth and leaf expansion (Black *et al.*, 2002).

4.4.2 Effect of nitrate availability on NRA of hybrid poplar clones

Soil and site characteristics were very contrasted between the two study sites and this dramatically affected N-form availability (Tables 4.1, 4.3, and 4.4). Lower NO_3 availability in the soil at Magog is probably related to the absence of fertilisation, lower cow density (low animal input of nutrients) and lower N mineralization rate (Table 4.1, 4.3 and 4.4). Lower nitrification rate at the Magog site may be the result of a combination of factors such as low soil pH, high soil moisture (imperfect drainage) and absence of fertilisation (Stanford and Epstein, 1974; Raison *et al.*, 1992; Bona *et al.*, 2008).

Important differences in the NO_3 availability in riparian soils of pastures appear to induce a clone-specific response in NRA. This resulted in a significant Site x Clone interaction, with clone 3570 having a particularly high NRA at the Bromptonville site, while NRA of the four other clones (3230, 3729, 915311 and 915508) was generally low and similar between clones and between sites (Figure 4.2). This suggests that clone 3570 has a particular ability to activate the nitrate reduction process in its leaves in response to a higher NO_3 availability in the soil.

Higher leaf NRA from all clones could be expected at the Bromptonville site given the highest NO_3 availability at this site. As reported by Black *et al.* (2002) and Rosenstiel *et al.* (2004), highest leaf NRA values were found in poplars grown in soils with the highest external NO_3^- concentrations. Our field-based study showed that this relationship is only true for clone 3570, independently of tree size (Figure 4.2, Table 4.5).

It could also be argued that NO_3 reduction process in hybrid poplars grown at the Bromptonville site was diluted in a much larger leaf and whole-tree biomass compared to the Magog site (Table 4.5). An inverse relationship between dry biomass and NRA was also reported in *Robinia pseudoacacia* (Johnson *et al.*, 1991). However, this dilution effect was not observed for clone 3570 in this study. At the whole-tree level, clone 3570 also had a much higher total leaf NRA at the Bromptonville site, while this value was much more similar between all five clones at the Magog site (low NO_3 availability) (Table 4.5). This trend was also observed for leaf N concentration in poplar leaves.

Although, clone 3570 has the highest NRA and the highest leaf N concentration of all five clones, it is also the clone with the slowest growth rate at both sites (Table 4.5). Furthermore, at the whole-tree level, clone 3570 did not have a particularly high quantity of N accumulated and its leaves. Thus, NRA observed during the 5th growing season was neither a good indicator of mean aboveground biomass accumulation nor of N accumulation at the end of the 6th growing season (Table 4.5). Dykstra (1974) also reported that leaf NRA was not an index of N assimilation in hybrid poplars. However, this author observed that the poplar clone with the highest NRA had a significantly higher dry stem weight, dry leaf weight, and height growth. This was not the case in our field study.

Other components of productivity that have important genetic variation among poplar species may have affected clone growth, whether they are structural or physiological (Bradshaw *et al.*, 2000). This include leaf morphology and leaf growth (Ridge et al., 1986), leaf photosynthetic capacity (Barigah *et al.*, 1994), nutrient requirements (Heilman and Norby, 1998), nutrient-use efficiency (Lodhiyal and Lodhiyal, 1997), water-use efficiency (Blake *et al.*, 1984), light-use efficiency (Cannell *et al.*, 1988), phenotypic plasticity in response to differential N availability (Cooke *et al.*, 2005), early-rooting ability and rooting patterns (Green *et al.*, 2003; Block *et al.*, 2006; Zalesny *et al.*, 2009), size, distribution and orientation of leaves and branches (Isebrands and Michael, 1986; Ceulemans *et al.*, 1990; Dunlap and Stettler, 1998), wood density (Pliura *et al.*, 2007), etc. A favourable combination of many of these factors explains the superior growth of selected hybrid poplar clones (Bradshaw *et al.*, 2000).

