UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE DES PEUPLEMENTS DE MÉLÈZE DANS LES TOURBIÈRES DE LA RÉGION DU LAC DUPARQUET, ABITIBI

MÉMOIRE
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AVANT-PROPOS

Le présent mémoire est constitué des trois articles suivants:

Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. «Gradient analysis in *Larix laricina* dominated wetlands in Canada's southeastern boreal forest». Canadian Journal of Botany 79: 444-456.

Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. «Radial growth analysis of *Larix laricina* from Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks». Écoscience 8: 127-138.

Girardin, M.P., Tardif, J. et Bergeron, Y. soumis. «Dynamics of eastern larch stands in relation to larch sawfly outbreaks in the Northern Clay Belt of Quebec». Canadian Journal of Forest Research 0: 00-00.

La création du protocole expérimental, la récolte, l'analyse statistique des données ainsi que la rédaction des trois manuscrits furent réalisées par l'auteur principal. La contribution des co-auteurs fut essentiellement de financer le projet, superviser les étapes de terrain, les analyses statistiques et la rédaction. Leurs commentaires et suggestions quant aux choix des analyses et à la structure des manuscrits furent grandement appréciés. Ce mémoire de maîtrise et les trois articles qu'il comporte constituent donc une contrubution originale de Martin P. Girardin.

REMERCIEMENTS

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RÉSUMÉ

Les populations de mélèze laricin (*Larix laricina* (Du Roi) K. Koch) sont principalement confinées aux milieux hydriques où la croissance des arbres est limitée par le mauvais drainage, la faible disponibilité en éléments nutritifs, l'absence d'oxygène au niveau des racines et la basse température des sols. Des épisodes périodiques de défoliation par la tenthrède du mélèze (*Pristiphora erichsonii*) constitueraient aussi un facteur important influençant la croissance et la dynamique des peuplements. Le mémoire suivant a été consacré à 1) déterminer les principaux facteurs écologiques associés à la distribution de la végétation des tourbières à mélèzes rencontrées sur les rives du Lac Duparquet, au sud-ouest de la forêt boréale québécoise; 2) déterminer les facteurs contrôlant la croissance radiale du mélèze et 3) déterminer les facteurs influençant la dynamique des peuplements de mélèze.

L'étude de la végétation réalisée dans quatre peuplements distribués dans la région du Lac Duparquet indique que la répartition des espèces à l'intérieur de ces milieux était principalement reliée à la distance de la rive, c'est à dire à la tolérance des espèces aux crues printanières. Des relations significatives ont aussi été observées avec la concentration en nitrates du substrat (en relation avec l'abondance de *Kalmia angustifolia* et d'*Alnus rugosa*), son pH et sa conductivité. Un lien a été démontré entre les propriétés chimiques et physiques de la nappe phréatique et la distribution des espèces, notamment le pH, la conductivité, la profondeur et la concentration en carbone. L'interférence lumineuse s'est également révélée un facteur important sous le couvert de *Thuja occidentalis*. De plus, nous avons noté que la distribution de certaines espèces végétales est représentative de conditions environnementales particulières (pH, hauteur de la nappe, effet de compétition, etc). Les espèces indicatrices des milieux sont, entre autres, *Larix laricina*, *Spiraea alba*, *Kalmia angustifolia*, *Picea mariana*, *Alnus rugosa*, *Betula pumila*, *Thuja occidentalis*, *Trientalis borealis*, *Abies balsamea*, *Betula papyrifera*, *Fraxinus nigra*, *Onoclea sensibilis* et *Eleocharis smallii*.

Les analyses des patrons de croissance radiale, des cernes manquants et des cernes à bois terminal pâle de tiges de mélèze ont montré l'existence de plusieurs épidémies de la tenthrède au cours du dernier siècle. Par l'observation de ces caractéristiques, nous avons détecté des évidences de périodes d'épidémie pour les années 1895-1912, 1937-1942 et 1955-1962. Toutefois, les analyses dendrochronologiques utilisant le mélèze et une espèce non-hôte de la tenthrède (*Picea mariana*) laissent aussi supposer qu'il y aurait eu des périodes d'épidémies au début des années 1920, à la fin des années 1970 et au début des années 1980. Les analyses dendroclimatiques ont à leur tour montré que les hauts niveaux des eaux de mai et de septembre, de même que les précipitations d'août, étaient les principaux facteurs influençant la croissance radiale du mélèze (relations négatives). Une relation positive avec l'indice de sécheresse a aussi été observée. Fait intéressant, depuis les années 1960, la variabilité inter-annuelle dans la croissance du mélèze croissant en bordure du Lac Duparquet est à la hausse. De même, l'effet négatif des niveaux des eaux du mois de mai sur la croissance est plus important.

L’analyse de la distribution des classes d’âge a principalement permis d’identifier trois périodes de régénération du mélèze au cours des 150 dernières années: 1840-1890, 1900-1920 et 1935-1950. Suite à l’analyse dendrochronologique, deux de ces périodes (1900-1920 et 1935-1950) de recrutement ont été apparentées aux épidémies de la tenthrède mentionnées ci-haut (1895-1912 et 1955-1962). En induisant la mortalité du couvert dominant, la tenthrède du mélèze permettrait la survie d’une régénération préétablie, ainsi que l'augmentation de la production de graines chez les arbres ayant survécu.

Ces travaux nous ont permis d’illustrer l’existence d’un gradient complexe à l’intérieur des communautés de mélèzes du Lac Duparquet, gradient expliqué par le régime nutritif, la compétition et le régime hydrique. Par contre, les relations les plus importantes ont été obtenues à partir de l’étude de la dynamique des peuplements, notamment entre les patrons de recrutement de mélèze et les épisodes de la tenthrède. Les résultats ont, entre autres, démontré que les épidémies de la tenthrède n’affectaient pas l’ensemble du peuplement mais avaient un effet plutôt local (dynamique de trouées). Ces peuplements devraient être étudiés d’une façon plus approfondie afin de déterminer la taille de ces trouées et plus précisément les facteurs induisant leur formation.

Mots clés : *Larix laricina*; analyse de végétation; inondation; analyse canonique des correspondances; *Kalmia*; *Alnus*; *Thuja occidentalis*; *Picea mariana*; dendrochronologie; insectes; climat; bois terminal pâle; *Pristiphora erichsonii*; fonction de réponse.

INTRODUCTION GÉNÉRALE

1.1 SUJET

Le mélèze laricin (*Larix laricina* (Du Roi) K. Koch) est abondamment distribué dans les tourbières nord-américaines de l'Atlantique jusqu'au centre de l'Alaska (Johnston 1990). Principalement confiné aux milieux humides en zones subarctique, boréale et tempérée (Nairn *et al.*, 1962; Schooley et Pardy, 1981; Bergeron *et al.*, 1982; Martineau, 1985; Johnston, 1990), il peut également être observé sur des sols minéraux. En milieu humide, sa croissance est principalement limitée par la présence d'un mauvais drainage, la faible disponibilité en éléments nutritifs, l'absence d'oxygène et la basse température du sol (Bergeron *et al.*, 1982; Kozlowski, 1982). Du fait qu'il a une distribution très vaste, le mélèze est en mesure de tolérer des conditions climatiques très variées (Johnston 1990)

1.2 PROBLÉMATIQUE

Des travaux historiques portent à croire que les peuplements de mélèze ont été fortement menacés dans le passé, notamment en raison d'une épidémie sévère de la tenthrède du mélèze (*Pristiphora erichsonii*), au cours des années 1870 et 1900 (Turnock, 1972; frère Marie-Victorin, 1995). Toutefois, bien peu d'informations existent dans la documentation scientifique sur l'effet de ce facteur sur la croissance du mélèze, et encore moins, sur la dynamique des peuplements. À cela s'ajoute l'effet des récents changements climatiques qui risquent non seulement d'interférer avec la dynamique des peuplements de mélèze, mais également avec l'ensemble des espèces composant ces communautés.

1.3 ÉTAT DES CONNAISSANCES

Le succès de l'établissement d'une espèce en tourbière dépend principalement de la qualité du drainage. Les effets variés résultant d'une inondation prolongée sont en majorité crées par une déficience en oxygène du substrat (Kozlowski, 1984). On y retrouve entre autres un taux élevé de bactéries anaérobies, induisant la formation de toxines (Zinkal *et al.*, 1974; Crawford, 1983; Kozlowski, 1984; Lieffers et Rothwell, 1986; Yamamoto *et al.*, 1987). Une inhibition de certains échanges physiologiques au niveau des racines suite à la pourriture de celles-ci serait également créée, particulièrement l'évacuation des toxines accumulées par la plante, (Zinkal *et al.*, 1974; Crawford, 1983; Kozlowski, 1984; Lieffers et Rothwell, 1986; Yamamoto *et al.*, 1987).

Bien que la tolérance aux conditions hydriques soit d'une importance capitale pour le succès d'une espèce végétale dans ces milieux, il n'en demeure pas moins que plusieurs relations ont été observées entre la distribution des espèces et certains autres paramètres environnementaux tels que les concentrations du substrat et de l'eau en éléments cationiques (H, Ca, Zn, etc.) et nutritifs (NH_4, NO_3, P, K)(Vitt et Bayley, 1984; Glaser *et al.*, 1990; Jean et Bouchard, 1993; Jeglum et He, 1995). Cependant, plusieurs de ces études sont contradictoires en ce qui a trait au rôle accordée aux paramètres chimiques (nitrates, pH, conductivité, etc) dans la distribution des communautés végétales. Ainsi, Jeglum et He (1995) ont mentionné que les gradients pH-calcium et nitrates de la tourbe seraient responsables de la plus grande part de la variabilité dans la distribution de la végétation. Au contraire, Jean et Bouchard (1993) n'ont observé que de faibles relations entre la distribution végétale et le gradient nutritif, alors que Glaser *et al.* (1990) n'ont observé que de faibles relations avec le gradient cationique.

Certains auteurs auraient attribué ces divergences dans la distribution des espèces végétales aux types de perturbations retrouvées dans les milieux étudiés (Heinselman, 1970; Vitt et Bayley, 1984; Jean et Bouchard, 1993; Jeglum et He, 1995). Comme de nombreux autres milieux forestiers, les tourbières sont sujettes aux régimes de perturbations (Heinselman, 1970; Johnston, 1990). Bien que le feu à l'intérieur de ce type d'environnement soit relativement rare (Curtis, 1959) (conditions relativement humides), il n'en demeure pas moins que le feu d'un bassin versant pourrait avoir une influence considérable sur les propriétés chimiques de la tourbe et la composition en espèces du sous-bois (Heinselman, 1970; Jeglum et He, 1995). Il en sera de même pour les modifications anthropiques apportées au régime du bassin hydrographique (barrage ou coupe) (Jean et Bouchard, 1996).

En Amérique du Nord, les changements climatiques des trois derniers siècles ont fait l'objet de plusieurs études dendrochronologiques (Stockton et Meko, 1983; Jacoby et

D'Arrigo, 1989; Bergeron et Archambault, 1993; Tardif et Bergeron, 1997). Pour la période de 1840 à aujourd'hui, plusieurs changements ont été observés. On note, entre autres, une période de réchauffement de 1840 à 1960 (maximum dans les années 1940, Jacoby et D'Arrigo, 1989), suivie d'une période de refroidissement de 1960 à 1970 suivie d'un réchauffement vers des valeurs supérieures à celles des années 1940 (Boden, Kanciruk et Farrell, 1990; Lau et Weng, 1999). Depuis 1850, la tendance générale d'augmentation de la température est aux environs de 0,5 à 0,7^{o}C (Jones, Wigley et Kelly, 1982; Wigley, Jones et Kelly, 1986; Jacoby et D'Arrigo, 1989; Jones et Briffa, 1992; Karl *et al.*, 1993).

Par ailleurs, des changements climatiques très rapides ont été notés depuis 1980 (Lau et Weng, 1999). Durant la première moitié des années 1990, un accroissement de la fréquence de périodes chaudes (El nino) a été enregistré, avec cependant une amplitude moindre que celles enregistrées dans les années antérieures. Une augmentation des précipitations a aussi été observée (près de 17%), notamment au cours de la deuxième moitié du vingtième siècle (Bradley *et al.*, 1987; Karl *et al.*, 1993; Groisman et Easterling, 1994; Groisman *et al.*, 1994).

La tenthrède du mélèze est l'un des plus importants défoliateurs en Amérique du Nord et son origine possiblement européenne a longtemps été débattue. Bien que le débat semble se diriger vers un statut indigène (Jardon *et al.*, 1994b), il n'en reste pas moins que plusieurs espèces parasitoïdes européennes ont été introduites dans le but d'y faire la lutte (Muldrew, 1955; Turnock, 1972). Bien que certaines introductions aient eu un taux de succès acceptable, certaines ont par contre soulevé de fortes inquiétudes. L'introduction de *Mesoleius tenthredinis* (après une épidémie de tenthrède dévastatrice de 1890 à 1910) dans les années 1910 a connu deux décennies de succès, jusqu'à l'apparition d'une souche de tenthrède résistante (Lejeune, 1955; Turnock, 1972). Aujourd'hui, la tenthrède est rapportée comme étant toujours présente au Québec (Jardon *et al.*, 1994a; 1994b; Arquillère *et al.*, 1990)

Dans la région du Lac Duparquet, plusieurs études ont montré l'incidence des changements climatiques sur la dynamique des peuplements forestiers et la croissance arborescente, ceci pour la période postérieure au Petit Age Glaciaire (ca. 1850). D'abord, une diminution significative du nombre de feux et de l'amplitude de la surface brûlée a été observée (Bergeron et Archambault, 1993). Ceci serait entre autres attribué à une diminution de l'occurrence des périodes de sécheresse pour cette région. De même, Tardif et Bergeron (1997) ont rapporté une augmentation de l'amplitude des inondations printanières, indiquée par un accroissement de la hauteur et de la fréquence des cicatrices glacielles enregistrées par le cèdre blanc (*Thuja occidentalis* L.). De même, une augmentation de la croissance radiale du frêne noir (*Fraxinus nigra*) fut reliée à un accroissement de la saison de croissance. Une saison hivernale de moins en moins longue serait en effet liée à une fonte plus rapide de la neige au printemps (Karl *et al.*, 1993; Brown et Goodison, 1996). Enfin, en raison de l'accroissement de la sévérité des inondations, Tardif & Bergeron (1999) ont également rapporté un déplacement des populations de frêne noir en plaines de débordement vers des milieux à élévation supérieure.

1.4 OBJECTIFS ET HYPOTHÈSES

Le premier objectif de la présente étude était de mettre en relation les divers gradients environnementaux (éléments nutritifs, pH, distance du bassin d'eau, type de substrat, lumière, etc.) avec le patron de distribution de la végétation, dans un environnement non perturbé. Une étude réalisée par Denneler *et al.* (1999) concluait que les phénomènes physiques reliés aux inondations, notamment l'effet des vagues, constituaient les facteurs principaux contribuant à la présence ou à l'absence des espèces végétales, entre autres le mélèze, en milieu humide. Cependant, cette étude n'a pas pris en compte les interactions biologiques entre les espèces et l'impact de la distance de la rive sur le gradient nutritif de l'eau et du substrat. Nous tenions donc à tester l'hypothèse de la présence d'un gradient complexe formé des paramètres physiques, chimiques et biologiques.

Le deuxième objectif de l'étude était de reconstituer, par la méthode dendrochronologique, les dernières épidémies de la tenthrède ayant eu cours dans la région du Lac Duparquet. Une analyse dendroclimatique a aussi été effectuée afin d'établir les relations entre la croissance du mélèze et les facteurs de température, précipitation, niveau d'eau et sécheresse. Suite aux observations de Tardif et Bergeron (1997), rapportant entre autres un accroissement de la fréquence et de la sévérité des inondations printanières sur le Lac Duparquet, nous supposions que le stress hydrique printanier serait la composante la plus importante reliée à la croissance radiale du mélèze. Par contre, il se pourrait que les épidémies de la tenthrède rapportées dans l'ensemble du Canada (Turnock, 1972) aient aussi affecté la croissance du mélèze dans la région à l'étude.

Le troisième objectif avait pour but d'établir les relations entre les facteurs climatiques et épidémiologiques et les périodes de recrutement du mélèze. Nous nous attendions, entre autres, à ce que l'occurrence des épidémies de tenthrède soit un facteur des plus importants dans la dynamique des populations, notamment en induisant la mortalité de l'ensemble du couvert dominant.

1.5 AIRE D'ÉTUDE

La zone à l'étude est située dans la région de l'Abitibi, 700 km au Nord de Montréal (48°28'N, 79°17'O) et comprend six tourbières. Parmi celles-ci, trois sont adjacentes au Lac Duparquet et couvrent chacune une superficie allant d'environ 0.25 km^2 à 0.5 km^2 (Fig. 1.1). On y retrouve une pente relativement faible et un terrain peu accidenté, composé à quelques endroits de monticules de *Sphagnum* spp. et de dépressions (moins de 30 cm de dénivellation). Ces dernières exposent souvent la nappe phréatique. Ces tourbières sont situées au sud-est du Lac Duparquet et leurs berges sont sujettes à l'effet de vagues (Denneler et al. 1999). Deux sont composées uniquement de mélèze (II et III), alors qu'une comprend du mélèze, de l'épinette noire et du cèdre (I). La tourbière II fut divisée en deux zones (nord et sud) lors de l'étude de la croissance radiale du mélèze en raison de la grande superficie couverte par le peuplement de mélèze.

Une quatrième tourbière est située en bordure de la rivière Magusi, ouest du Lac Duparquet (Fig. 1.1). Cette tourbière est caractérisée par une montée alluviale créée par la déposition minérale suite aux crues printanières. Le terrain est similaire aux trois autres tourbières, quoi que plus accidenté en raison d'un plus grand nombre de débris ligneux jonchant le sol. La superficie couverte par cette tourbière est relativement petite, soit environ 0.1 km^2. Elle comprend également les trois espèces arborescentes nommées ci-haut.

Une cinquième tourbière est située en bordure du Lac Soisson (Fig. 1.1). Ce lac de moins de 0.5 km^2 est indirectement en contact avec le Lac Duparquet via la Rivière Kanasuta. Cette tourbière est relativement petite, soit environ 0.1 km^2. Le Lac Soisson n'expose pas ses berges à un effet de vague important. La tourbière est par contre exposée aux crues printanières. Celle-ci est aussi composée de mélèze, d'épinette noire et de cèdre. Le terrain est d'une pente faible similaire aux autres tourbières et peu accidenté.