As proposed earlier by Dykstra (1974), we suggest that important NRA differences reflect the genetic assemblage, or parentage, of the five unrelated clones. Four of the five clones used in this study (3230, TxD; 3729, NxM, 915311, MxB and 915508, DNxM) had at least one parental species from the *Tacamahaca* section of the *Populus* genus (*P. balsamifera*, *P. trichocarpa*, *P. maximowiczii*). These four clones share another similarity; they all had relatively low NRA in comparison to clone 3570 (Figures 4.1 and 4.2). On the other hand, clone 3570, a DxN hybrid that has both of its parental species from the *Aigeiros* section, was the only clone that had an increased NRA on the nitrate-rich Bromptonville site. Dykstra (1974) also reported that leaf NRA in *P. deltoides* x *P. nigra* was much higher than in *P. tristis* x *balsamifera* at all substrate availabilities.

The relatively low leaf NRA in hybrid poplar clones that have a *Tacamahaca* section genetic contribution may be related to the soil N-form preferences of these clones. As pointed out by Desrochers *et al.* (2007), *P. balsamifera* and two other clones related to the

Tacamahaca section were better adapted for NH_4 uptake, rather than that of NO_3 . This is consistent with the fact that that poplars from the *Tacamahaca* section are generally less nutrient demanding and better adapted to lower site fertility, lower soil pH and cooler climates, than poplars from the *Aigeiros* section (Zsuffa *et al.*, 1977; Dickmann, 2001; Cooke and Rood, 2007; Périnet, 2007).

Conversely, research on Eastern cottonwood (*P. deltoides.*) suggests that a 60–80% NO_3 (balanced with NH_4) solution optimizes whole-plant growth (Woolfolk, 2000). Moreover, Woolfolk and Friend (2003) found that greatest total root length, specific root length, and N concentration of roots in enriched patches occurred at the 80:20 NO_3:NH_4 ratio. This evidence supports the fact that poplars from the *Aigeiros* section generally grow best on nutrient-rich alluvial deposits found in warmer temperate regions (Dickmann, 2001). High leaf NRA in response to high NO_3:NH_4 ratio has also been reported in red ash (*Fraxinus pennsylvanica*), a common early succession species of rich alluvial bottomlands (Truax *et al.*, 1994b).

Nevertheless, although different poplar species and hybrids may have soil N-form preferences, trees from the genus *Populus* are considered generalist pioneer species, capable of thriving on low and high NO_3 or NH_4 sites (Min *et al.*, 2000). This would also explain why NO_3 was the main factor controlling biomass growth, C sequestration and N accumulation of all five clones in the same experimental design (Fortier *et al.*, 2010a, b).

Finally, a clearer portrait of NRA in the set of clones studied here may have been obtained if NRA in roots had been tested in parallel to leaf NRA. Given that very low NRA was found in leaves of some clones (particularly clone 915508), it could also be suggested that NO_3 assimilation is relatively important in the roots of some clones and hybrid types, as shown by Min *et al.* (1998) in trembling aspen (*P. tremuloides*). Given the high genetic variability in physiological traits of poplar species, generalisations such as that nitrate assimilation is almost entirely restricted to leaves in poplars (Black *et al.*, 2002), should be made with caution.

Future research is needed to clearly understand soil N-form preferences among unrelated hybrid poplar clones and its potential relationship with NRA. If this relationship is proven, NRA could provide interesting information on the suitability and adaptability of different hybrid poplar clones to various plantation environments (clear-cut sites, agricultural sites, abandoned farmland, riparian buffers, contaminated sites)

4.5 Conclusion

Although poplars are commonly used as model trees (Bradshaw *et al.*, 2000), it is clear from this study and others, that important physiological differences exists concerning N assimilation among the different poplar species, hybrids and clones. Leaf NRA differences of more than one order of magnitude were observed between the hybrid poplar clones used in this study, with clone 3570 always having the highest NRA. Important differences in NO_3 availability in riparian soils of pastures appear to induce a clone-specific response in NRA only seen in clone 3570. These important NRA differences may reflect the genetic assemblage or parentage of the five unrelated clones, and possibly influence soil N-form preferences.

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CONCLUSION GÉNÉRALE

Les résultats présentés dans les deux premiers chapitres de cette thèse ont mis en lumière le fort potentiel des bandes riveraines de peuplier hybride pour produire du bois et de la biomasse, ainsi que pour séquestrer du carbone et des nutriments (N et P) en milieu agricole. La démonstration de ce potentiel constitue une contribution majeure dans les domaines de l'agroforesterie et des services écosystémiques dans les paysages agricoles. Le peuplier hybride est actuellement employé partout dans le monde en milieu tempéré (Canada, États-Unis, Argentine, Chili, Europe, Inde, Chine, etc.). Cette essence pourrait donc facilement être implantée dans la zone riveraine de divers paysages agricoles des régions tempées de façon à créer des biens alternatifs (bois et biomasse) tout en améliorant l'agroenvironnement. L'Organisation des Nations Unies (ONU) semble d'ailleurs manifester un intérêt particulier pour les solutions agroforestières qui visent la production de biomasse en zone riveraine (A. Gold, communication personnelle). Dans un contexte mondial d'expansion des pratiques agricoles intensives (Millenium Ecosystem Assessment 2005), il semble plus que jamais important de développer des solutions d'aménagement viables sur le plan économique. Cela permettra de contrebalancer les coûts associés à la restauration de la zone riveraine, ce qui améliorera probablement l'acceptabilité sociale des projets de restauration.

Dans les régions tropicales et subtropicales, d'autres espèces à croissance rapide pourraient être employées, à l'instar du peuplier hybride en régions tempérées, dans des systèmes agroforestiers riverains similaires à ceux étudiés dans le cadre de cette thèse. Parmi ces essences on retrouve notamment le balsa (*Ochroma pyramidale*) et les espèces du genre *Cecropia*, les « peupliers des tropiques d'Amérique du Sud» (D. Gagnon, communication personnelle).

Cette thèse nous a également permis de constater que le potentiel du peuplier hybride à générer certains services écologiques dans la zone riveraine est très variable d'un site à l'autre. Des écarts de croissance d'environ un ordre de grandeur ont été observés entre les sites, essentiellement en raison de la fertilité du sol. Le principal facteur qui a influencé la croissance des peupliers et, par conséquent, leur capacité à séquestrer du C et des nutriments, a été la disponibilité en NO_3 dans le sol riverain. Cette forte disponibilité en NO_3 a été observée sur les sites où l'on pratique un élevage plus intensif du bétail (fertilisation annuelle du pâturage, densité élevée d'animaux). Ainsi, le peuplier hybride semble être un arbre idéal pour intercepter la pollution azotée qui provient de la fertilisation agricole. Non seulement le peuplier hybride croît plus vite lorsque l'azote est plus abondant dans le sol, mais on retrouve également l'azote en plus forte concentration dans ses tissus, ce qui a un effet synergétique sur l'accumulation totale de l'azote dans l'arbre (Jarrell et Beverly, 1981). Cette synergie positive a également été observée pour l'accumulation du phosphore aux sites de Bromptonville et de St-Isidore-de-Clifton.

Dans une étude paneuropéenne, il a été montré que l'efficacité des bandes riveraines pour enlever l'azote du sol est négativement corrélée à la charge en azote qui rejoint la bande riveraine (Sabater *et al.*, 2003). Parallèlement, on sait également que plus le sol riverain est saturé en phosphore plus les risques de lessivage de ce nutriment vers le cours d'eau sont importants lors d'événements de fort ruissellement ou d'inondation (Stutter *et al.*, 2009). L'utilisation d'essences très exigeantes sur le plan nutritionnel, comme le peuplier hybride, serait donc à recommander pour créer des «points chauds» d'enlèvement des nutriments en excès (N et P), particulièrement dans la zone riveraine qui borde les cultures annuelles dont les sols sont surfertilisés et souvent saturés en N et P (Di et Cameron, 2002; CAAAQ, 2007), mais également dans les pâturages fertilisés où la densité d'animaux est élevée. De plus, il est primordial de ne pas exclure les petits cours d'eau et les fossés de drainage de nos stratégies d'aménagement riverain, car ces derniers constituent souvent la première porte d'entrée des nutriments excédentaires dans le réseau hydrographique (Parkyn *et al.*, 2005; Wigington *et al.*, 2005).