La sixième tourbière est située à environ 1 km au nord-ouest du Lac Duparquet, à l'est du Rapide Danseur. Elle est traversé par la route 388 (chemin Matheson) (Fig. 1.1). Cette tourbière n'est pas soumise au crues printanières du Lac Duparquet. On n'y retrouve une composition mixte de mélèze, d'épinette noire et de cèdre de chacun des côtés de la route. Cependant, du côté sud, la végétation au sol est fortement dominée par des espèces arbustives et de *Sphagnum* spp., alors que du côté nord le sol est dénudé et majoritairement composé de *Carex* spp.. Du côté nord, un grand nombre de dépressions est observé contrairement au côté sud. La végétation au sol étant différente des deux côtés de la route, les conditions de drainage auraient été modifiées lors de la construction de la route dans les années 1930-1940. L'échantillonnage de cette tourbière s'est principalement déroulé du côté nord.

1.5 STRUCTURE DU MÉMOIRE

Le présent mémoire est constitué de trois articles:

1. Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. «Gradient analysis in *Larix laricina* dominated wetlands in Canada's southeastern boreal forest». Canadian Journal of Botany 79: 444-456.

2. Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. «Radial growth analysis of *Larix laricina* from Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks». Écoscience 8: 127-138.

3. Girardin, M.P., Tardif, J. et Bergeron, Y. soumis. «Dynamics of eastern larch stands in relation to larch sawfly outbreaks in the Northern Clay Belt of Quebec». Canadian Journal of Forest Research 0:00-00.

Le premier article, intitulé en français «Analyse des gradients dans les tourbières dominées par le mélèze dans le sud-est de la forêt boréale canadienne», visait à répondre au premier objectif. Afin de déterminer quels facteurs étaient les plus liés à la distribution de la végétation, les données de recouvrement en espèces provenant de l'échantillonnage de 186 quadrats ont été comparées aux données environnementales (concentrations en éléments nutritifs, pH, hauteur de la nappe phréatique, etc).

Le deuxième article, «Analyse de la croissance radiale de *Larix laricina* dans la région du Lac Duparquet en relation avec le climat et les épidémies de tenthrède», visait à reconstituer les périodes d'épidémie de la tenthrède du mélèze (*Pristiphora erichsonii*) dans la région du Lac Duparquet ainsi que d'étudier l'effet des fluctuations climatiques sur la croissance radiale de l'espèce. Pour ce faire, des carottes (n = 230) ont été récoltées sur 115 arbres, sablées, interdatées et chacun des cernes fut mesuré selon la méthode standard. Les périodes épidémiques ont été identifiées à partir de la morphologie des cernes alors que les relations entre la croissance radiale et le climat ont été étudiées de façon statistique.

Le troisième article, «Dynamique des peuplements de mélèze en relation avec les épidémies de la tenthrède », visait à établir l'impact des épidémies de la tenthrède sur le recrutement en mélèze. Cet article avait également comme objectif secondaire de déterminer si un effet des changements climatiques pouvait être observé sur la dynamique des peuplements. Cet article expose les résultats d'une analyse des structures d'âge à l'intérieur de 12 quadrats échantillonnés dans les peuplements de mélèze autour du Lac Duparquet. Des analyses de la croissance radiale et de la croissance en hauteur ont été effectuées afin d'établir les relations entre les périodes de recrutement et les épidémies de la tenthrède.

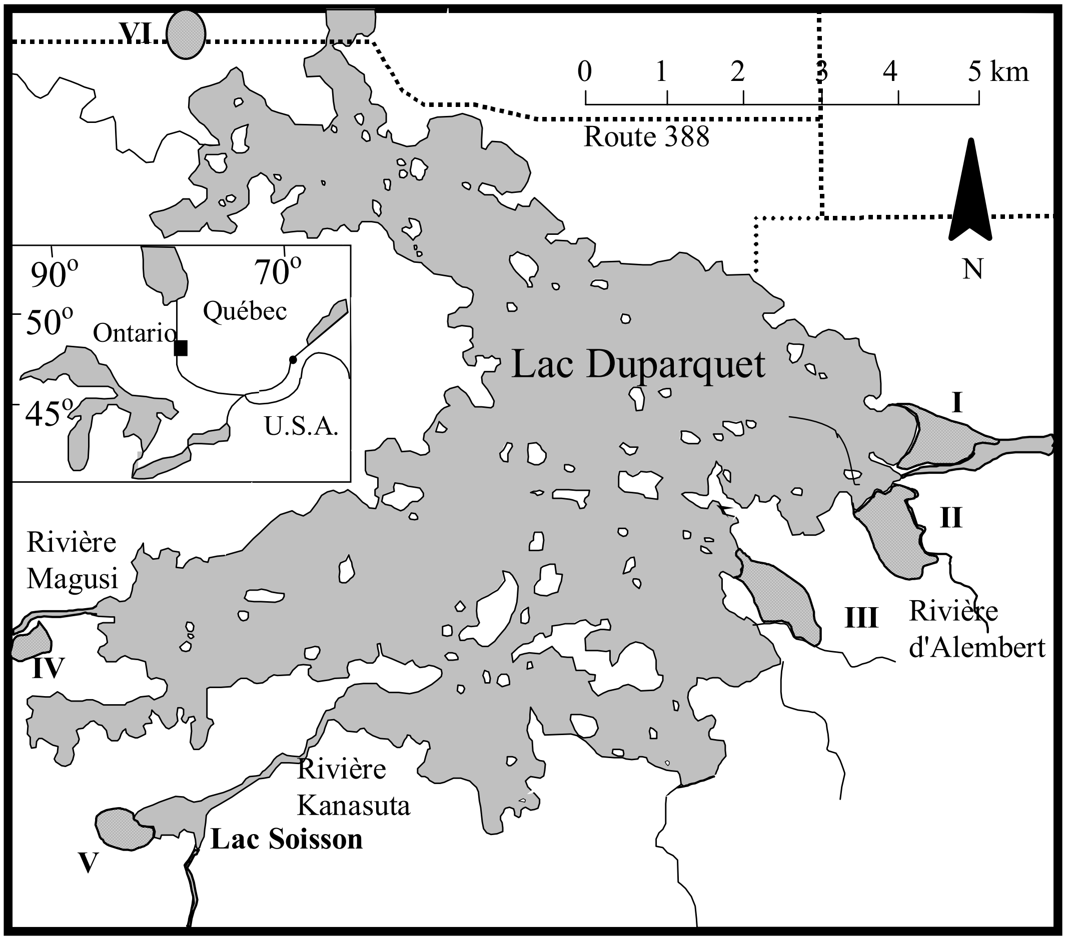

Figure 1.1 Carte illustrant le positionnement des six tourbières échantillonnées en 1998 et 1999 par rapport au Lac Duparquet, Abitibi, Québec.

ARTICLE I: ANALYSE DES GRADIENTS DANS LES TOURBIÈRES DOMINÉES PAR LE MÉLÈZE DANS LE SUD-EST DE LA FORÊT BORÉALE CANADIENNE

Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. Gradient analysis in *Larix laricina* dominated wetlands in Canada's southeastern boreal forest. Canadian Journal of Botany 79: 444-456.

2.1 ABSTRACT

With the objective of understanding how vegetation was structured in four *Larix laricina* dominated wetlands in north-western Québec, 186 point-centred quarters were sampled in four stands. For each point, both biotic and abiotic variables were collected and species cover was recorded. Divisive hierarchical classification analysis (Twinspan) identified nine vegetation clusters: i) *Larix laricina* & *Spiraea alba*, ii) *Larix laricina* & *Kalmia angustifolia*, iii) *Larix laricina*, *Picea mariana* & *Alnus rugosa*, iv) *Larix laricina* & *Betula pumila*, v) *Thuja occidentalis* & *Trientalis borealis*, vi) *Abies balsamea* & *Betula papyrifera*, vii) *Fraxinus nigra* & *Onoclea sensibilis*, viii) *Alnus rugosa* and xiv) *Eleocharis smallii*. Results of the canonical correspondence analyses indicated that the distribution of these clusters was mainly related to (i) distance from shore, (ii) shade (canopy cover), (iii) substrate nitrate concentration (in relationship with the abundance of *Kalmia angustifolia* and *Alnus rugosa*), (iv) substrate pH (in relationship with the abundance of *Sphagnum* spp.) and (v) substrate conductivity. Several characteristics of the water table also affected the species distribution, including pH, depth and carbon concentration. Further studies should address the effect of the presence of *Kalmia angustifolia* and of *Alnus rugosa* on larch growth.

Keywords: larch; wetland; vegetation analysis; flooding; boreal forest.

2.2 RÉSUMÉ

Dans le but de comprendre la distribution de la végétation dans quatre tourbières dominées par *Larix laricina* dans la forêt boréale du Nord-Ouest du Québec , 186 quadrants centrés sur le point ont été échantillonnés à l'intérieur de quatre sites. Pour chacun des points, des variables abiotiques et biotiques ont été récoltées et le recouvrement des espèces a été noté. L'analyse par classification divisive hierarchique (Twinspan) produit neuf groupements végétaux: i) *Larix laricina* & *Spiraea alba*, ii) *Larix laricina* & *Kalmia angustifolia*, iii) *Larix laricina*, *Picea mariana* & *Alnus rugosa*, iv) *Larix laricina* & *Betula pumila*, v) *Thuja occidentalis* & *Trientalis borealis*, vi) *Abies balsamea* & *Betula papyrifera*, vii) *Fraxinus nigra* & *Onoclea sensibilis*, viii) *Alnus rugosa* et xiv) *Eleocharis smallii*. Les analyses canoniques des correspondances ont indiqué que la distribution de ces groupements était principalement reliée à (i) la distance à la rive, (ii) l'interférence lumineuse et certaines caractéristiques du substrat, entre autre (iii) la concentration en nitrate du substrat (notamment en relation avec l'abondance de *Kalmia angustifolia* et d'*Alnus rugosa*), (iv) le pH (en relation avec l'abondance de *Sphagnum sp.*) et (v) la conductivité. Un lien a été démontré entre les caractéristiques de la nappe phréatique et la distribution des espèces, notamment en relation avec le pH, la profondeur et la concentration en carbone. Des études plus approfondies devraient être conduites afin de déterminer l'impact de la présence des espèces *Kalmia angustifolia* et *Alnus rugosa* sur la croissance du mélèze.

Mots clés: mélèze; tourbière; analyse de végétation; inondation; forêt boréale.

2.3 INTRODUCTION

The study of ecological gradients has been widely used as an approach for defining interactions between plant species and their spatial distribution in relation to physical, chemical and biological factors. In floodplains and wetlands, it has been shown that most of the partitioning between species (including trees, shrubs and herbaceous species) is related to soil moisture, i.e. in relation to the elevation above a water body or to the depth of the water table (Keddy 1983; Tardif and Bergeron 1992; Jeglum and He 1995). Thus, emphasis was put on discussing the importance the period, frequency and duration of flooding on species establishment, which mainly depends on their tolerance of flooding (Robertson et al. 1978; Keddy 1983; Kenkel 1986; Glaser et al. 1990; Shipley et al. 1991; Tardif and Bergeron 1992; Jean and Bouchard 1993; Jeglum and He 1995).

In wetland environments, studies have also shown that the main ecological gradient is not composed of a single factor, but elevation or distance from the shore does however account for large-scale variability (Robertson et al. 1978; Vitt and Bayley 1984; Kenkel 1986). Complex gradients combining peat thickness - moisture gradients and pH – calcium gradients were previously found by Jeglum and He (1995). Moreover, herbaceous plants and shrub species are sometimes distributed as a function of fine scale factors (or secondary gradients), which are responsible for more heterogeneous patterns. Microtopographic relief, resulting from the erosion and deposition of materials during spring flooding, for example, creates a multitude of micro-environmental conditions which lead to a patchy distribution of plant species (Wistendahl 1958; Robertson et al. 1978; Hardin and Wistendahl 1983).

In the definition of wetland community types, a study conducted by Kenkel (1986) in the western Ontario boreal forest stressed the importance of the nutrient gradient, and suggested that the distinction between oligotrophic and eutrophic peatland types should be based on nutrient status. However, Jeglum and He (1995) discussed the controversy surrounding the explanation of species distribution in relation to nutrient gradients. Many studies have produced contradictory results relative to the importance of this complex gradient, mostly concerning the relationships between nitrates and cations and species abundance. As an example, in wetlands of the northern Ontario clay belt, Jeglum and He (1995) reported that the pH-calcium gradient and the nitrogen gradient were responsible for the majority of the explained variation in plant distribution. In contrast, Jean and Bouchard (1993) observed little correlation between plant distribution and nutrient variables. Similarly, Glaser et al. (1990) found little correlation between vegetation and the cation gradient.

Some authors attribute this lack of consistency to the effect of multiple factors, such as changes in natural disturbance regimes (fire frequency and climate change: Vitt and Bayley 1984; Kenkel 1986; Glaser et al. 1990; Jean and Bouchard 1993) or anthropogenic disturbances (water level changes: Jean and Bouchard 1993; Jeglum and He 1995). It seems that the significance of the nutrient gradient may be dependent on the presence or absence of disturbances, which maintain community structure in successionnal stages and produce changes in abiotic conditions (Vitt and Bayley 1984; Jean and Bouchard 1993). Heinselman (1970) also insisted on the difficulty of predicting the development of wetlands because of their different history, the local topography, the circulation of water, erosion and global climatic changes.

This study follows an earlier study undertaken by Denneler et al. (1999) at Lake Duparquet in the south-western boreal forest of Québec. In their study, Denneler et al. (1999) concluded that physical phenomena related to flooding, notably wave effects, were the main factors contributing to the presence or absence of larch (*Larix laricina* (Du Roi) K.Koch) in the wetlands of Lake Duparquet. However, their study did not include other species or account for biological interactions, such as shading or nutrient interference, and the influence of distance from the shore on the chemical properties of the substrate and of the water table. The first objective for this study was to define the main plant communities in stands dominated by larch on the shores of Lake Duparquet. The second objective was to determine which ecological factors were associated with species' distribution in the wetlands of Lake Duparquet.

2.4 STUDY AREA

The study area is located on the shores of Lake Duparquet, 700 km north of Montreal in the Abitibi region, south-western Québec (48°28'N, 79°17'O)(Figure 2.1). This large lake (50 km^2) drains northward through the Duparquet River towards James Bay. The region is part of the Northern Clay Belt of Québec and Ontario, a geomorphological feature resulting from sediments deposited during the maximum extension of the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Mean annual temperature is 0.8°C and total annual precipitation varies from 800 to 900 mm (Environment Canada 1993). The mean frost-free period is 64 days, but frost can occur at any time of the year (Anonymous 1982).

Four larch stands were selected along the shores of Lake Duparquet using aerial photographs (years 1926, 1945 and 1994). These stands were chosen because the water level of the lake has not been purposefully modified in the past and no lethal fires (Bergeron 1991) have been reported since the mid nineteenth century (Bergeron 2000). Also, no logging has occurred inside the study stands, nor within the wetland watersheds. All stands showed a mixed dominance of larch, black spruce (*Picea mariana* Mill.) and white cedar (*Thuja occidentalis* L.).

2.5 METHODS

2.5.1 Field sampling

In August 1999, for each selected stand (BL1, BL2, CC, MAG, Fig. 2.1), three to four transects (a, b, c, d) were placed perpendicularly to the water bodies (stream, river or lake) with a distance of 50 to 100 metres between each. A total of seven transects were put in place perpendicular to the lake (BL1a-b-c-d, BL2a, CCa-b), and six perpendicular to streams or rivers (BL2c, CCc-d, MAGa-b-c). One transect (BL2b) was located between Lake Duparquet and the D'Alembert River. From the shoreline to the upper limit of the distribution of larch, sampling points were located at 30m to 40m intervals. A total of 186 points were sampled (number of points per stand: BL1: 52, BL2: 50, CC: 60, MAG: 24).

For each point, distance from the shore was recorded. The point-centred quarter (PCQ) method was used to determine tree (diameter at breast height [DBH] > 5cm) species importance values at the sample points (Cottam and Curtis 1956; Lindsey et al. 1958; Warde and Petranka 1981; Barbour et al. 1987). In each of four quadrants, DBH, height and distance of the nearest tree to the point centre were measured. A cut-off point of 15m from the point centre was established, and a missing value was recorded when no tree was found within this distance.

Regeneration (height < 1 m), shrub and herbaceous species cover was determined in 1m^2 quadrats located over each of the 186 PCQs. After measurement of the shrub height, percent cover was assigned for each species using coverage classes ($0 < 1 < 1\%$; $1\% \leq 2 < 5\%$; $5\% \leq 3 < 25\%$; $25\% \leq 4 < 50\%$; $50\% \leq 5 < 75\%$; $75\% \leq 6 < 100\%$; 7 = 100%; Daubenmire ???? Voir Gagnon et Bouchard 1981 CanJBot) Tardif and Bergeron 1992). For species located outside the 1m^2 quadrats (cut-off point at 2m from the point centre), a cover of 0.5% was given. Marie-Victorin (1995) was used for vascular plant nomenclature. Non-vascular plants were included in the study in two categories: *Sphagnum* spp. and Bryophytes (which includes the cover of all mosses other than *Sphagnum* spp.).

At each PCQ, the number of dead trees was estimated in a 5m radius. The cut-off point of 5m was chosen because in most cases this was a representative sample of the quantity of logs and snags observed in the PCQ vicinity. Afterward, a tree cover class within a 5m radius was assigned following the Montague and Givnish (1996) criteria: (i) dominant: complete penetration of light from the top and partially from the sides; (ii) codominant: complete penetration of light from the top and low penetration from the sides; (iii) intermediary: partial penetration of light from the top and no penetration from the sides; (iv) suppressed: no penetration of light.

In each 1m^2 quadrat, substrate was identified as peat, hummock or clay, and logs on the ground were noted as present or absent. Wherever peat occurred, its minimal depth (up to 130 cm) was measured by using a graduated stick. Also, depth of the water table (soil surface as the reference level) was measured and corrections were made following daily measurements of the Lake Duparquet water level.

Samples of substrate and soil water from the water table (when present) were taken in each 1m^2 quadrat to determine pH, nitrate and ammonium concentration, and conductivity (Heinselman 1970). Water samples were taken at a depth of 30 cm to avoid the influence of recent rainfalls. Mineral nitrogen (NH_4^+ and NO_3^-) was extracted from substrate samples (2g) in 40 ml of a KCl solution (Maynard and Kalra 1993). Afterwards, water table and substrate samples were frozen until injection analysis using a Tecator FIAStar 5020. For the substrate, the measurement of pH and conductivity was conducted by adding distilled water to the substrate samples in a 4:1 ratio (by volume). A carbon concentration index was also determined for water table samples by measuring the absorbency at a 465-nm wavelength (Stevenson 1982).

2.5.2 Data analysis

In this study, both understory and overstory plant species were analysed simultaneously. The following formulas were used to calculate tree species importance values in each PCQ. The parameters d_A and D_A respectively stand for diameter and distance to the PCQ (in metre) of trees species A (for details, see Mueller-Dombois and Ellenberg (1974), and Barbour et al. (1987)):

[1] Importance value of species A = $(RD_A + RB_A + PI_A)/3$

[2] RD_A = Relative density of species A = (No of trees of species A/4)*100

[3] RB_A = Relative basal area of species A = (basal area of A / $\sum$ of all basal areas)*100

[4] Basal area of species A = $\sum \pi d_A^2/4$

[5] PI_A = Proximity index of species A = $[\sum((15-D_A)/15)*100]$ / No of trees of species A

In equation [5], the number 15 stands for the distance to the cut-off point. For the understory, each coverage class of shrub and herbaceous species was scaled to 100 using the median of each class.

The environmental matrix contained a total of 21 variables for each of the 186 PCQs: relative distance from the shore (distance scaled to 100), longitude and latitude (degree), minimal peat thickness (m), average shrub and tree height (m), canopy classes (dominant, codominant, intermediary and suppressed), average distance between trees and point centre (m), presence/absence of logs on the ground (binary variable), number of dead trees (counts), percent of surface in pools (% of the substrate surface covered by the water table (Heinselman 1970)), pH (substrate and water table samples), conductivity (μMhos; substrate and water table samples), nitrate and ammonium concentrations (μgml^{-1}; soil and water table samples), carbon concentration index (water table samples only) and water table depth (cm).

The water table level was adjusted so that it was a positive value by adding ten to each measurement (Ter Braak and Smilauer 1998). For the analysis of cations, Heinselman (1970) suggested correcting the values for conductivity (which accounts for all ions) to eliminate for the effects of H+ ions. However, because the conductivity values obtained in this study were superior to the critical value of 4.1 suggested by Heinselman (1970), no correction factor was applied. Finally, for the PCQs located on clay and hummocks (N= 16), no water table was found within a 30cm depth, which resulted in missing values for pH, nitrate, ammonium, and conductivity in the environmental matrix. This has important effects in the ordination analyses because the CANOCO program recognises all missing values as zeros (Ter Braak and Smilauer 1998). To overcome this problem, missing values were replaced by the mean value of each corresponding variable.

Vegetation groups were determined using the Twinspan method (Hill 1979), which as the advantage of using indicator species. Default parameters were conserved. Gradient lengths were calculated using detrended correspondence analysis (DCA, Legendre and Legendre 1998) and environment-species relationship analysis was done with canonical correspondence analysis (CCA). Both methods have the advantage of preserving the χ^2 distance, which has the property of excluding every pair of zeros in the quantification of the object-descriptors relationship (Legendre and Legendre 1998). Note that the detrended canonical correspondence analysis (DCCA) method was avoided, as suggested by Legendre and Legendre (1998), notably because detrending methods are largely arbitrary when interpreting complex gradients (Wartenberg et al. 1987). A forward selection of environmental variables was done and variables significant at $p<0.05$ were preserved in the CCA models (999 permutations were generated). The CANOCO software (Version 4.0, Ter Braak and Smilauer 1998) was used in all ordination analyses.

In this study, because the environmental variables, understory and overstory were sampled at different scales, the assessment of associations between trees and environmental variables should be made with caution. The same caution applies when interpreting interspecific associations between the tree species and the understory species. Also, caution should be taken when interpreting relationships between environmental variables and species when only a small number of PCQs are clustered in a common vegetation type.

2.6 RESULTS

2.6.1 Vegetation analysis

Nine vegetation clusters (or vegetation types), were defined with Twinspan (Figure 2.2). Our classification was mainly based on the dominance of pseudospecies in the Twinspan division and on the dominant tree species. Species coverage, importance values and frequencies are given in Table 2.1; environmental variables are given in Table 2.2; average tree species height, density and importance values are given in Table 2.3. Tree importance values and densities were calculated following the formula of Barbour et al. (1987), and a correction factor was applied to account for quadrants in which tree species were absent (Warde and Petranka 1981).

Larch trees dominate four of the nine clusters. The understory of the first cluster (*Larix laricina* & *Spiraea alba*) is mainly composed of *Alnus rugosa*, *Betula pumila*, *Cornus stolonifera*, *Spiraea alba* and *Cassandra calyculata* (Table 2.1). Regeneration is mainly composed of balsam fir (*Abies balsamea* Mill.), black spruce and larch, whereas black spruce and larch dominate the overstory (Tables 2.1 and 2.3). A total of 38 understory species are present, compared to 37, 32 and 34, respectively, for the other larch clusters. Peat is the main substrate in this environment. The tree cover class indicates a very open tree crown, with trees smaller on average than those of other vegetation types (Table 2.2).

In the second larch cluster (*Larix laricina* & *Kalmia angustifolia*), dominant understory species are *Kalmia angustifolia*, *Andromeda glaucophylla*, *Myrica gale*, *Ledum groenlandicum*, *Cassandra calyculata* and *Smilacina trifolia* (Table 2.1). In this cluster, *Sphagnum* covers the surface almost entirely. Regeneration is similar to the preceding cluster, although black spruce and larch seedlings are present at higher frequencies. This part of the gradient is mostly dominated by larch; black spruce is found in only five of the 78 PCQs (Table 2.1 and 2.3). Water analysis shows a high carbon concentration, whereas the pH values for the substrate and the water table are at their lowest (Table 2.2). The tree crown is slightly more suppressed than in the preceding cluster, and the PCQs are generally distributed further away from the shore.

The third cluster (*Larix laricina, Picea mariana* & *Alnus rugosa*) is mainly characterised by an increase in the abundance of *Picea mariana* (both in the understory and the overstory, Table 2.1). Although larch density is less than half of the value found in the preceding cluster (Table 2.3), the average importance value is almost similar due to an increase in tree basal area. Also, the tallest larch trees are present in this cluster, averaging 10.4 m tall (Table 2.3). In the understory, dominant species are *Alnus rugosa*, *Ledum groenlandicum*, *Myrica gale* and *Betula pumila,* and *Sphagnum* abundance is relatively low. A deep water table, high pH and high carbon and ammonium concentrations in water table samples are associated with this cluster (Table 2.2). The shrub cover is relatively high in this vegetation type.

The understory of the fourth larch cluster (*Larix laricina* & *Betula pumila*) is mostly dominated by *Prunus virginiana*, *Alnus rugosa*, *Calamagrostis canadensis*, *Cassandra calyculata*, *Cornus stolonifera*, *Equisetum* spp., *Trientalis borealis* and *Smilacina trifolia* (Table 2.1). *Sphagnum* covers the ground surface entirely and larch dominates the overstory (low cover but very tall trees, Table 3). White cedar is abundant, consisting of relatively short trees (1.9 m average), not in a dominant position (Table 2.3). No clear environmental variables strongly characterise this cluster (Table 2.2).

White cedar completely dominates the fifth cluster, *Thuja occidentalis* & *Trientalis borealis*, although black spruce and larch are present in moderate numbers (Table 2.1, Table 2.3). Regeneration is equally divided between white cedar, black spruce and larch, and the understory is largely composed of *Alnus rugosa*, *Ledum groenlandicum*, *Carex trisperma* and *Carex* spp.. In this cluster, a total of 34 understory species are present. The tree cover class is near the intermediary class, indicating a higher level of suppression of light from the tree crown (Table 2.2). Analysis of the water table shows high pH and area occupied by pools, and low nitrate and ammonium concentrations (Table 2.2). As for the substrate, it has high nitrate and ammonium concentrations. This vegetation type occurs in the part of the distance gradient most elevated and away from shore (Table 2.2)

Abies balsamea is dominant in the sixth cluster (*Abies balsamea* & *Betula papyrifera*) with *Betula papyrifera*, and at a distance from the shore equivalent to the fourth cluster type (Table 2.2). Although white cedar and black spruce are found occasionally, larch is almost never present, and its seedlings are never present (Table 2.1). A few very tall white cedars are present (Table 2.3). The understory is dominated by *Sphagnum*, *Maianthemum canadense* and *Alnus rugosa,* and 34 other understory species are present (Table 2.1). In this environment, a decrease in peat thickness and a high water table (indicating high moisture conditions) are observed (Table 2.2). As indicated by the high tree cover class, a small amount of light penetrates the tree crown to reach the understory. Analyses also show that the water table has high cation and dissolved carbon concentrations. As for the substrate, high conductivity and high nitrate-ammonium concentrations are observed.

Fraxinus nigra, *Thalictrum pubescens*, *Cornus stolonifera* and *Rubus pubescens* mainly dominate the seventh cluster (*Fraxinus nigra* & *Onoclea sensibilis*) (Table 2.1). The tree canopy closure is similar to that observed in the fifth cluster, but most of the PCQs for this vegetation type are located close to open water. *Viola pallens* and *Onoclea sensibilis* are also common in this cluster, composed of a total of 26 understory species. *Thuja occidentalis* and *Abies balsamea* also occur. Peat is generally absent in this vegetation type (Table 2.2), although some PCQs occur on the borders of wetlands where the peat does not exceed 40 cm in thickness. In such places, the substrate surface is almost entirely covered by the water table (large percent area consisting of pools).

Two clusters have no tree species and both are located beside water bodies. *Cornus stolonifera*, *Alnus rugosa*, *Calamagrostis pubescens*, *Myrica gale* and *Smilacina trifolia* dominate the 8th cluster (*Alnus rugosa*) (Table 2.1). A few larch seedlings are present. In this environment, the water table is deep, rich in cations, nitrate and carbon (Table 2.2). Peat thickness ranges from 10 cm to 90 cm. As for the 9th cluster, *Eleocharis smallii*, it is dominated by *Salix discolor*, *Lysimachia terrestris*, *Calamagrostis canadense*, *Spiraea alba*, *Myrica gale*, *Sium suave*, *Eleocharis smallii* and *Juncus pelocarpus* (Table 2.1). Fine mineral sediment is the common substrate of this cluster, with the exception of a few PCQs located on peat (less than 2 cm thick). The substrate of this vegetative type is rich in nitrate and pH values are very high (Table 2.2).

2.6.2 Spatial distribution

Figure 2.3 represents the spatial location of the vegetation clusters using the 186 point GPS data and the aerial photographs. It illustrates the confinement of *Eleocharis smallii* and *Fraxinus nigra* & *Onoclea sensibilis* clusters near the shore (relative distance close to 0%) and the *Thuja occidentalis* & *Trientalis borealis* and *Abies balsamea* & *Betula papyrifera* clusters at the upper limit (relative distance near 100%). Larch clusters are mainly distributed in specific stands. The *Larix laricina* & *Kalmia angustifolia* and *Larix laricina*, *Picea mariana* & *Alnus rugosa* clusters are not found in the MAG stand, whereas the *Larix laricina* & *Betula pumila* cluster is not found in the CC stand. As for the *Alnus rugosa* cluster, it is only found adjacent to the lakeshore.

2.6.3 Detrended correspondence analysis

The detrended correspondence analysis results indicate that the lengths of the first and second gradients are 4.451 and 3.989. Thus, the vegetation data set responded to the requirements formulated by Borcard et al. (1992) and Legendre and Legendre (1998), i.e. the necessity to have gradients longer than four (SD>4) and a unimodal distribution of species for a proper application of canonical correspondence analysis.

2.6.4 Canonical correspondence analyses

Canonical correspondence analysis for the entire vegetation data set indicates that the axes of the species ordination are significantly correlated with their respective environmental axes ($p<0.001$). Eigenvalues and species-environment correlation coefficients for the first and second axes are respectively $E_1=0.369$, $E_2=0.284$, $r_1=0.815$ and $r_2=0.815$. Figure 2.4

illustrates the significant variables retained at $p<0.05$. Only the highest correlations are discussed in the text. The first axis is mainly related to the *Fraxinus nigra* & *Onoclea sensibilis* cluster in relation to soil pH and nitrate concentration (positive relationships between these variables and this cluster), and with peat thickness (negative relationship). We also found that the *Abies balsamea* & *Betula papyrifera* cluster is largely influenced by the second axis in relation to the opening of the tree crown (cover class), percent area of pools and tree mortality (positive relationship). However, a negative relationship is found between this cluster and the carbon index. The second axis is also related to the *Eleocharis smallii* cluster because of the following variables: soil nitrate concentration (positive relationship), average tree height, relative distance from shore and peat thickness (all negative relationships).

To concentrate the CCA analysis on clusters dominated by larch, the three outlier clusters (*Fraxinus nigra*, *Eleocharis smallii* and *Abies balsamea* & *Betula papyrifera)* were eliminated from the data matrix (total of 26 PCQ), as suggested by Peet (1980). This ordination produced a projection of the *Larix laricina* & *Betula pumila* cluster on the first axis in relation to soil pH, soil conductivity, soil nitrate concentration, percent area of pools (positive relationships) and the water carbon index (negative relationship, Figure 2.5). The cluster *Thuja occidentalis* & *Trientalis borealis* is also highly associated with the first axis by the percent area of pools and the tree cover class (positive relationships). The distribution of *Larix laricina* & *Spiraea alba* and *Alnus rugosa* clusters along the second axis is related to the shrub height (positive relationship), tree height and the distance from the shore (negative relationships). Eigenvalues and species-environment correlation coefficients for the first and second axes are respectively $E_1=0.252$, $E_2=0.177$, $r_1=0.900$ and $r_2=0.806$ (significance of all canonical axes at $p<0.01$).

A third canonical correspondence analysis was conducted using only the tree, sapling and seedling data (Fig. 2.6). Only the PCQs containing at least one tree species were used in this analysis (total of 162 PCQs). Eigenvalues and species environment correlation coefficients for the first and second axes are respectively $E_1=0.458$, $E_2=0.282$, $r_1=0.819$ and $r_2=0.806$ (significance of all canonical axes at $p<0.001$). Significant relationships are present between *Picea mariana* and *Larix laricina* and the water table depth and the peat thickness (all positive relationships). *Abies balsamea*, *Betula papyrifera* and *Fraxinus nigra* are both negatively associated to these variables, but they are positively associated to a high number of dead trees and the tree cover class. Relationships also exist between *Thuja occidentalis* and the distance from the shore, percent area of pools, substrate and water pH (all positive relationships), and average tree height (negative relationship). Finally, larch and black spruce regeneration occurs mainly where a deep water table is found.

2.7 DISCUSSION

The wetlands studied around Lake Duparquet are similar to the minerotrophic swamp forest and poor minerotrophic swamp forest described by Heinselman (1970) and by Vitt and Bayley (1984), notably because of the concave topography and the observed species. In explaining vegetation distribution, our results tend to support the existence of a complex gradient formed by nitrate, pH, conductivity (measure of the content in cations) and peat thickness. This gradient is mostly formed by the substrate variables, whereas the water table variables account for only a fraction of the explained variability. The opening of the tree crown (tree cover class) and the distance from the shore are also important parameters in explaining species distribution.

2.7.1 Understory species

Nutrient conditions, as indicated by nitrate concentration and pH, are strongly associated with understory species distribution. Among the clusters significantly related with the nitrate concentration is the *Alnus rugosa* cluster, found only a few metres from the lakeshore. This cluster is positively correlated with high concentrations of NH_4 and NO_3. Able to fix atmospheric nitrogen via its root nodules, *Alnus rugosa* may have contributed to the enrichment of the substrate following decomposition of its leaves (Daly 1966; Bares and Wali 1979; Ringius and Sims 1997; Schwintzer and Tjepkema 1997). The same observation can be extended to the cluster *Larix laricina*, *Picea mariana* & *Alnus rugosa*, where *A.*

rugosa is also found abundantly. Vitt and Bayley (1984) also observed a relationship between the wetland nutrient status and the presence of this shrub.

In contrast with the *Alnus rugosa* and nitrate concentration relationship, a negative relationship occurs between the nitrate concentration and the increasing abundance of *Kalmia angustifolia*. However, it is not clear if *Kalmia* abundance is related to the lack of soil nitrate, and if it has an effect on the growth of other species. Inderjit and Mallik (1999) have suggested that *Kalmia* could dominate microsites that were nutrient poor prior to its colonisation. However, it has previously been shown that *Kalmia* leaf litter decreases the substrate nitrate concentration by its mobilisation into *Kalmia* litter, either by a chelate process or by leachate (Facelli and Pickett 1991; Inderjit and Mallik 1996). As for the effects of *Kalmia* on the growth of other species, interference with larch growth may be possible, as was previously found for black spruce seedlings (Inderjit and Mallik 1996; Inderjit and Mallik 1999; Zhu and Mallik 1994). Zhu and Mallik (1994) have shown that *Kalmia* has an allelopathic effect on the primary roots of black spruce, which results in deficient regeneration.

The substrate pH is among the strongest gradients in this study, and we suspect *Sphagnum* spp. of partially influencing its values. The relationships between pH and *Sphagnum* spp. has been briefly discussed by Vitt and Bayley (1984). They mentioned that areas of low pH suggest stagnant waters in which a lowering of pH could be caused by a cation exchange with *Sphagnum* spp. (calcium and magnesium ions replaced with hydrogen ions). In some peatlands, the acidification of the water table would increase along a distance gradient as the *Sphagnum* spp. density increases away from the source waters (Vitt and Bayley 1984). Our results are not as clear as those found by Vitt and Bayley (1984), because the most important *Sphagnum* spp. cover observed in this study (found in the *Larix laricina* & *Betula pumila* cluster) correlates with high pH values. On the other hand, we did observe very low pH values in the *Larix laricina*, *Picea mariana* & *Alnus rugosa* cluster, which also has high *Sphagnum* spp. cover.

The most likely explanation for this contradiction is the input of mineral rich water in the *Larix laricina* & *Betula pumila* vegetation type, which could alter the alkalinity of the stagnant water (Glaser et al. 1990). Many of the *Larix laricina* & *Betula pumila* PCQs are located beside clusters of *Thuja occidentalis* & *Trientalis borealis* and *Fraxinus nigra* & *Onoclea sensibilis*. In accordance to Heinselman (1970) and Johnston (1990), the vegetation type *Thuja occidentalis* & *Trientalis borealis* may be benefiting from an input of mineral rich soil water, whereas the *Fraxinus nigra* & *Onoclea sensibilis* vegetation type is located on beach ridges subject to mineral deposition following spring floods (Bergeron and Bouchard 1983; Bergeron et al. 1983). Both of these vegetation types have high pH values and high conductivity, and it may be possible that the adjacent *Larix laricina* & *Betula pumila* vegetation type also benefited from the cation input. The cation exchange from *Sphagnum* spp. in the *Larix laricina* & *Betula pumila* vegetation type could thus be counteracted by an additional input of calcium and magnesium from the watershed or the rivers.