Pour maintenir à long terme un fort potentiel de captage des nutriments en zone riveraine, une récolte périodique des peupliers est inévitable en bordure des cultures agricoles et des pâturages qui sont continuellement fertilisés (Dosskey, 2001; Dorioz *et al.*, 2006).

Dans cet esprit, la récolte des peupliers en fin d'été alors qu'ils ont encore leurs feuilles maximiserait l'exportation de l'azote et du phosphore à l'extérieur du système riverain, afin d'éviter une éventuelle saturation du sol.

Il semble également judicieux sur le plan sylvicole de profiter des excès de fertilisants agricoles pour produire rapidement de la matière ligneuse en zone habitée. Soulignons que des rendements en volume de bois atteignant 40 m^3 ha^{-1} an^{-1} ont été obtenus après six ans dans la bande riveraine du pâturage de Bromptonville en Estrie. Cela laisse présager que des rendements similaires et, mêmes supérieurs, pourraient être obtenus dans les régions agricoles chaudes et dominées par des cultures intensives (ex : bandes riveraines en bordure des cultures de maïs grain en Montérégie). De tels rendements pourraient également justifier l'aménagement de bandes riveraines plus larges, ce qui permettrait de maximiser l'enlèvement des nutriments excédentaires, tout en intensifiant la production ligneuse sur de faibles superficies, tel que le propose le concept de triade (Hunter, 1990; Messier *et al.*, 2003).

Les travaux de drainage et de redressement des cours d'eau en milieu agricole ont dénaturé plus de 30 000 km de cours d'eau naturels et ont créé environ 10 000 km de fossés verbalisés (Beaulieu, 2001). Notre étude montre que le peuplier hybride peut produire un rendement moyen de 18 m^3 ha^{-1} an^{-1} (tous sites et tous clones confondus) dans des bandes riveraines de 4,5 m de large (trois rangées d'arbres avec une densité de 2222 tiges ha^{-1}), ce qui équivaut à 18 m^3 par 1.1 km de cours d'eau protégé par des bandes riveraines de 4.5 m de largeur sur chaque berge. En multipliant la longueur du réseau hydrographique qui a été dénaturé et la longueur du réseau de drainage par la productivité moyenne du peuplier hybride en bande riveraine, on obtient un potentiel de production qui s'élève à environ 650 000 m^3 ha^{-1} an^{-1}. Cette quantité de bois correspondrait à un peu plus de 2 % des volumes de bois récoltés en forêt au Québec en 2006-2007 (Gouvernement du Québec, 2009). Une telle production de bois dans un contexte d'afforestation permettrait également de diversifier l'économie des régions agricoles et de générer des crédits de carbone éventuellement monnayables.

Soulignons que l'approche d'aménagement utilisée pour implanter les bandes riveraines dans cette étude est également peu coûteuse (aucune préparation de terrain et un arrosage d'herbicide de 1 m^2 par plant la première année). Cela se compare avantageusement aux coûts actuels associés à l'aménagement d'une plantation en milieu agricole au Québec (labourage-hersage en préparation de terrain et hersage 2 à 3 fois par an pendant 3 à 4 ans pour l'entretien).

Néanmoins, il serait réducteur de croire que les bandes riveraines de peuplier hybride sont uniquement intéressantes pour produire du bois et séquestrer du C et des nutriments dans une perspective d'aménagement intensif et de réduction de la pollution agricole diffuse. Les résultats du chapitre 3 montrent que les bandes riveraines créent, à mesure qu'elles croissent, une ambiance forestière en termes de conditions lumineuses. Ce phénomène ne semble pas affecter négativement l'abondance et la richesse des espèces végétales indigènes et de milieux humides en sous-couvert. Toutefois, à mesure que la canopée se referme, on observe une exclusion des espèces végétales introduites et de milieux mésiques.