2.7.2 Overstory species

The water table depth and the distance from the shore are among the most important variables related with tree species distribution. The periodic fluctuations of the water table with Lake Duparquet spring floods could limit the establishment of many trees, shrubs and herbaceous species (Kenkel 1986; Denneler et al. 1999). Various effects resulting from prolonged flooding are reported; these would mainly be related to oxygen deficiency in the rooting zone (Kozlowski 1984). Some possible effects are decay in the root system, a high anaerobic metabolism from bacteria (responsible for the production of compounds toxic to seedlings) and a decrease in nutrient uptake (leading to lower plant productivity) (Zinkal et al. 1974; Crawford 1983; Kozlowski 1984; Lieffers and Rothwell 1986; Yamamoto et al. 1987). Thus, the absence of tree species in the *Alnus rugosa* and *Eleocharis* clusters is probably related to the frequency and duration of flooding, such that tree seedling survival is difficult (Brown et al. 1988). Nevertheless, as mentioned by Denneler et al. (2000), these parts of the stands are also highly exposed to wave effects and the physical damages created by the wave activity may explain to a large degree the absence of tree establishment.

As observed in the ordination results, the tree cover class explains a large part of the variability in tree distribution. Larch is known to be shade intolerant and less competitive than other tree species such as black spruce and white cedar (Montague et Givnish 1990; Johnston 1990). When all tree species co-occurred (in clusters *Larix laricina* & *Betula pumila* and *Thuja occidentalis* & *Trientalis borealis*), larch was often not in a dominant position, and the density of its regeneration was in many cases lower than that of spruce and of cedar. Therefore, we may speculate that in these clusters, either black spruce or white cedar will gradually replace larch. The flooding and the low water table depth could thus help maintain larch in the vegetation types *Larix laricina* & *Spiraea alba* and *Larix laricina* & *Kalmia angustifolia* (lower on the distance gradient and/or lower water table depth), because seedling establishment of white cedar and black spruce, less tolerant than larch to flooding, is limited (Johnston 1990). Johnston (1990) mentioned that black spruce might also show a lack of reproduction under a dense white cedar cover. In our study, black spruce was mostly scattered throughout the mixed stands and very limited in abundance.

The last variable that has a large influence on tree establishment is peat thickness. Although *Abies balsamea* and *Betula papyrifera* occupy a variety of habitats (in the present study they were found on beach ridges, on clay deposits, and on thin water saturated organic deposits), their establishment does not seem to be successful on thick organic deposits. The same observation can be extended to *Fraxinus nigra* found on the river beach ridges and immediately besides on the thin water saturated organic deposits. It is reported that *Fraxinus nigra*, in water saturated sites, will grow best where the water is constantly moving, so that the substrate remains aerated (Johnston 1990). As for *Betula papyrifera* and *Abies balsamea*, *s*oil moisture may have been the most restrictive parameter (Johnston 1990). Larch and black spruce are therefore the most successful species on the stagnant water saturated peat layer.

2.8 CONCLUSION

The distribution of plant species in the Lake Duparquet wetlands is mainly associated with nutrient conditions, as indicated by nitrate concentration, pH and conductivity, and under the influence of peat thickness, water table depth, tree cover class and distance from the shore. In accordance with the results of Vitt and Bayley (1984), we found a relationship between *Sphagnum* spp. cover and low substrate pH. However, this relationship was reversed in some parts of the stands where it is possible that periodic flooding, by adding calcium and magnesium to the substrate, may compensate for the pH lowering caused by *Sphagnum* spp.. A comparison of samples taken at intervals throughout an entire season could elucidate this question. Moreover, because significant relationships were found between nitrate availability and *Alnus rugosa* abundance, and low nitrate levels and *Kalmia angustifolia* abundance, further studies should be conducted to determine if the substrate chemical conditions are actually caused by the presence of these two shrub species. These studies could also be focused on the effects of the abundance of these shrubs on the growth of larch trees, saplings and seedlings.

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Table 2.1 Understory and overstory species relative frequency (F) and cover (C) in each of the vegetation clusters

	Vegetation clusters (no of samples)																	
	1 (N=19)		2 (N=78)		3 (N=24)		4 (N=10)		5 (N=22)		6 (N=11)		7 (N=7)		8 (N=7)		9 (N=8)	
Herbs and Shrubs	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%
Thalictrum pubescens	-	-	-	-	-	-	-	-	**5**	2	**18**	2	**86**	26	**14**	15	-	-
Lycopus uniflorus	-	-	-	-	-	-	-	-	-	-	**27**	2	**86**	8	**14**	15	**25**	15
Glyceria canadensis	-	-	**6**	4	-	-	**20**	1	-	-	**9**	16	-	-	**29**	8	-	-
Carex oligosperma	-	-	**4**	6	-	-	-	-	-	-	-	-	**14**	15	-	-	**13**	1
Lysimachia terrestris	-	-	-	-	-	-	**10**	1	-	-	**9**	2	**14**	15	-	-	**63**	12
Calamagrostis canadensis	**42**	10	**10**	10	-	-	**40**	6	**50**	3	**55**	17	**57**	14	**86**	34	**63**	29
Salix discolor	**5**	15	**1**	1	-	-	-	-	**5**	6	-	-	-	-	-	-	**63**	40
Spiraea alba	**63**	11	-	-	**4**	15	**10**	3	-	-	**9**	4	**57**	11	**86**	19	**63**	10
Sium suave	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**75**	2
Juncus pelocarpus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**63**	11
Eleocharis smallii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**100**	17
Prunus virginiana	**32**	15	**9**	6	**8**	2	**30**	23	**9**	9	**36**	11	**14**	1	**29**	32	-	-
Glyceria borealis	**16**	18	**1**	1	**4**	15	-	-	-	-	**18**	10	-	-	**14**	3	-	-
Cornus stolonifera	**68**	21	**1**	1	**8**	1	**80**	31	**41**	3	**82**	13	**86**	26	**57**	14	-	-
Carex lacustris	**37**	21	**3**	8	**8**	20	**20**	19	-	-	**27**	47	-	-	**14**	3	**25**	15
Viburn lentago	**21**	4	-	-	-	-	**10**	15	-	-	-	-	-	-	**29**	8	-	-
Potentilla palustris	**37**	7	**1**	15	**13**	6	**80**	6	**9**	2	-	-	-	-	**14**	15	**50**	5
Rubus pubescens	**47**	11	-	-	**25**	8	**100**	13	**64**	11	**82**	42	**71**	24	**29**	9	-	-
Iris versicolor	**11**	1	**5**	1	-	-	**50**	1	**18**	9	**9**	2	**29**	1	-	-	**25**	9
Smilacina trifolia	**68**	8	**83**	18	**58**	6	**100**	9	**82**	9	**55**	14	**29**	9	**57**	21	-	-
Myrica gale	**47**	30	**99**	26	**79**	21	**30**	5	**73**	9	**55**	4	-	-	**100**	49	**88**	47
Carex sp.	**68**	14	**95**	14	**92**	21	**90**	12	**95**	29	**73**	14	**71**	12	**43**	10	**13**	15
Alnus rugosa	**100**	19	**83**	12	**100**	30	**100**	21	**100**	22	**91**	38	**71**	18	**71**	20	-	-
Cassandra calyculata	**89**	46	**90**	25	**96**	27	**100**	27	**82**	24	**45**	2	-	-	**29**	26	-	-
Carex trisperma	**11**	15	**59**	15	**33**	14	**10**	15	**55**	18	**27**	12	-	-	**14**	15	-	-
Betula pumila	**100**	15	**96**	16	**88**	21	**90**	23	**18**	5	**27**	14	-	-	**29**	19	-	-
Lonicera villosa	**42**	8	**13**	16	**13**	3	**60**	10	**32**	7	**27**	22	-	-	-	-	-	-
Ledum groenlandicum	**47**	18	**83**	22	**92**	48	**100**	27	**100**	20	**64**	8	**14**	15	-	-	-	-
Vaccinium oxycoccos	**5**	15	**56**	11	**63**	33	**60**	12	**14**	3	-	-	-	-	-	-	-	-
Kalmia angustifolia	**5**	3	**78**	17	**13**	10	**30**	1	**23**	11	**27**	28	-	-	-	-	-	-
Carex canescens	**32**	13	**9**	9	**4**	15	**20**	9	-	-	**9**	16	-	-	-	-	-	-
Andromeda glaucophylla	**63**	14	**92**	19	**79**	17	**70**	14	**32**	8	-	-	-	-	-	-	-	-
Amelanchie sp.	**26**	8	**5**	8	**4**	3	**20**	8	-	-	-	-	-	-	-	-	-	-
Vaccinium myrtilloides	-	-	**18**	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix pedicellaris	**58**	13	**31**	6	**42**	9	**20**	15	-	-	-	-	-	-	-	-	-	-
Salix bebbiana	**5**	38	**23**	12	**4**	1	-	-	**5**	2	-	-	-	-	-	-	-	-
Kalmia polifolia	**11**	9	**18**	10	**8**	2	-	-	-	-	-	-	-	-	-	-	-	-
Carex tenuiflora	-	-	**5**	15	**4**	3	-	-	-	-	-	-	-	-	-	-	-	-
	1		2		3		4		5		6		7		8		9	
	F%	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%	**F%**	C%

Sphagnum sp.	**84**	12	**97**	40	**75**	12	**100**	44	**86**	28	**73**	44	**29**	26	-	-	-	-
Carex paupercula	**21**	5	**13**	4	-	-	**20**	15	**5**	2	**18**	10	-	-	-	-	-	-
Carex disperma	-	-	**6**	7	**29**	32	-	-	**23**	16	**18**	16	-	-	-	-	-	-
Viola pallens	**11**	9	-	-	-	-	-	-	**5**	4	**55**	11	**57**	18	-	-	-	-
Triantalis borealis	**11**	9	-	-	-	-	**40**	2	**59**	5	**45**	5	**29**	2	-	-	-	-
Onoclea sensibilis	-	-	-	-	-	-	-	-	-	-	-	-	**86**	19	-	-	-	-
Nemopanthus mucronatus	**16**	30	**1**	1	-	-	**50**	14	**5**	2	**9**	2	**29**	8	-	-	-	-
Maianthemum canadense	**5**	3	-	-	**29**	10	**40**	15	**50**	6	**82**	21	**43**	10	-	-	-	-
Galium labradoricum	**11**	2	-	-	-	-	**40**	2	**5**	2	**18**	2	**14**	1	-	-	-	-
Equisetum sp.	**32**	11	**18**	2	**21**	16	**90**	12	**68**	8	**73**	6	**71**	7	-	-	-	-
Cystopteris fragilis	**11**	20	**1**	3	-	-	-	-	**5**	2	**45**	8	**14**	1	-	-	-	-
Cornus canadensis	-	-	-	-	**4**	3	-	-	**45**	3	**36**	24	**14**	1	-	-	-	-
Carex intumescens	-	-	-	-	-	-	-	-	-	-	**55**	7	**29**	8	-	-	-	-
Grass sp.	-	-	**1**	15	**13**	23	-	-	**5**	38	**18**	8	-	-	-	-	-	-
Mosses	**89**	5	**73**	7	**75**	1	**90**	10	**82**	8	**100**	14	**71**	12	-	-	-	-
Trees and regeneration																		
*Abies balsamea **	**5**	25	**5**	44	**8**	38	-	-	**59**	32	**82**	45	**43**	42	-	-	-	-
*Betula papyrifera **	-	-	**1**	1	**4**	1	**10**	1	**14**	2	**82**	2	**29**	1	-	-	-	-
*Fraxinus nigra **	-	-	-	-	-	-	**10**	1	**9**	2	**9**	2	**86**	16	-	-	-	-
*Larix laricina **	**37**	46	**63**	38	**67**	30	**50**	50	**77**	41	-	-	**29**	38	**14**	50	-	-
*Picea mariana **	**11**	33	**29**	36	**79**	37	**70**	33	**82**	45	**18**	34	**14**	33	-	-	-	-
*Thuja occidentalis **	-	-	-	-	-	-	**70**	20	**73**	45	-	-	**14**	20	-	-	-	-
*Larix laricina ***	**63**	29	**99**	79	**96**	66	**90**	49	**64**	25	**9**	6	-	-	-	-	-	-
*Thuja occidentalis ***	-	-	-	-	-	-	**70**	20	**86**	49	**9**	7	**29**	13	-	-	-	-
*Picea mariana ***	**11**	3	**6**	2	**46**	17	**50**	19	**27**	10	**9**	10	-	-	-	-	-	-
*Abies balsamea ***	-	-	-	-	-	-	-	-	**5**	1	**73**	45	**29**	17	-	-	-	-
*Betula papyrifera ***	-	-	**3**	16	-	-	-	-	**9**	2	**55**	21	-	-	-	-	-	-
*Fraxinus nigra ***	-	-	-	-	-	-	-	-	**5**	1	**9**	4	**86**	57	-	-	-	-

Legende

F%: Species frequencies

C%: Covers (shrub and herb species) and importances values (tree species)

1- Larix laricina & Spiraea alba; 2- Larix laricina & Kalmia augustifolia; 3- Larix laricina, Picea mariana & Alnus rugosa; 4- Larix laricina & Betula pumila;

5- Thuja occidentalis & Trientalis borealis; 6- Abies balsamea & Betula papyrifera; 7- Fraxinus nigra & Onoclea sensibilis; 8- Alnus rugosa; 9- Eleocharis Smali

**Seedlings and saplings,*

***Trees*

Table 2.2 Average and standard deviation of variables recorded in each vegetation clusters

Vegetation clusters (no. of samples)

	1 (N=19)		2 (N=78)		3 (N=24)		4 (N=10)		5 (N=22)		6 (N=11)		7 (N=7)		8 (N=7)		9 (N=8)	
	AV	SD	**AV**	SD	**AV**	SD	**AV**	SD	**AV**	SD	**AV**	SD	**AV**	SD	**AV**	SD	**AV**	SD
Average distance among trees	**1.7**	1.5	**1.4**	0.9	**1.4**	0.9	**1.2**	0.9	**1.0**	0.9	**0.5**	0.7	**0.8**	0.4	-	-	-	-
Average tree height	**6.4**	4.9	**9.5**	2.8	**9.7**	3.7	**8.6**	2.4	**8.0**	3.2	**8.6**	4.4	**9.3**	1.8	-	-	-	-
Carbon index	**0.06**	0.02	**0.11**	0.03	**0.07**	0.02	**0.04**	0.01	**0.06**	0.03	**0.10**	0.06	**0.08**	0.02	**0.07**	0.02	-	-
Cover	**1.1**	0.3	**1.6**	0.6	**1.8**	0.5	**1.6**	0.5	**2.8**	1.0	**3.5**	1.1	**2.9**	1.1	**1.0**	0.0	**1.0**	0.0
Mortality	**3**	3	**4**	3	**5**	3	**6**	4	**5**	3	**9**	9	**5**	3	**1**	2	**0**	0
Peat depth	**0.96**	0.27	**1.01**	0.27	**0.94**	0.16	**0.97**	0.36	**0.99**	0.24	**0.68**	0.43	**0.20**	0.33	**0.63**	0.17	**0.05**	0.06
Relative distance	**33**	21	**51**	24	**52**	21	**61**	31	**82**	18	**66**	45	**2**	6	**9**	3	**0**	0
Shrubs height	**1.52**	0.35	**1.30**	0.38	**1.62**	0.34	**1.74**	0.34	**1.26**	0.48	**1.66**	0.67	**1.77**	0.95	**1.39**	0.26	**1.25**	0.12
Soil conductivity	**124.9**	42.2	**111.0**	36.6	**121.5**	37.6	**120.9**	25.8	**148.5**	44.9	**162.7**	57.0	**129.0**	44.2	**125.7**	34.2	**137.7**	49.5
Soil NH_4	**15.40**	9.14	**14.03**	6.60	**26.38**	10.18	**14.76**	12.86	**20.34**	5.03	**21.65**	15.21	**16.03**	14.67	**24.86**	7.90	**10.71**	8.79
Soil pH	**5.65**	0.52	**4.90**	0.37	**5.55**	0.41	**5.82**	0.43	**5.94**	0.55	**5.67**	0.59	**5.75**	0.47	**5.33**	0.37	**6.11**	0.56
Soli NO_3	**0.03**	0.05	**0.02**	0.02	**0.03**	0.02	**0.02**	0.01	**0.05**	0.06	**0.05**	0.05	**0.03**	0.02	**0.09**	0.08	**0.18**	0.42
% in pools	**2**	2	**2**	3	**5**	6	**8**	5	**17**	10	**14**	19	**5**	9	**0**	1	**0**	0
Water table depth	**20**	9	**24**	10	**25**	11	**17**	4	**24**	10	**15**	9	**10**	9	**26**	13	-	-
Water conductivity	**64.37**	11.86	**65.30**	8.76	**68.38**	10.89	**66.65**	23.84	**74.17**	15.80	**74.92**	25.74	**67.26**	1.13	**71.71**	14.15	-	-
Water NH_4	**0.08**	0.02	**0.09**	0.03	**0.08**	0.02	**0.07**	0.02	**0.06**	0.02	**0.07**	0.01	**0.08**	0.01	**0.08**	0.01	-	-
Water NO_3	**0.48**	0.35	**0.46**	0.35	**0.73**	0.37	**0.30**	0.26	**0.37**	0.23	**0.58**	0.43	**0.45**	0.13	**0.75**	0.57	-	-
Water pH	**6.88**	0.36	**6.09**	0.51	**6.61**	0.29	**7.12**	0.36	**6.82**	0.57	**6.67**	0.29	**6.63**	0.37	**6.66**	0.25	-	-
Water C/N index*	**0.13**	-	**0.38**	-	**0.11**	-	**0.20**	-	**0.26**	-	**0.15**	-	**0.14**	-	**0.22**	-	-	-

Legends

AV: Average value

SD: Standard deviation

1- Larix laricina & Spiraea alba; 2- Larix laricina & Kalmia augustifolia; 3- Larix laricina, Picea mariana & Alnus rugosa; 4- Larix laricina & Betula pumila; 5- Thuja occidentalis & Trientalis borealis; 6- Abies balsamea & Betula papyrifera; 7- Fraxinus nigra & Onoclea sensibilis; 8- Alnus rugosa; 9- Eleocharis smallii

* Note that a low ratio indicates that plant growth may be limited by poor nutrient conditions

Table 2.3 Height, density and cover of the tree species

	Vegetation clusters								
	1	2	3	4	5	6	7	8	9
Average height (m)									
Abies balsamea	-	-	-	-	6.3	10.1	10.2	-	-
Betula papyrifera	-	4.8	-	-	6.5	9.6	-	-	-
Fraxinus nigra	-	-	-	-	6.9	5.4	7.3	-	-
Larix laricina	6.3	9.6	10.4	10.4	7.1	2.7	-	8.4	-
Picea mariana	0.7	0.7	1.8	0.9	4.1	15.4	4.0	-	-
Thuja occidentalis	-	-	-	1.9	4.0	10.1	1.4	-	-
Density (ha)									
Abies balsamea	-	-	-	-	7.9	223.3	89.1	-	-
Betula papyrifera	-	2.0	-	-	15.7	105.8	-	-	-
Fraxinus nigra	-	-	-	-	7.9	11.8	445.3	-	-
Larix laricina	27.2	258.7	207.5	98.3	196.6	11.8	-	1.0	-
Picea mariana	4.7	6.8	43.2	43.0	55.0	35.3	-	-	-
Thuja occidentalis	-	-	-	79.9	353.8	11.8	89.1	-	-
Cover (m^2/ha)									
Abies balsamea	-	-	-	-	0.04	3.32	3.15	-	-
Betula papyrifera	-	0.01	-	-	0.04	1.35	-	-	-
Fraxinus nigra	-	-	-	-	0.05	0.03	11.93	-	-
Larix laricina	0.63	4.54	4.32	2.78	3.96	0.41	-	0.06	-
Picea mariana	0.02	0.09	0.25	0.75	0.77	2.24	-	-	-
Thuja occidentalis	-	-	-	5.28	9.61	3.17	6.32	-	-

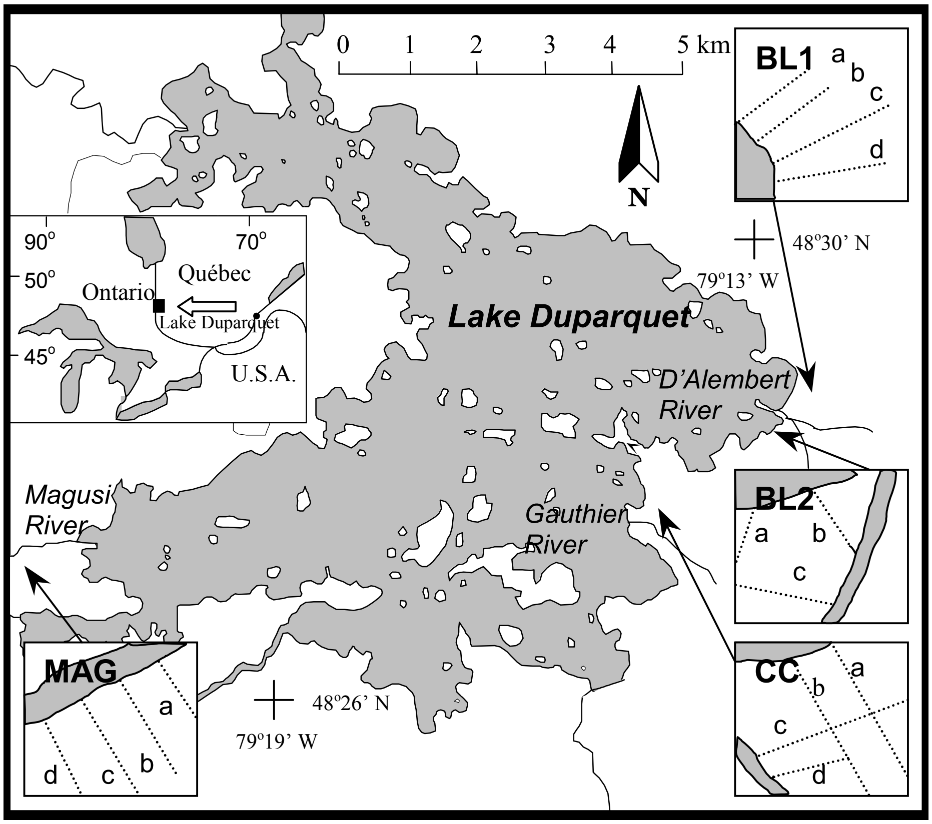

Figure 2.1 Map of Lake Duparquet showing the location of the four *Larix laricina* stands studied: BL1, BL2, CC and MAG. Lengths of the longest transects for each stands are respectively 500, 720, 720 and 240 metres.

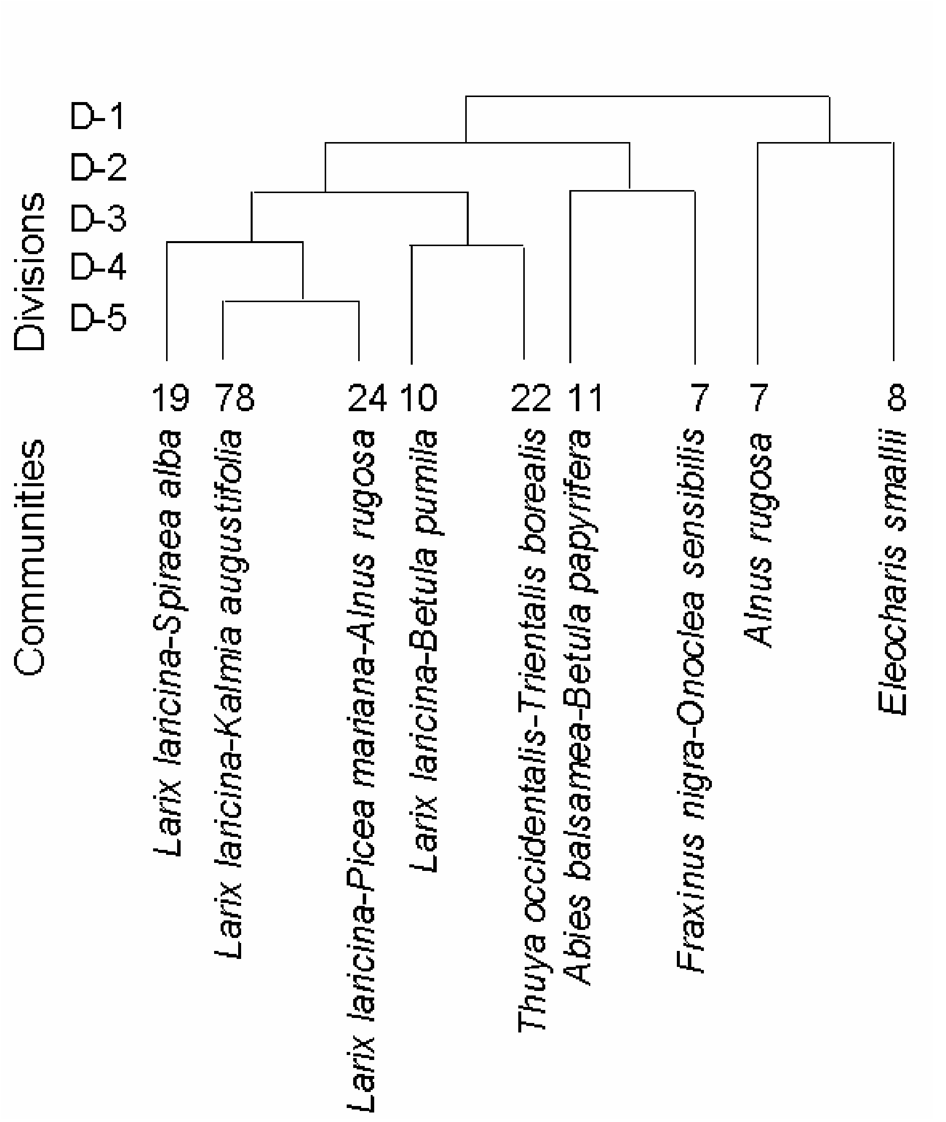

Figure 2.2 Vegetation clusters retained after the Twinspan divisive hierarchical classification analysis.

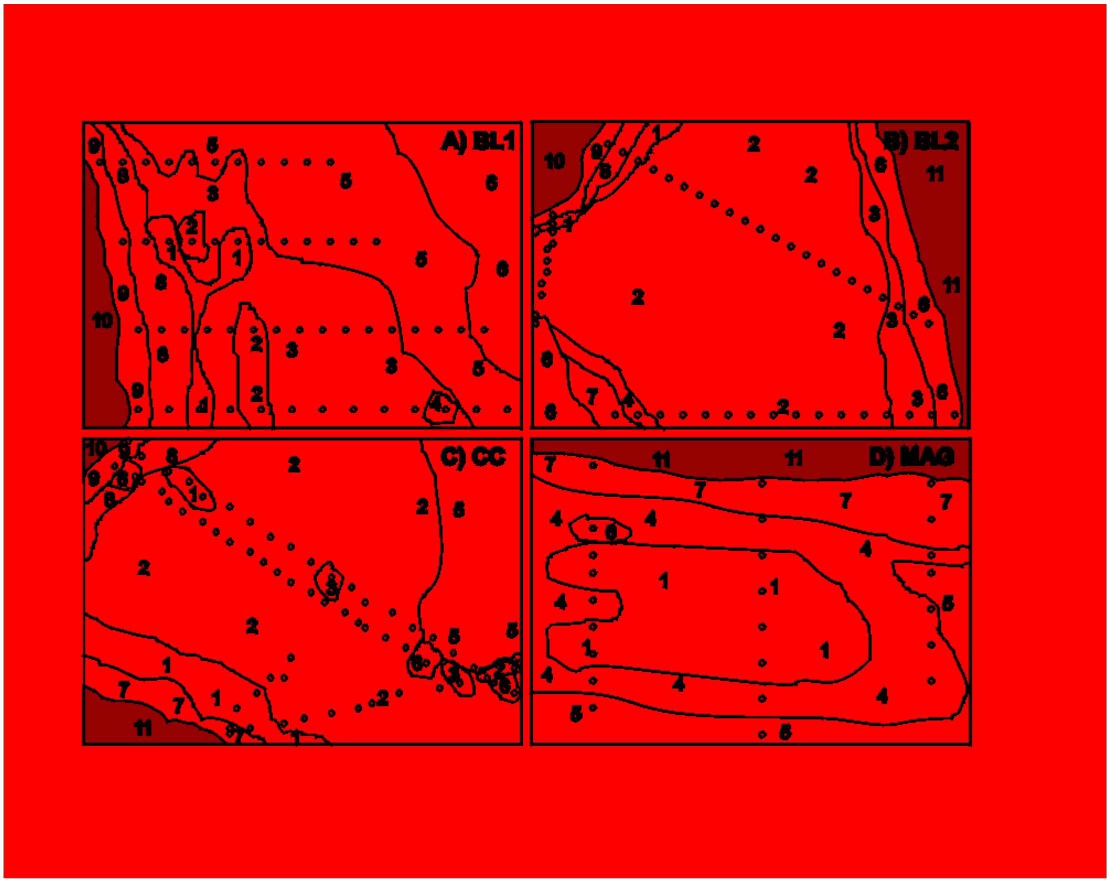

Figure 2.3 Spatial location of the nine vegetation clusters and the 186 PCQs in the studied stands a) BL1, b) BL2, c) CC and d) MAG. The contours were hand drawn from GPS data, field notes and aerial photographs. Legend: 1- *Larix laricina* & *Spiraea alba*; 2- *Larix laricina* & *Kalmia angustifolia*; 3- *Larix laricina*, *Picea mariana* & *Alnus rugosa*; 4- *Larix laricina* & *Betula pumila*; 5- *Thuja occidentalis* & *Trientalis borealis*; 6- *Abies balsamea* & *Betula papyrifera*; 7- *Fraxinus nigra* & *Onoclea sensibilis*; 8- *Alnus rugosa*; 9- *Eleocharis smallii*; 10- Lake Duparquet and 11- rivers.

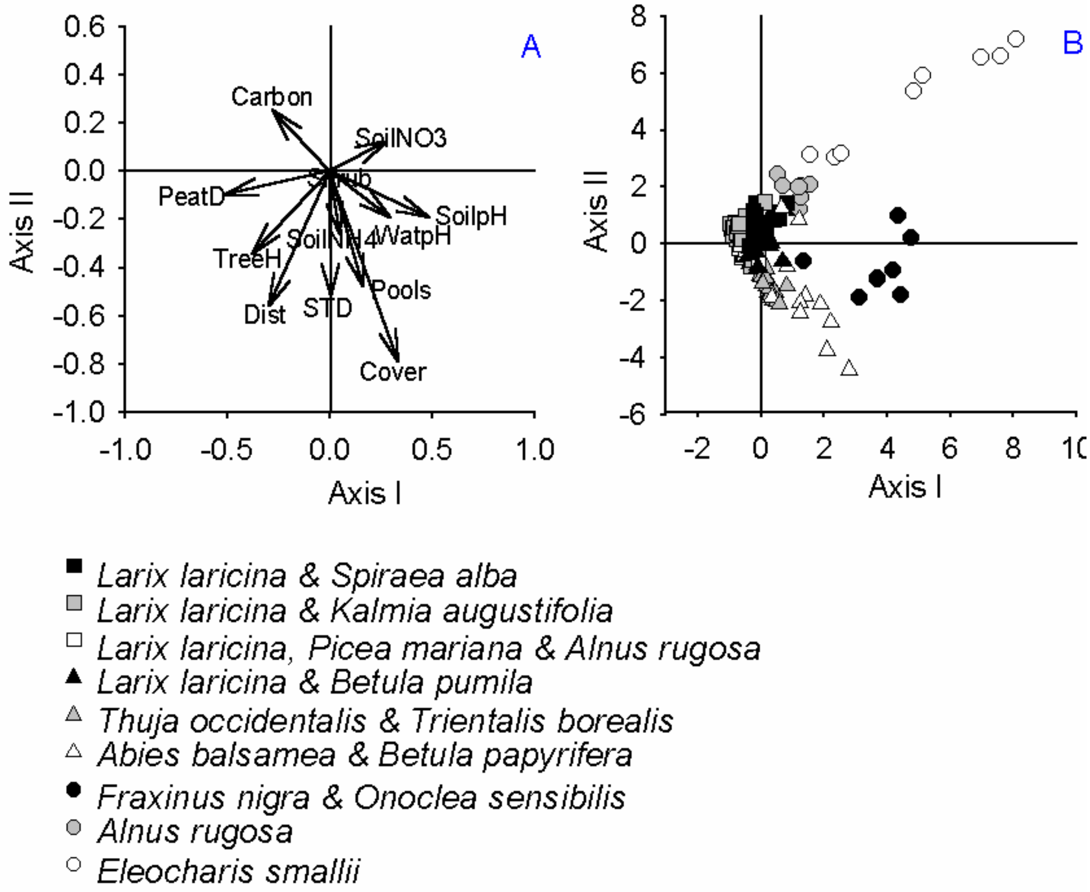

Figure 2.4 Results of the canonical correspondence analysis (CCA) conducted on all PCQs sampled around Lake Duparquet. (A) The bi-plots yield approximates the correlation coefficient between descriptors and environmental factors and also among descriptors and environmental factors themselves. Variables with arrows at sharp angles are positively correlated, and the length of an arrow represents the size of the coefficient. By contrast, obtuse angle between variables indicates negative correlation. See Table 2.2 for abbreviation meanings. (B) The position along the first two axes of the CCA of all 186 PCQs and the nine vegetation clusters.

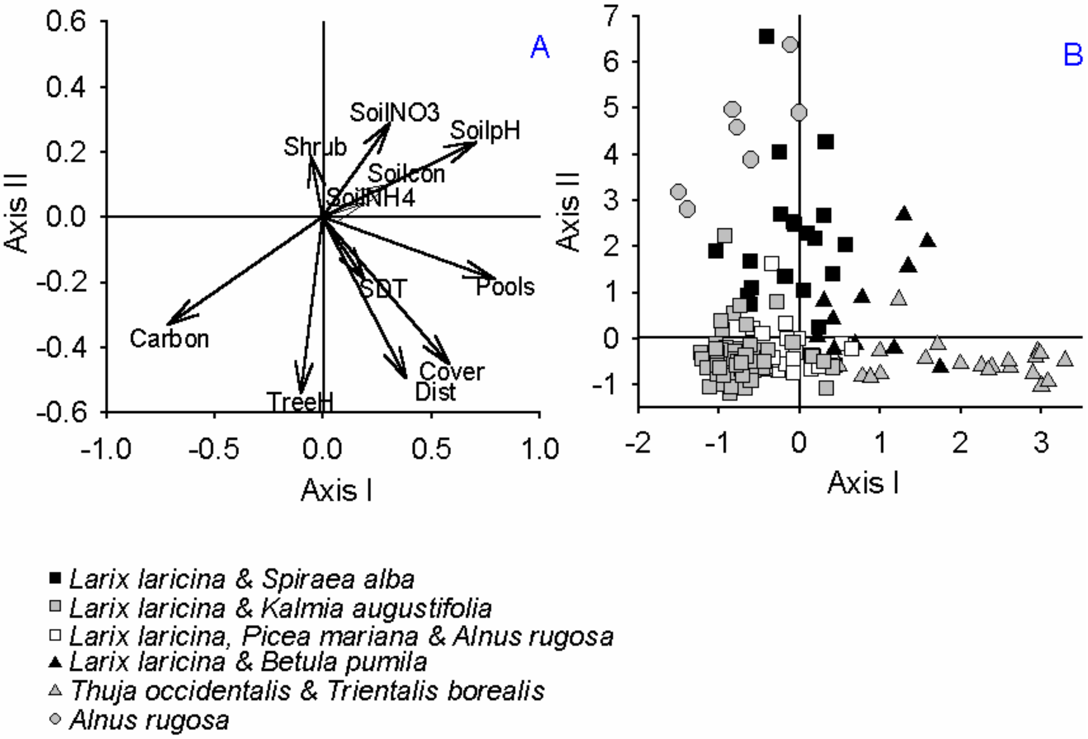

Figure 2.5 Results of the canonical correspondence analysis (CCA) after the elimination of the outlier vegetation clusters.