Ces résultats suggèrent que les bandes riveraines de peuplier hybride pourraient également être aménagées pour créer des corridors forestiers permanents dans une perspective de conservation de la biodiversité en milieu agricole (habitat, interconnexion entre les boisés de ferme et les massifs forestiers, réduction de la température des cours d'eau, etc.). Dans ce type de bandes, des coupes partielles pourraient être réalisées et suivies d'un enrichissement en sous-couvert avec des espèces indigènes (feuillus nobles, pin blanc, arbustes, plantes de sous-bois forestier, etc.) de façon à créer des bandes boisées s'apparentant aux forêts riveraines naturelles (Gardiner *et al.*, 2004). Par la suite, ces bandes boisées pourraient faire l'objet d'un aménagement extensif ou écosystémique de façon à maintenir un certain potentiel d'enlèvement des nutriments excédentaires tout en conservant des attributs structuraux, fonctionnels et compositionnels (ex : chicot, bois mort au sol, débris ligneux dans le cours d'eau, etc.). Enfin, dans les zones où la pollution diffuse n'est pas un enjeu, ces bandes boisées pourraient tout simplement être protégées. Bref, les bandes riveraines de peuplier hybride apparaissent comme un outil de restauration multifonctionnel et polyvalent qui peut être employé dépendamment de l'objectif poursuivi par le propriétaire (réduction de la pollution diffuse, production de bois ou de biomasse, séquestration de C, création de corridors forestiers) (Figure C.1).