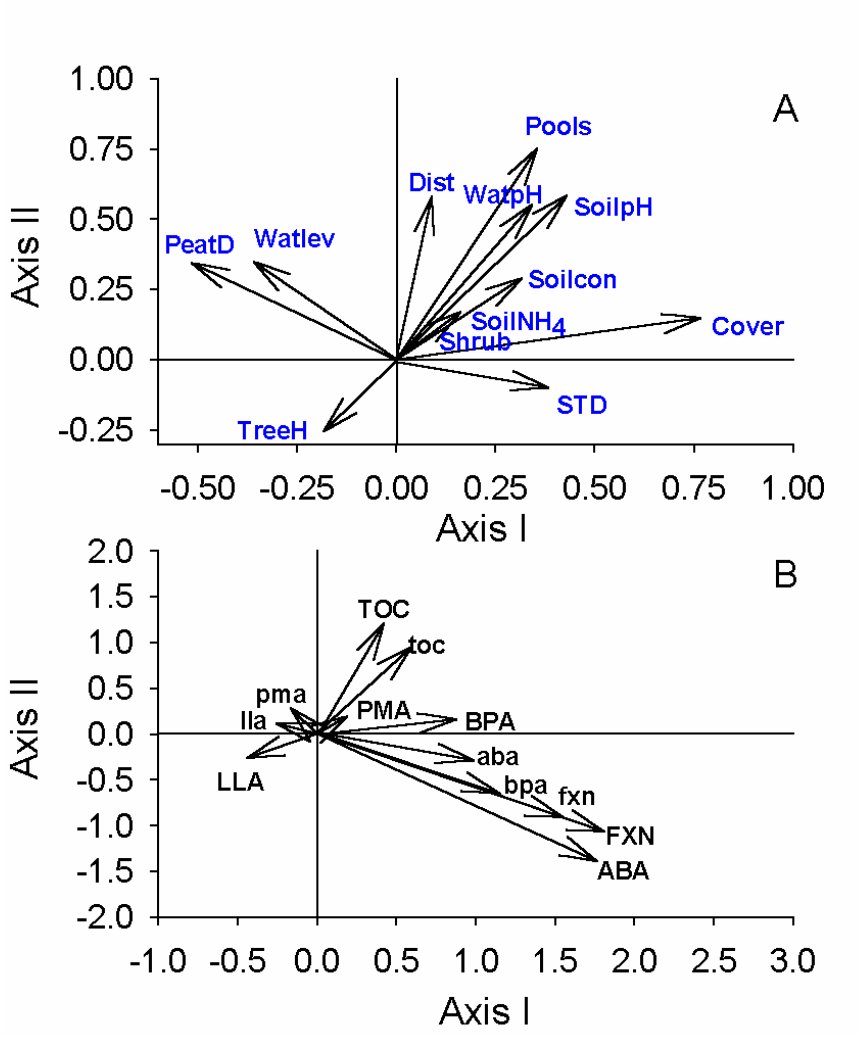

Figure 2.6 Results of the canonical correspondence analysis (CCA) conducted on the six tree species: LLA = *Larix laricina*; PMA = *Picea mariana*; TOC = *Thuja occidentalis*; BPA = *Betula papyrifera*; FXN = *Fraxinus nigra* and ABA = *Abies balsamea*. Capital letters are for trees, lower case letters for seedlings and saplings.

ARTICLE II: ANALYSE DE LA CROISSANCE RADIALE DE *LARIX LARICINA* DANS LA RÉGION DU LAC DUPARQUET EN RELATION AVEC LE CLIMAT ET LES ÉPIDÉMIES DE TENTHRÈDE

Girardin, M.P., Tardif, J. et Bergeron, Y. 2001. Radial growth analysis of *Larix laricina* from Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks. Écoscience 8: 127-138.

3.1 ABSTRACT

A dendrochronological study was done at six sites dominated by eastern larch (*Larix laricina* (Du Roi) K.Koch) in Québec's southwestern boreal forest. The objectives were to reconstruct periods of larch sawfly (*Pristiphora erichsonii*) outbreak in the region and to determine which climatic factors (precipitation, temperature, water level or drought) explained the greatest variation in the radial growth of larch. From the presence of light latewood rings, followed by periods of growth suppression, we identified larch sawfly outbreaks for the years 1895 to 1912, 1937 to 1942, and 1955 to 1962. We suspect that additional outbreaks occurred in the early 1920s, late 1970s and early 1980s as well, though at the same time as spruce budworm outbreaks (*Choristoneura fumifera* (Clem.)). Response function analysis showed negative relationships between larch radial growth and May and August precipitation and May and September water level, and demonstrated positive relationships with May drought index and previous year September drought index. These results suggest that flooding in the early growing season and excessive water levels at the end of the growing season may negatively affect larch radial growth. Our results also indicate an increase in the year to year variation in radial growth in larch sites subjected to flooding. This may reflect the increase in the Lake Duparquet water level at the spring break up.

Keywords: Larch, dendrochronology, insects, climate, light latewood, *Pristiphora erichsonii*, response function, water level.

3.2 RÉSUMÉ

Une étude dendrochronologique a été réalisée dans six sites dominés par le mélèze (*Larix laricina* (Du Roi) K.Koch) à la limite sud de la forêt boréale dans l'ouest du Québec. Les objectifs visés étaient de reconstituer les périodes de défoliation par la tenthrède du mélèze (*Pristiphora erichsonii*) au cours du 20e siècle et de déterminer quels facteurs physiques (précipitation, température, niveau d'eau et humidité du substrat) expliquent le plus la variabilité de la croissance radiale du mélèze. D'après l'occurrence des cernes à bois final pâle suivis de périodes de réduction de croissance, nous rapportons la présence d'épidémies de la tenthrède du mélèze au cours des années 1895 à 1912, 1937 à 1942 et 1955 à 1962. Nous avons aussi des indications de la présence de la tenthrède au début des années 1920, à la fin des années 1970 et au début des années 1980, bien que des épidémies de la tordeuse des bourgeons d'épinette (*Choristoneura fumifera* (Clem.)) aient été rapportées aux mêmes moments. L'analyse des fonctions de réponse indique des relations négatives entre la croissance radiale du mélèze et les précipitations de mai et août et les niveaux d'eau de mai et septembre de l'année en cours. Des relations positives ont été obtenues avec l'indice de sécheresse pour les mois de septembre de l'année précédente et mai de l'année en cours. Ces résultats suggèrent que les inondations en début et en fin de saison de croissance ont un effet négatif sur la croissance radiale. Enfin, les résultats démontrent une augmentation des variations inter-annuelles dans la croissance des peuplements de mélèze soumis aux inondations du Lac Duparquet. Ceci pourrait faire suite à l'augmentation des niveaux d'eau lors de la débâcle printanière.

Mots-clés: mélèze, dendrochronologie, insectes, climat, bois final pâle, *Pristiphora erichsonii*, fonction de réponse, inondation.

3.3 INTRODUCTION

Populations of eastern larch (tamarack, *Larix laricina* (Du Roi) K. Koch) are mainly confined to hydric sites in subarctic, boreal and temperate North American forests (Nairn *et al.*, 1962; Schooley & Pardy, 1981; Bergeron *et al.*, 1982; Martineau, 1985; Johnston, 1990). The growth of this species is limited by water saturated conditions (Bergeron *et al.*, 1982), low nutrient availability, absence of oxygen in soils, and low soil temperature (Kozlowski, 1982). In these environments, particularly in wetlands next to water bodies, larch distribution is influenced by its tolerance to the frequency, duration and timing of spring flooding (Robertson *et al.*, 1978; Kenkel, 1986; Tardif & Bergeron, 1992; Denneler, Bergeron & Bégin, 1999).

A climatic analysis conducted in the northern Québec temperate forest by Jean & Bouchard (1996) revealed negative relationships between larch growth and high spring and autumn water levels. These authors also reported that both monthly precipitation and temperature play a major role in controlling larch radial growth (Jean & Bouchard, 1996). Similar results were found in Québec's northern boreal forest by Kaminski (1997), who reported a negative effect of May precipitation on larch radial growth. A positive effect of June precipitation, which was attributed to a possible depletion of the meltwater reserve in the soil, was also observed (Kaminski, 1997).

In addition to climate, the radial growth of larch may be seriously affected by defoliation by the larch sawfly (*Pristiphora erichsonii*) (Coppel & Leius, 1955; Rose & Lindquist, 1980; Turnock, 1972; Jardon, Filion & Cloutier, 1994a; 1994b). In northern Québec, Jardon, Filion & Cloutier (1994a) found six periods of suppressed radial growth between 1847 and 1993 corresponding to sawfly outbreaks: 1847-1861, 1883-1890, 1894-1906, 1907-1911, 1938-1952 and 1984-1989. Arquillère *et al.* (1990) also mentioned sawfly epidemics in the same region for the periods 1905 to 1908 and 1940 to 1946. In the southwestern Québec boreal forest, field records indicate severe infestations for the years 1939, 1940, 1955 and from 1959 to 1965 (Ministère de l'Énergie et des Ressources, Québec, rapports annuels 1937-1982). Smaller outbreaks were also reported during the 1970 to 1982 period. It has also been suggested that, to a lesser extent, larch may be defoliated during severe spruce budworm (*Choristoneura fumifera* [Clem.]) outbreaks (Johnston, 1990). In the Lake Duparquet region, spruce budworm outbreaks have been reported during the periods 1919 to 1929, 1930 to 1950 and 1970 to 1985 (Morin, Laprise & Bergeron 1993).

Our first objective was to reconstruct larch sawfly outbreaks for the twentieth century in the Lake Duparquet region (northwestern Québec), using dendrochronological methods. This brings additional data, which may be compared with other information sources for observation of the outbreaks spatial progression. Our second objective was to determine the main climatic factors (mean monthly water level, average temperature, total precipitation and drought index) influencing larch radial growth. A dendrochronological study conducted by Tardif & Bergeron (1997b) on white cedar (*Thuja occidentalis* L.) revealed that Lake Duparquet water levels at spring breakup have increased in height (~100 cm) and frequency over the past 150 years. We were thus suspecting that the spring flooding regime has played an important role in larch growth, notably over the last few decades. Six study sites were chosen in relation to a gradient of severity of the spring flooding on the shore of Lake Duparquet (Denneler, Bergeron & Bégin, 1999).

3.4 STUDY AREA

The study area is located in the forests surrounding Lake Duparquet in the Abitibi region, Québec (48^{o}28’N, 79^{o}17’W, Fig.3.1). The lake covers an area of 50 km^2 and drains northward via the Duparquet River towards James Bay. The region is part of the Northern Clay Belt of Québec and Ontario, associated with the maximum extension of postglacial lakes Barlow and Ojibway (Vincent & Hardy, 1977). Mean annual temperature is 0.8^{o}C and total annual precipitation varies from 800 to 900 mm (Environment Canada, 1993). The mean frost-free period is 64 days, although frost may occur at any time of the year (Anonymous, 1982).

Six larch stands from the Lake Duparquet area were selected for this study, including all larch stands surrounding Lake Duparquet (Fig. 3.1). The lake water regime has not been modified in the past. The six sites were chosen along a gradient of flooding severity (Denneler, Bergeron & Bégin, 1999). Sites BL1, BL2, BL3 and CC are all subject to flooding and wave action from Lake Duparquet (Denneler, Bergeron & Bégin, 1999). Site LS is subject to flooding from Lake Soisson, a much smaller lake (~700 m wide in contrast to ~10 km for Lake Duparquet, Fig. 3.1). Site CM, being non-riparian, is not subjected to any external flooding.

Site BL1 is dominated by larch at its lowest points and by cedar (*Thuja occidentalis* L.) in its highest parts, with some black spruce (*Picea mariana* [Mill.] BSP.) scattered throughout. Sampling was conducted in the lower section, 200 to 400m from the shore. Three other sites (BL2, BL3 and CC) are pure larch stands, while the fifth site, on the shore of Lake Soisson (LS), is a mixed stand of larch, black spruce and white cedar, with an understory composed of white cedar, black spruce and balsam fir (*Abies balsamea* [L.] Mill.). The sixth site is located just off Matheson road (CM). This site, also dominated by larch, black spruce and white cedar, was disturbed by the construction of the road early in the twentieth century and more recently by the establishment of claim trails. On the north side of the road, the ground is poorly colonized by vegetation (*Carex* sp.) and decomposition is far more advanced than on the other sites, suggesting that drainage may have been modified following road construction. For this site, sampling was conducted on the northern side at a minimal distance of 50 m from the road and 20 m from the land claim trails. All study sites are located on organic deposits (>0.6 m thick) where the depth to the water table is at least 20 cm.

3.5 METHODS

3.5.1 Sampling

In this study, the largest diameter larch and black spruce trees were sampled for each site at the end of the 1997, 1998 and 1999 growing seasons (each site being 2 to 4 ha). A total of 118 larch trees were sampled from which two to three cores per tree were taken at 1.5 m above ground. Some cores were rejected (2 in site BL1, 2 in BL3 and 4 in CM) because of young age and presence of compression wood. Generally, such cores show low correlation with the reference chronologies (Stokes & Smiley, 1968). A total of 230 cores (115 trees) were retained for the study (Table 3.1). As for black spruce, 50 cores from 26 trees were considered.

3.5.2 Development of chronologies

The cores were prepared following the standard procedure proposed by Stokes & Smiley (1968) and Swetnam, Thompson & Sutherland (1988). Visual cross-dating was done using the method described in Yamaguchi (1991). A Velmex Uni Slide micrometer (0.001 mm precision) was used to measure ring width and cross-dating was validated using the COFECHA program (Holmes, Adams & Fritts, 1986). Pointer years for the cross-dating of larch were 1996, 1992, 1984, 1979, 1976, 1973, 1967, 1964, 1962, 1961, 1960, 1956, 1922 and 1895. For black spruce, these years were 1984, 1962, 1960, 1956 and 1922. Both species had similar growth sequences, notably for years 1920 to 1922, 1960 to 1965, 1983 to 1985 and 1990 to 1997.

To remove the effect of the age/size-related trend, a spline function giving a 50% frequency response of 45 years was applied to the measured series (Cook & Peters, 1981). This was done to produce the standard chronologies. Residual chronologies were computed in the same manner as the standards, but in this case the series were averaged using residuals from autoregressive modelling of the detrended measurement series (Cook & Holmes, 1986; Holmes, Adams & Fritts, 1986). This resulted in chronologies with a strong common signal and without persistence. Both chronologies were constructed using ARSTAN (Holmes, 1983; Cook, 1985).

A common interval analysis, which contains the maximum possible number of data in a rectangular matrix (length of common interval times number of series), was performed for the 1935 to 1996 period. Finally, Pearson correlations were calculated among site residual chronologies.

3.5.3 Sawfly outbreak identification

Outbreak periods of the larch sawfly were first identified using the criteria described by Harper (1913) and Jardon, Filion & Cloutier (1994a). These periods are characterized by 1) the presence of a light latewood ring without a decrease in the width of the whole tree-ring (thin-walled latewood cells, Harper 1913); 2) a decrease in radial growth; and 3) an increase in the presence of missing or incomplete rings. Light latewood rings are characterized by a reduction in the thickeness of latewood cells. This is a response to a lack of assimilated products that supply the cells during the current growth year (Harper, 1913; Filion & Cournoyer, 1995; Liang, Filion, & Cournoyer, 1997).

To better identify the larch sawfly outbreak periods, a chronology of black spruce growing on sites BL1 and LS (Fig. 3.1) was used for a non-host comparison analysis. The rationale of the host/non-host comparisons are fully described in Swetnam, Thompson & Sutherland (1985). Essentially, the effects of current or past insect outbreaks are detectable when a decrease in the growth of the host species occurs, with no corresponding decrease in the non-host species. Analysis of the host and non-host chronologies was done with the OUTBREAK program following the BUDWORM options (Holmes & Swetnam, 1996). In this analysis, the non-host chronology (black spruce residual chronology) was subtracted from each host series (larch individual residual series) to reduce the common effects of climatic variation. Years in which the normalized series were negative were recorded as possible outbreak period. However, if the period identified did not reach a threshold for maximum growth reduction (-1.28 in standard deviation) or a minimum length for sawfly outbreaks (in this case it was fixed at four consecutive years), then this period was eliminated as a possible outbreak. The minimum length of outbreaks was fixed at four years to eliminate possible effects of individual tree responses to a yearly, specific environmental condition. It was also reported that larch cannot survive more than three years of complete defoliation and more than eight years of moderate defoliation (Ives & Nairn, 1966; Nairn *et al.*, 1962). As for the thresholds with a standard deviation of –1.28, our trials revealed that the percentage of trees in possible outbreak periods was stable inside the interval –1.10 to –1.40.

3.5.4 Climate and hydrology relationships

The effects of hydrological and climatic fluctuations on larch radial growth were analyzed using both correlation analyses (Briffa & Cook, 1990; Fritts, 1976) and response function analyses (Fritts *et al.*, 1991). The bootstrap response function analysis provides a test of significance of the stability of the regression coefficients within a specific time period by repeated, random sampling of the data (Guiot, 1993). A weight was associated with each monthly variable, expressing the separate relative effects of several climatic factors on ring width (Fritts, 1976). This method offers the advantage of avoiding errors caused by collinearity among variables and providing a more realistic estimate of tree response to climate. All climatic analyses were performed using PRECON (Fritts *et al.*, 1991) and 999 bootstrap iterations were generated.

As an estimate of the Lake Duparquet water level, hydrological data (mean monthly river discharge) from the Harricana River station (1915-1998), 100 km east of Lake Duparquet (48°36’N, 78°06’O), were used in the absence of data closer to Lake Duparquet. Tardif & Bergeron (1997b) reported that both hydrological systems respond to the same regional climate. Regional mean monthly temperature and total monthly precipitation (1896-1997) from Tardif & Bergeron (1997a) were used in our analyses of temperature and precipitation variables (May from the previous year of growth up until September of the current year). These regional series were computed using data from eight weather stations distributed within *ca* 100km of Lake Duparquet. The mean of the monthly drought index from the Canadian Fire Code (1915-1996) calculated from Iroquois Falls (100 km to the

West [48°45'N, 80°40'W]) daily data (May to September of the previous and present years; Tardif & Bergeron, 1997a) was also used as a measure of substrate moisture content.

All dendroclimatic analyses were conducted for the period 1915 to 1996. This period was chosen to preserve a constant degree of freedom in all analyses. A second response function analysis using data for the period 1962 to 1996 was nevertheless calculated to assess the response to climate in the more recent years and as a verification test to confirm that there was no major interference from the outbreak periods. This was to test that similar responses to climate were occurring in both intervals.

3.6 RESULTS

3.6.1 Tree-ring statistics of larch

A large amount of the total variance was accounted for by the first eigenvector, and trees collected in pure larch stands (BL1, BL2, BL3 and CC) generally had higher mean sensitivity and standard deviation (Table 3.1). In contrast, high autocorrelation was observed in the standard chronologies of sites LS and CM. First-order autocorrelation values from residual chronologies were very low. The common pattern among trees is reflected by the strong intercore, inter-tree and intra-tree correlations and by the large amount of variance explained by the first principal component vector (52 to over 68%). Inter-tree correlations from pure stands are generally higher than those from mixed stands (LS and CM). Finally, Pearson correlations indicate a relatively high correlation among all site residual chronologies ($p < 0.01$, Table 3.2). The majority of larch trees sampled were established after 1875, as shown by the larch residual and standard chronologies (Fig. 3.2). According to the standard chronologies, variability in year to year growth was lower in sites CM and LS compared to all other larch chronologies (Fig. 3.2). This was particularly noticeable after the 1960s. These two sites also had the lowest mean sensitivity and standard deviation, and the highest autocorrelation (Table 3.1). No anthropogenic effects were observed at the CM site in relation to the construction of the road, suggesting that all trees were established after this period.

The chronologies obtained for larch show that during the second half of the XXth century, year to year fluctuations have increased. This is further illustrated by the major increase in mean sensitivity for the chronologies constructed from trees growing on the shore of Lake Duparquet (Fig. 3.3). This generalized increase in mean sensitivity supports the hypothesis that there is a common signal influencing radial growth. In contrast, this signal is less clear for the CM site after 1970 and less important for the LS site. An increase followed by a decrease in mean sensitivity was observed for all site chronologies for the periods 1885 to 1915 and 1945 to 1970.

3.6.2 Larch sawfly outbreaks

Three larch sawfly outbreak periods were determined using the criteria of Harper (1913) and Jardon *et al.* (1994a). The most recent outbreak appears to have started in 1955, and the period of growth suppression generally ended in 1962 (Fig. 3.2). Light latewood cells were observed to be most abundant in 1955 (3.1% of all series), 1957 (5.3%) and 1958 (14.6%) (Fig. 3.4). Missing or incomplete rings were sometime found for years 1959 (7.7% of all series), 1960 (4.8%), 1961 (0.5%), 1962 (0.4%) and 1964 (1.2%) (see Fig. 3.4 for site frequencies). The CM site was the site most affected by this last outbreak, as indicated by the high number of incomplete and missing rings, and evidence of growth suppression (Fig. 3.2 and Fig. 3.4f).

A second outbreak period was observed from 1937 to 1942, and light latewood rings were observed in 1937 for 4% of the individuals. No missing rings resulted from this outbreak (Fig. 3.4). The longest suppression period caused by the larch sawfly started in 1895 as indicated by the first light latewood ring (8.2% of all series), and ended around 1912. A light latewood ring also characterized the years 1896 (10.4%), 1897 to 1907, 1909 and 1910. A few missing rings occurred from 1897 to 1901, 1904 to 1906, 1909 and 1910 (Fig. 3.4).

The black spruce residual chronology, used as the non-host species, is presented in Figure 3.5. Two periods of minor growth suppression were observed in this chronology: 1930 to 1935 and 1910 to 1915. However, these periods of radial growth suppression did not coincide with any of the growth suppressions observed in larch chronologies.

Correlations between the host and non-host residual chronologies (Table 3.2) indicated that most of the series correlations were statistically significant. The two species would thus respond to similar environmental factors, a necessary condition for using OUTBREAK (Holmes & Swetnam, 1996).

Host and non-host analysis using the black spruce residual chronology (Fig. 3.5) and the larch residual chronologies revealed five periods of growth anomalies that could be identified as possible outbreak periods (Fig. 3.6). These periods were also observed using a white cedar chronology (from sites BL1, LS and CM) and a *Fraxinus nigra* chronology from Tardif & Bergeron, (1997a) as non-host species (not presented). The most recent possible outbreak period started in 1975. Maximum peaks in percent of trees characterized by a reduction in radial growth were observed from 1978 to 1980 and 1983 to 1986 (Fig. 3.6). A possible outbreak period was also observed from 1950 to 1961 with its maximum intensity occurring between 1957 and 1958. More than 95% of the trees were affected during this period, also coinciding with the one detected using the light latewood criteria. A third possible outbreak period occurred around 1935 and ended in 1946. Another one was found from 1916 to 1930 for which the maximum intensity was from 1923 to 1925. The BL1 and LS sites were the sites most affected during this period. The longest and most important period occurred from 1895 to about 1912. Over 80% of all series would have been affected for a period of ten years. This period was also detected using the light latewood criteria. Note that the periods reported here as possible outbreak periods do not correlate with any decrease in black spruce radial growth residual chronology (Figure 3.5). Note also that we voluntary omitted discussion of the 1874-1884 period because of the low sample depth.

3.6.3 Response to climate

The climate analysis performed for the period 1915-1996 indicated that larch stands located on the shores of Lake Duparquet (BL1, BL2, BL3 and CC) and Lake Soisson (LS) responded more to temperature and precipitation than to drought and river discharge (first response function models adjusted r^2, Fig. 3.7). However, growth in the Matheson site (CM) responded better to precipitation and river discharge, as shown by the higher adjusted r^2 of the response function models when compared to temperature alone (Fig. 3.7).

In the current year of growth (year $_t$), climatic conditions in May were found to be significantly correlated to the drought index (Fig. 3.7, all six sites). This same relationship was observed for August precipitation. Also, BL3, LS and CM sites showed a negative relationship with the September river discharge. Observation of the climatic conditions in the previous year of growth suggested that for LS and CM sites, October precipitation in year $_{t-1}$ had a negative effect on growth of year $_t$ (Fig. 3.7).

The analysis conducted using the 1962-1996 interval indicated that during the last 34 years, larch growth was most strongly associated to precipitation and river discharge, although drought and temperature were also important factors associated to the variation in radial growth (Fig. 3.7, second response function models adjusted r^2). In the current year of growth (year $_t$), a positive relationship with the May drought index (BL2, BL3, CC, LS and CM sites) and a negative relationship with May river discharge (BL1, BL3 and LS) indicated a negative effect of flooding early in the growing season. This was shown on the CM site by a negative relationship with the March river discharge (see response function) and a change in the correlation sign. A positive relationship between the September drought index in year $_{t-1}$ and the larch radial growth in year $_t$ was also observed (BL1, BL2 and CM sites).

3.7 DISCUSSION

Larch growth in the wetland forests surrounding Lake Duparquet was influenced by a common factor. This was highlighted by a high mean sensitivity (similar to that obtained by Arquillère *et al.* (1990) and Jardon, Filion & Cloutier 1994b), a high variance in the first eigenvector and a high correlation among trees and sites. In contrast, the lower correlation and signal-to-noise ratio obtained in the CM site could be attributed to a slight effect of competition, notably for light (see Fritts (1976) for competition effects). In similar mixed larch and cedar stands of the lake Duparquet area, the tree cover is dense, with little light reaching the ground (Girardin, Tardif & Bergeron, 2001).

3.7.1 Sawfly outbreaks

Based on appearance of the light latewood rings, growth suppression periods and observations made by the Ministère de l'Énergie et des Ressources Québec (rapports annuels 1937-1982), we conclude that larch sawfly outbreaks occurred in the Lake Duparquet region for the periods 1895 to 1912, 1937 to 1942, and 1955 to 1962. We also suspect possible outbreaks in the early 1920s, at the end of the 1970s, and in the early 1980s. Although no light latewood ring were observed, we found a low frequency of missing rings in years 1979 and 1980. Field observations by the Ministère de l'Énergie et des Ressources (rapports annuels 1937-1982) reported high densities of the sawflies in 1979 and 1980. However, since spruce budworm outbreaks were occurring at the same time (1919-1929, 1930-1950 and 1970-1985; Morin, Laprise & Bergeron, 1992), it may be possible that factors other than the larch sawfly contributed to the growth suppression observed in these periods. Furthermore, although less literature exists on the subject, it has been reported that the larch casebearer *(Coleophora laricella)* could also be a serious defoliator in eastern North America (Rose & Lindquist, 1980; Johnston, 1990). Several severe outbreaks have caused extensive mortality in some areas of the United States (Wilson, 1977).

In our study, light latewood rings were not observed in all trees nor in all outbreak periods. Similar results were obtained by Filion & Cournoyer (1995). As was mentioned by these authors, the variation among trees and sites may reflect variation in the intensity of the defoliation. Furthermore, according to Liang, Filion & Cournoyer (1997), tree age and outbreak frequency could explain some variation found in the expression of this character in tree-rings.

Climate is an important factor in the dynamics of the larch sawfly, notably in relation to water level fluctuations. Lejeune (1955) reported that one or two weeks of high water levels in late summer induces heavy mortality of sawfly larvae populations. High water levels in spring (for several weeks) would also induce high mortality of the pupae population. An observation that suggests a relationship between the sawfly and water levels relates to the 1937 outbreak in the LS and CM sites, where radial growth was more affected than at the other, more flood-prone sites. The CM site was not subject to spring flooding because of its non-riparian position. Furthermore, these two sites were characterized by a lower water table than those at Lake Duparquet, and thus it is believed that they are subjected less to prolonged flooding. This situation is similar to the 1984-1989 outbreak studied by Tailleux & Cloutier (1993). These authors observed a strong decrease in growth of inland larch, in contrast to coastal site trees where no significant effect of the sawfly outbreak could be detected. Jardon, Filion & Cournoyer (1994b) also found similar results comparing mesic and hydric sites. In the present study, the same explanation can be extended to the observed delay of the 1955 outbreak, where the outbreaks recorded for the CM site occurred, on average, three years before sites located around Lake Duparquet (1958).

Further comparison between the outbreaks around Lake Duparquet with those of other studies mentioned previously (Arquillère *et al.* 1990; Jardon, Filion & Cournoyer, 1994a) revealed a similarity in the timing of the outbreaks from south to north. Although one of the outbreak on Lake Duparquet which was characterized by light latewood rings (1955-1962) was not observed in northern Québec, the two others (1895-1912 and 1937-1942) showed similar timing with those observed by Jardon, Filion & Cournoyer (1994a) for 1894-1906, 1907-1911 and 1938-1952 and Arquillère *et al.* (1990) for 1940-1942. In addition, the possible outbreak that may have occurred at the end of the 1970s and in the early 1980s coincides with the 1984-1989 outbreak reported by Jardon, Filion & Cournoyer (1994a).

3.7.2 Climate effects

In most of our sites, larch radial growth was highly influenced by hydric conditions in May, August, and September (first interval period). In all these cases, a negative relationship with growth was observed. It has previously been demonstrated that below average water table or reduced flooding may improve growth of wetland trees (Crawford, 1983; Lieffers & Rothwell, 1986; Macdonald & Lieffers, 1990). Hydric stress caused by prolonged flooding leads to a reduced recycling of organic matter since, in submerged soils, temperature is low, oxygen is absent and, thus, bacterial decomposition is retarded (Kozlowski, 1982; Tallis, 1983 and Macdonald & Lieffers, 1990). More specifically, Macdonald & Lieffers (1990) reported that in submerged conditions, there is a significant lack of nitrogen mineralization and depletion of mineral nutrition, which results in decreased carbon assimilation by larch. Moreover, oxygen deficiency in roots would decrease nutrient uptake in coniferous species, leading to lower plant productivity (Zinkal, Jeglum & Harvey, 1974). To overcome such anoxic problems, wetland trees have developed adventitious roots at the soil surface in order to maintain roots in the better aerated surface-peat layers (Rigg & Harrar, 1931; Denyer & Riley 1964; Gill, 1977). These adaptations serve as efficient exchange organs for the absorption of oxygen and for the diffusion of toxins out of the plant (ethanol, acetaldehyde and ethylene). However, Duncan (1954) reported that in an excessive drought, the alteration of these metabolic exchanges would cause growth reduction and sometimes death.

An interesting phenomenon observed in the Lake Duparquet area is the increase in larch mean sensitivity from about 1960. Year-to-year fluctuations in radial growth are more important, suggesting the existence of a stronger environmental signal. By comparing the 1915-1996 to the 1962-1996 response functions, we clearly observed the more important influence of hydric factors during spring on the radial growth of larch, notably from the May river discharge and the May drought index. This is in contrast to the non-riparian site (CM), where no relationship was found with the May river discharge.

3.8 CONCLUSION

This study has shown that sawfly outbreaks are an important component in growth trends in larch. Both flooding early in the growing season and hydric conditions at the end of the growing season also negatively influenced radial growth of larch in wetlands along the shore of Lake Duparquet. The hypothesized decrease in drought occurrence (Bergeron & Archambault, 1993; Bergeron & Flannigan, 1995) and increase in spring flooding (Tardif & Bergeron, 1997b) may also be responsible for the increase in larch mean sensitivity since the mid-twentieth century. This trend was not observed in our non-riparian site and thus may be related to an increase of inter-annual variability in Lake Duparquet water levels (Tardif & Bergeron, 1997b). Further studies on larch stand dynamics in relation to water levels will provide the information needed to confirm these hypotheses.

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Table 3.1 *Larix laricina* and *Picea mariana* residual chronology statistics.

	Larix laricina						*Picea mariana*
	BL1	BL2	BL3	CC	LS	CM	
Chronology length	1858-1998	1873-1998	1876-1996	1857-1996	1861-1998	1915-1998	1875-1998
Number of trees	19	15	24	20	19	18	26
Number of radii	36	31	48	40	39	36	50
Percentage of absent rings*	0.21	0.32	0.08	0.36	0.13	0.46	0.05
Mean ring width (mm)	1.59	1.41	1.39	1.03	1.30	1.20	0.54
Mean sensitivity	0.31	0.32	0.33	0.27	0.24	0.20	0.15
Standard-deviation	0.25	0.30	0.30	0.25	0.20	0.20	0.13
First order autorrelation	-0.05	0.11	0.08	0.01	-0.01	0.11	-0.06
First order autorrelation for standard chronologies	0.63	0.59	0.49	0.53	0.71	0.73	0.28
Common interval analysis	1935-1996	1935-1996	1935-1996	1935-1996	1935-1996	1935-1996	1935-1996
Number of trees	15	15	18	20	19	16	14
Number of radii	30	30	36	39	36	31	25
Signal to noise ratio	20.22	22.03	36.95	27.73	23.98	15.63	4.47
Variance in first PCA vector (%)	61.29	62.16	68.71	59.81	58.67	52.25	29.16
Intercore correlation	0.59	0.63	0.68	0.58	0.56	0.50	0.25
Intertree correlation	0.57	0.63	0.67	0.58	0.56	0.49	0.24
Intratree correlation	0.81	0.74	0.78	0.77	0.78	0.66	0.46

* Percentage of absent rings (1857-1998) are based on total number of cores and also account for incomplete rings

Table 3.2 Pearson correlation among sites residual chronologies for *Larix laricina* (BL1, BL2, BL3, CC, LS and CM) and *Picea mariana* (PMA) for the interval 1919 to 1996. Critical values: $r = 0.27$; $p<0.01$, $r = 0.21$; $p<0.05$.

	BL1	BL2	BL3	CC	LS	CM	PMA
BL1	1.00						
BL2	0.88	1.00					
BL3	0.83	0.91	1.00				
CC	0.85	0.87	0.79	1.00			
LS	0.83	0.79	0.73	0.79	1.00		
CM	0.52	0.49	0.43	0.50	0.70	1.00	
PMA	0.34	0.40	0.41	0.36	0.21	0.15	1.00

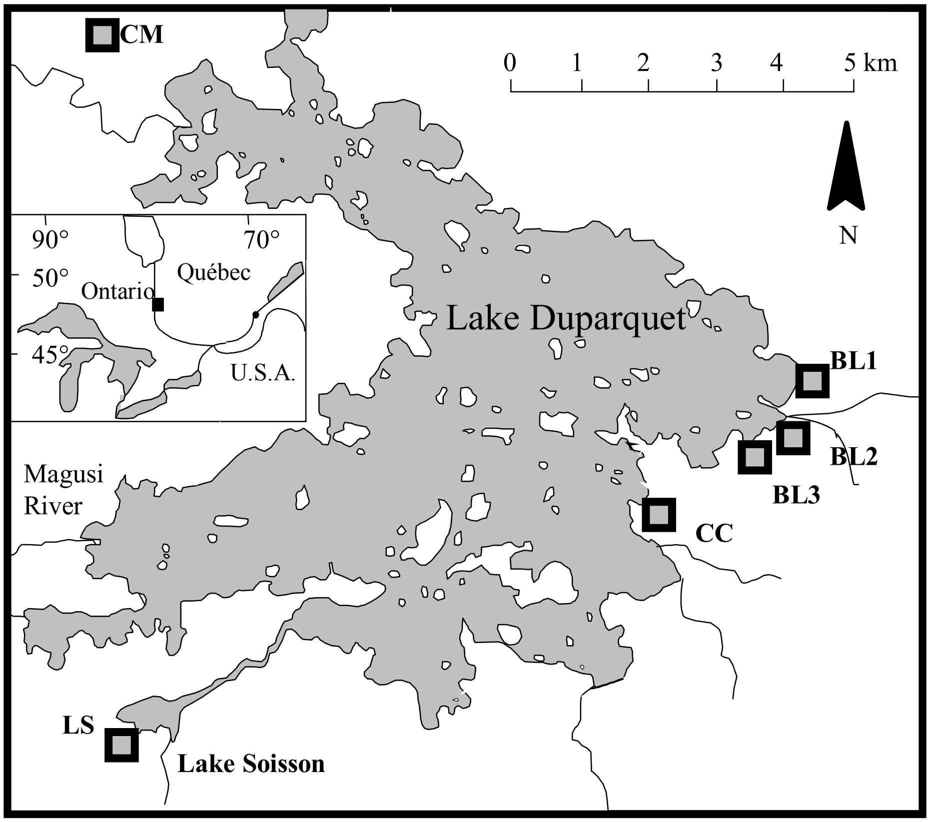

Figure 3.1 Map of the Lake Duparquet area showing the location of the six *Larix laricina* sites: BL1, BL2, BL3, CC, LS and CM.