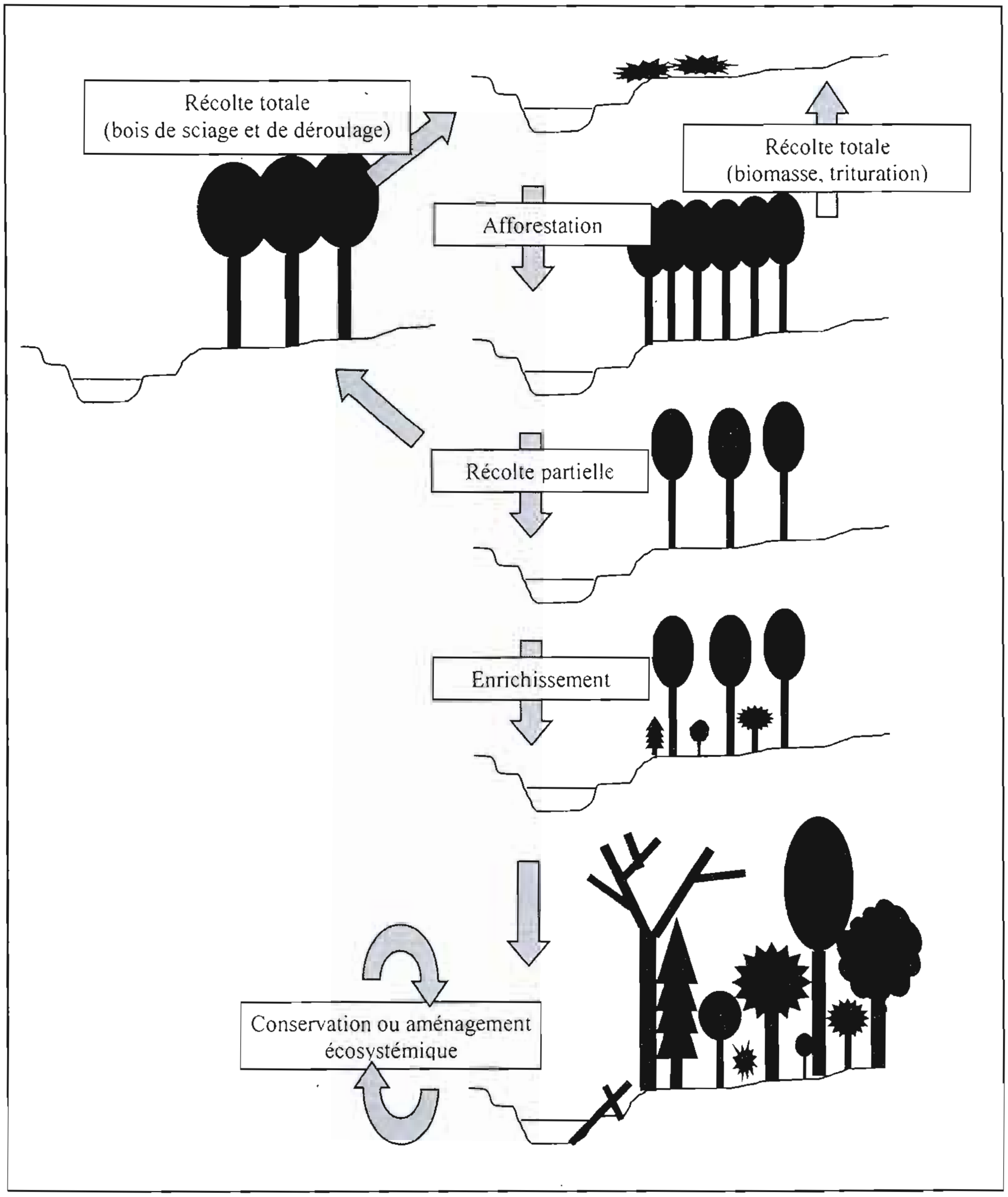

Figure C.1 Schématisation de différentes options d'aménagement possibles en partant d'une stratégie d'afforestation en milieu riverain agricole avec le peuplier hybride.

Cette thèse a également mis en lumière les importantes différences qui existent entre des clones de peuplier hybride non apparentés, notamment en terme de production de biomasse et de volume, de séquestration du carbone, d'accumulation des nutriments, d'architecture, d'ouverture de la canopée et d'activité de la nitrate réductase. Ces différences suggèrent d'abord que certains clones (3729 et 915311) sont plus propices que d'autres pour produire rapidement de la biomasse, et par conséquent séquestrer du C et des nutriments. Toutefois, d'autres clones qui poussent moins vite en bas âge (3570 et 3230) seront peut-être plus intéressants pour produire du bois de sciage et de déroulage sur de plus longues rotations en raison de leur rectitude et de leur plus faible branchaison.

Malgré sa forte croissance, nous avons montré que le clone 915311, un hybride entre *P. maximowiczii* et *P. balsamifera*, réduit considérable la biomasse des plantes en sous-couvert et, par conséquent, l'abondance des différents groupes d'espèces végétales. Cette situation est potentiellement défavorable tant sur le plan de la conservation que sur le plan de la lutte à la pollution diffuse. La végétation herbacée sous les peupliers est essentielle pour intercepter les sédiments et réduire l'érosion de surface; deux vecteurs importants pour le transport du phosphore vers le cours d'eau (McDowell *et al.*, 2001). Bien que la faible ouverture de la canopée sous le clone 915311 soit reliée à une faible biomasse végétale en sous-couvert, une évaluation plus approfondie du potentiel inhibiteur des composés chimiques secondaires contenus dans les feuilles de ce clone (apparenté au peuplier baumier) permettrait d'avoir un portrait plus complet des interactions peuplier : sol : plantes de sous-couvert (Schimel *et al.*, 1998). Les composés chimiques secondaires du peuplier baumier sont aussi des stimulateurs puissants de l'activité microbienne dans le sol, ce qui immobilise l'azote et réduit les pertes de ce nutriment (Schimel *et al.*, 1998). Parallèlement, le peuplier baumier possède une litière de moindre qualité (faible en N) , ce qui cause un enrichissement progressif du sol en carbone (Schimel *et al.*, 1998) et favorise potentiellement la dénitrification. Ces relations complexes illustrent bien le défi qui peut exister lorsque l'on cherche à aménager des bandes riveraines capables d'éliminer plusieurs polluants simultanément (Vidon *et al.*, 2010). Pour toutes ces raisons, il est recommandé d'opter pour une diversité de clones non apparentés pour augmenter la résilience face aux maladies et aux insectes, mais également pour ajouter de la diversité structurale et fonctionnelle, et ce tant dans le sol qu'au-dessus du sol. Nos résultats d'activité de la nitrate réductase vont d'ailleurs en ce sens, car ils suggèrent qu'il existe potentiellement d'importantes différences clonales en matière d'assimilation des différentes forme d'azote.

De manière générale, la forte croissance du peuplier hybride en zone riveraine nous porte à croire que cet arbre peut rapidement créer un environnement propice à la dénitrification bactérienne dans le sol, particulièrement sur les sites moins bien drainés (Gold *et al.*, 2001). Cette hypothèse doit toutefois être vérifiée. Une connaissance plus approfondie de la capacité des bandes riveraines de peuplier hybride à enrichir le sol riverain en carbone serait un atout dans ce contexte. Rappelons que la dénitrification est une fonction centrale pour l'enlèvement de l'azote dans la zone riveraine, particulièrement lorsque les arbres sont en dormance et qu'ils n'accumulent pas l'azote dans leur biomasse (Haycock et Pinay, 1993).

Une connaissance plus approfondie de l'architecture racinaire des différents clones pourrait également être utile pour comprendre de quelle manière les racines de peuplier colonisent les berges des cours d'eau. La stabilisation des berges est une autre fonction importante que procurent les arbres en milieu riverain, sachant qu'elle peut contribuer à réduire fortement les apports en sédiments et en phosphore dans les cours d'eau (Laubel *et al.*, 2003). Enfin, sur le plan de la conservation, il serait intéressant de réaliser des relevés fauniques (oiseaux, invertébrés dans la végétation, de la pédofaune et aquatiques, amphibiens, petits mammifères) pour évaluer la contribution des bandes riveraines de peuplier hybride en tant qu'habitat dans la matrice agricole. Cela permettrait également d'évaluer si les bandes constituent un refuge pour des espèces qui fournissent des services écologiques, comme la pollinisation et la lutte biologique. Par ailleurs, il pourrait également être envisageable de substituer le peuplier hybride pour des espèces indigènes (peuplier deltoïde et baumier) pour éviter tous problèmes possibles de pollution génétique (Broeck *et al.*, 2005).

Enfin, il faut garder à l'esprit que les bandes riveraines ne constituent pas une solution sans faille pour lutter contre la pollution agricole diffuse. Par exemple, les arbres sont peu actifs en matière d'accumulation d'éléments nutritifs de l'automne jusqu'au printemps, car ils sont en dormance. C'est également durant cette période de l'année que le réseau hydrographique augmente en densité (Wigington *et al.*, 2005) (Figure I.2) et que le phosphore est massivement exporté vers les cours d'eau lors de la fonte des neiges (Väänänen *et al.*, 2006). De même, lors de fortes pluies en terrain agricole argileux, une partie non négligeable des eaux de ruissellement riches en NO_3 n'infiltreront pas le sol riverain, ce qui exportera le NO_3 directement vers les cours d'eau (Wigington *et al.*, 2003). De plus, certaines fonctions de la bande riveraine qui permettent une réduction de la pollution diffuse génèrent également des impacts négatifs à d'autres échelles. Par exemple, lorsque les eaux chargées de NO_3 de la nappe phréatique rejoignent chroniquement la bande riveraine, la dénitrification produit des oxydes d'azote qui sont d'importants gaz à effet de serre (Hefting *et al.*, 2003). Cela met en perspective qu'une diversité d'approches, tant à l'échelle de la régie des cultures et des élevages, qu'en matière d'aménagement de l'ensemble du territoire agricole, doit être implantée pour prendre en charge des problématiques aussi complexes que la pollution diffuse et la conservation.

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