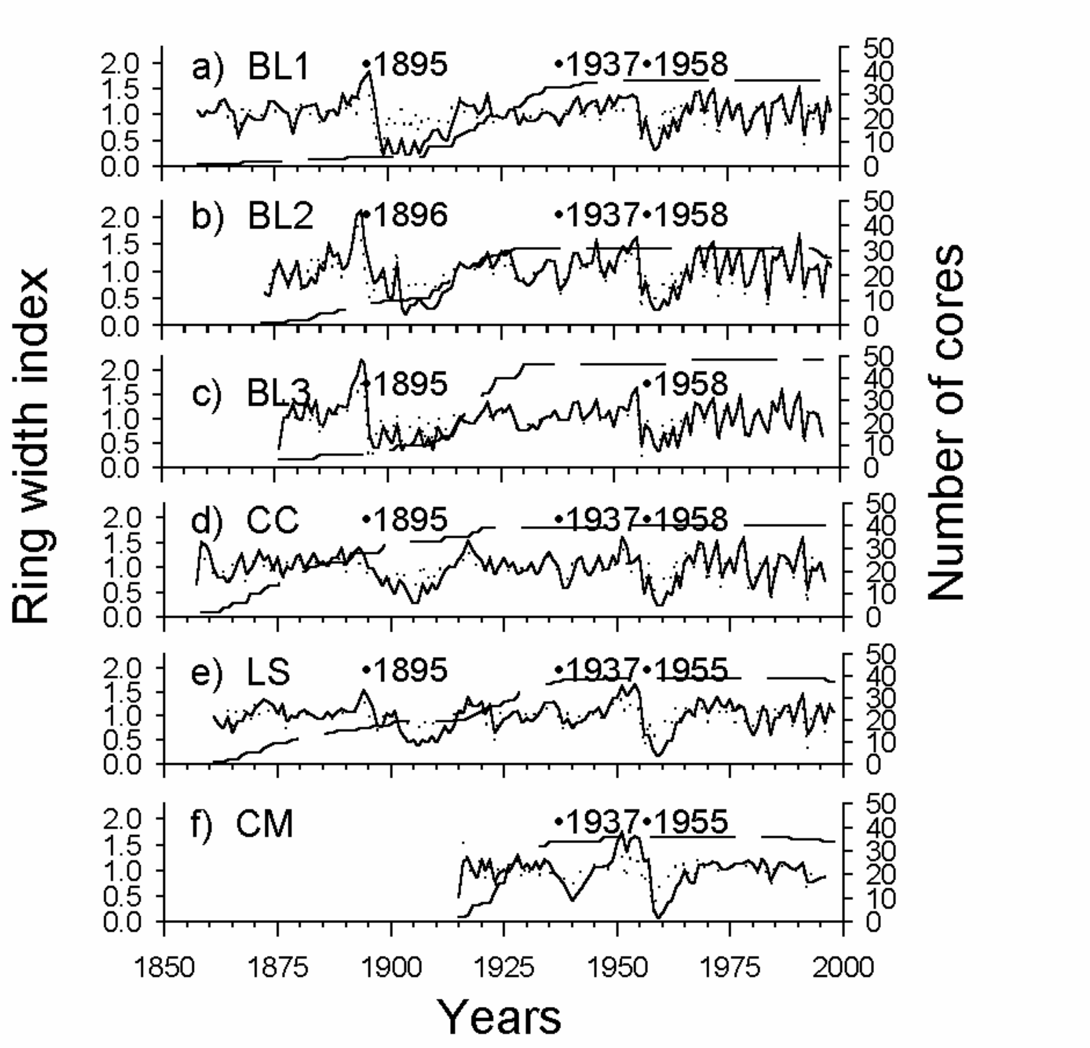

Figure 3.2 Standard (solid lines) and residual (dotted lines) chronologies for *Larix laricina* sites BL1, BL2, BL3, CC, LS and CM. Dates of the first appearance of a light latewood ring indicating sawfly outbreak periods are shown. The dashed lines represent sample depths.

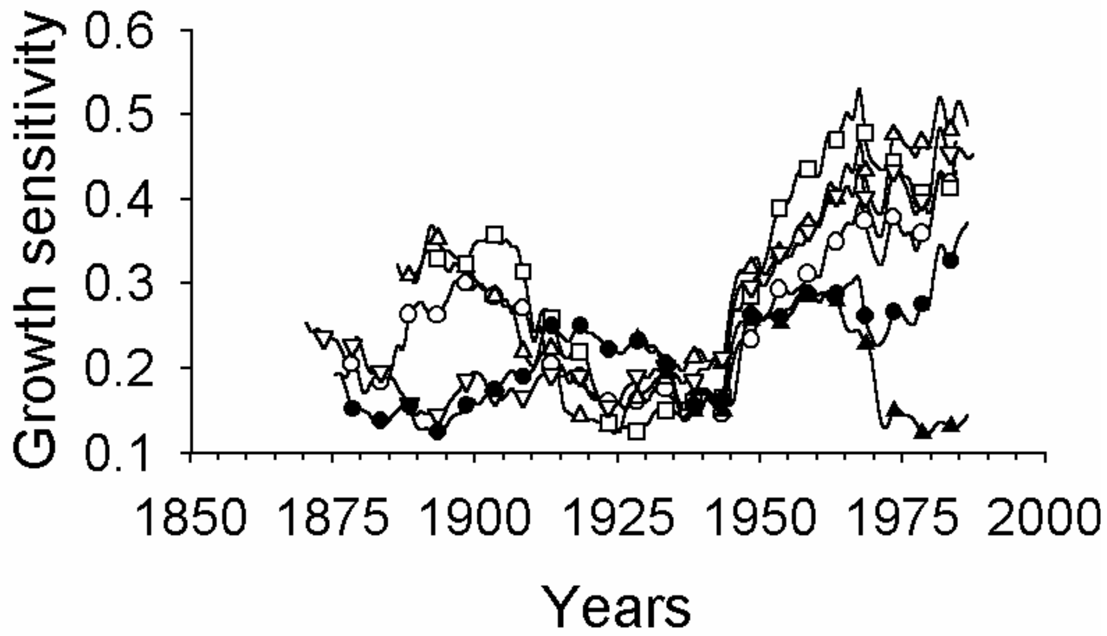

Figure 3.3 Mean sensitivity curves corresponding to the six sampled sites. Analysis was performed on residual chronologies using 25 years blocks lagged by one year. Sites shown are BL1 (empty circles), BL2 (empty up-triangles), BL3 (empty squares), CC (empty down-triangles), LS (filled circles) and CM (filled up-triangles).

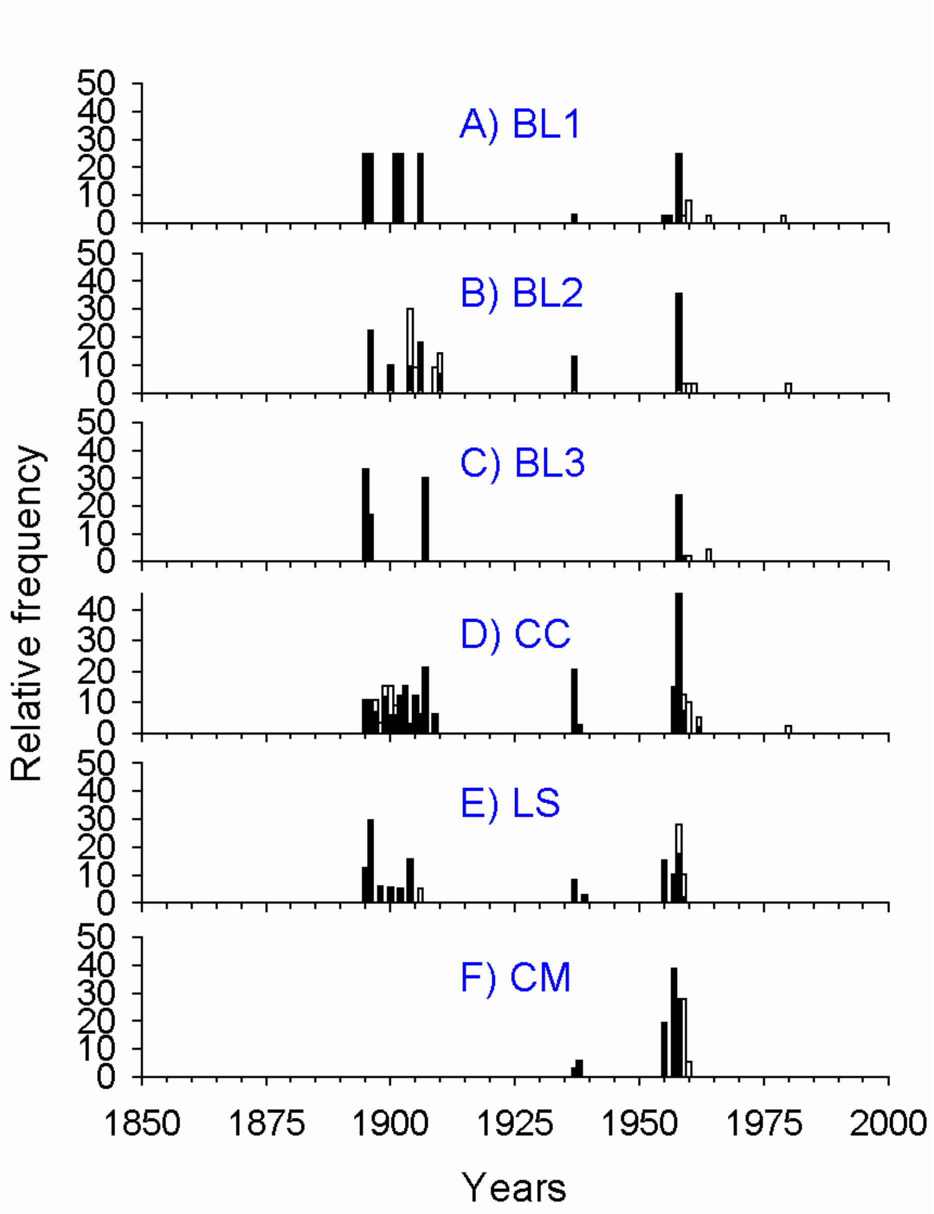

Figure 3.4 Stacked vertical bars chart showing relative frequencies of light latewood rings (filled bars) and missing rings (empty bars) for each sampled sites (A to F).

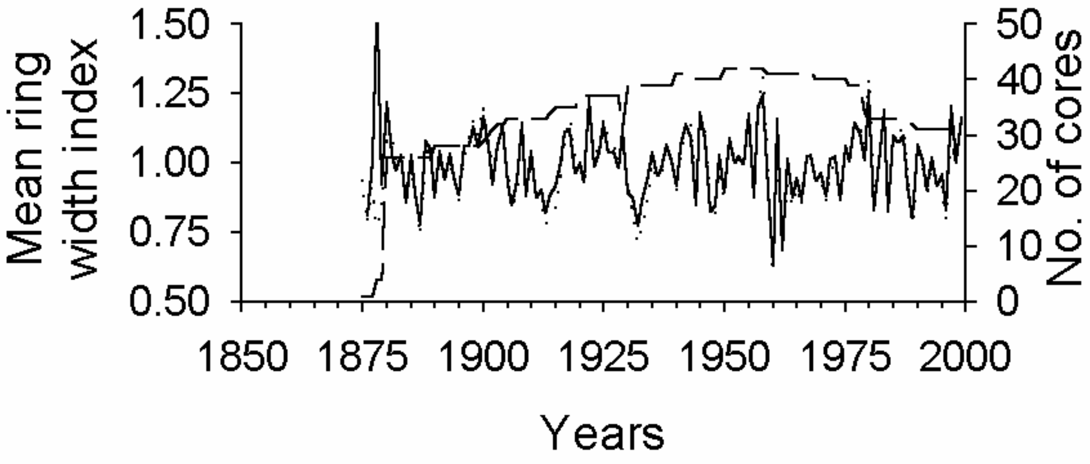

Figure 3.5 Standard (solid line) and residual (dotted line) chronologies of black spruce (*Picea mariana*). The dashed lines represent sample depths.

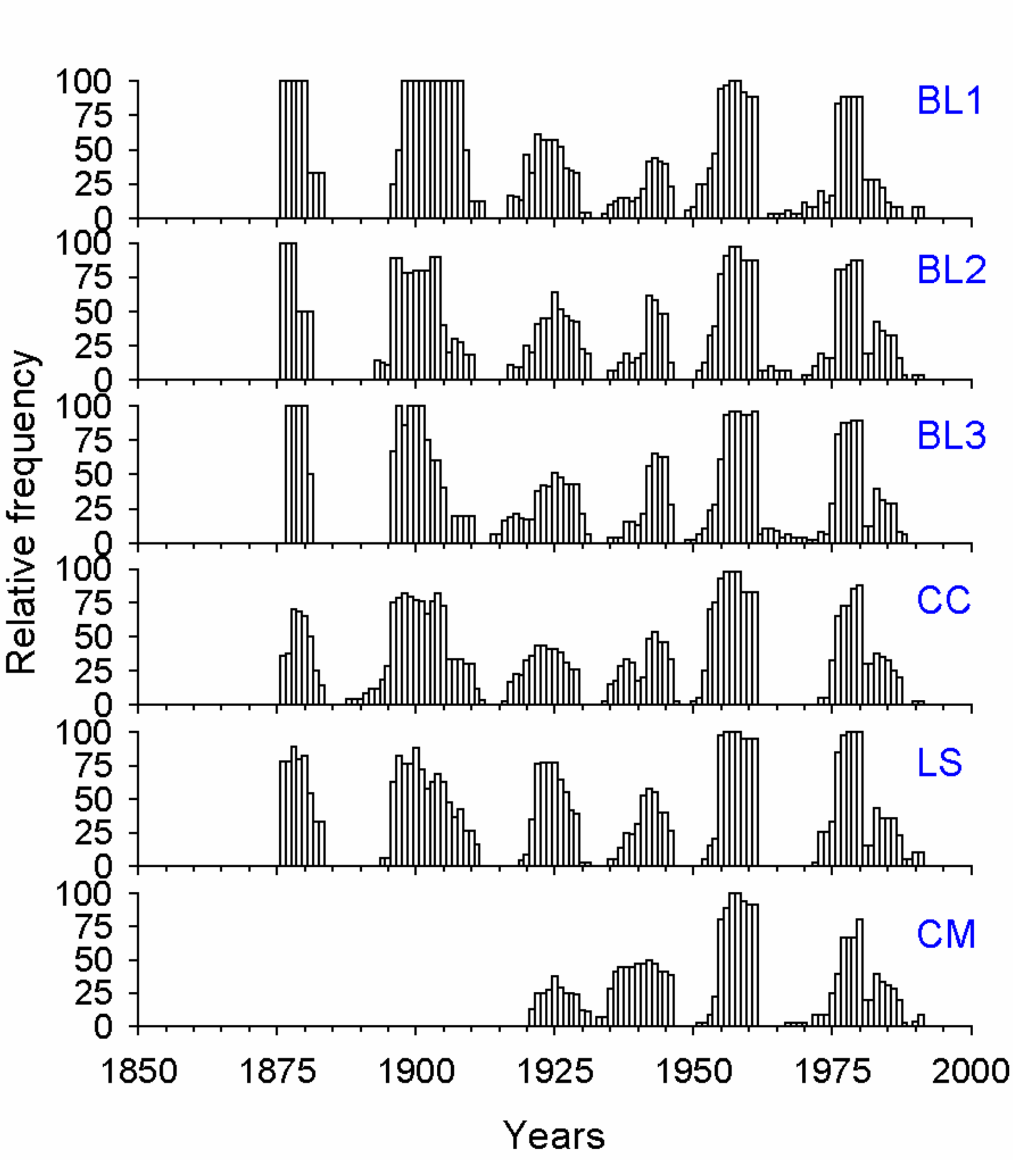

Figure 3.6 Vertical bars chart showing the percentage of larch series affected by a sawfly outbreak at a given year as identified by program OUTBREAK in the host and non-host analysis (*Picea mariana* as the non-host species).

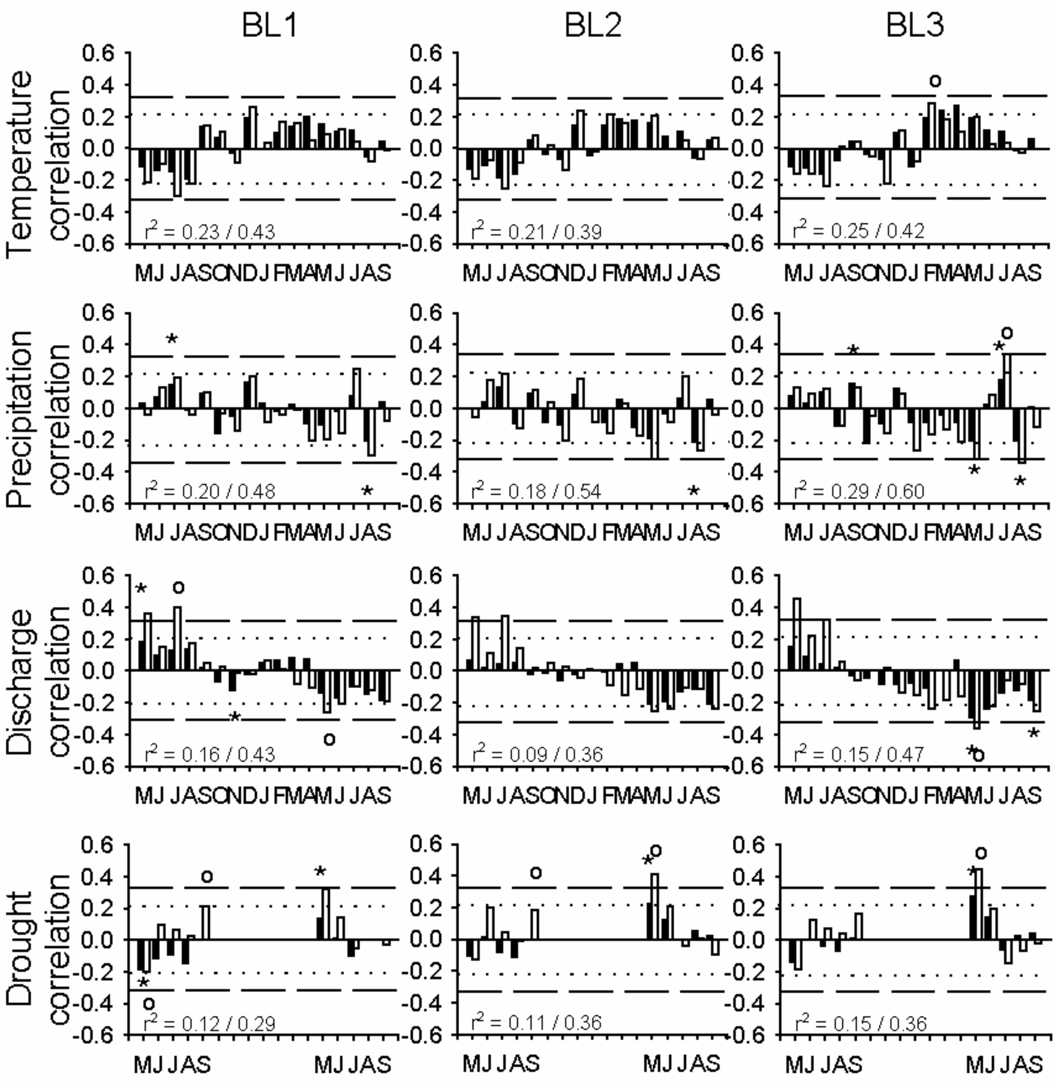

Figure 3.7a Pearson correlation coefficient between *Larix laricina* residual chronologies and temperature, precipitation, Harricana River discharge and drought index for the 1915 to 1996 (solid bars) and 1962 to 1996 intervals (empty bars). The sites shown are BL1, BL2 and BL3. The dotted lines and the dashed lines indicate a significant relationship at $p < 0.05$ (non-corrected significant level) for the 1915-1996 and 1962-1996 analyses, respectively. Significant variables ($p < 0.05$) tested separately with the response function analyses are shown by an asterisk (1915-1996) and a circle (1962-1996). First and second response function models r^2's are also indicated in order of analysis. Note that the increase of the r^2 from the first models to the second ones is only attributed to a decrease in the degrees of freedom (this is due to a decrease in the time interval studied).

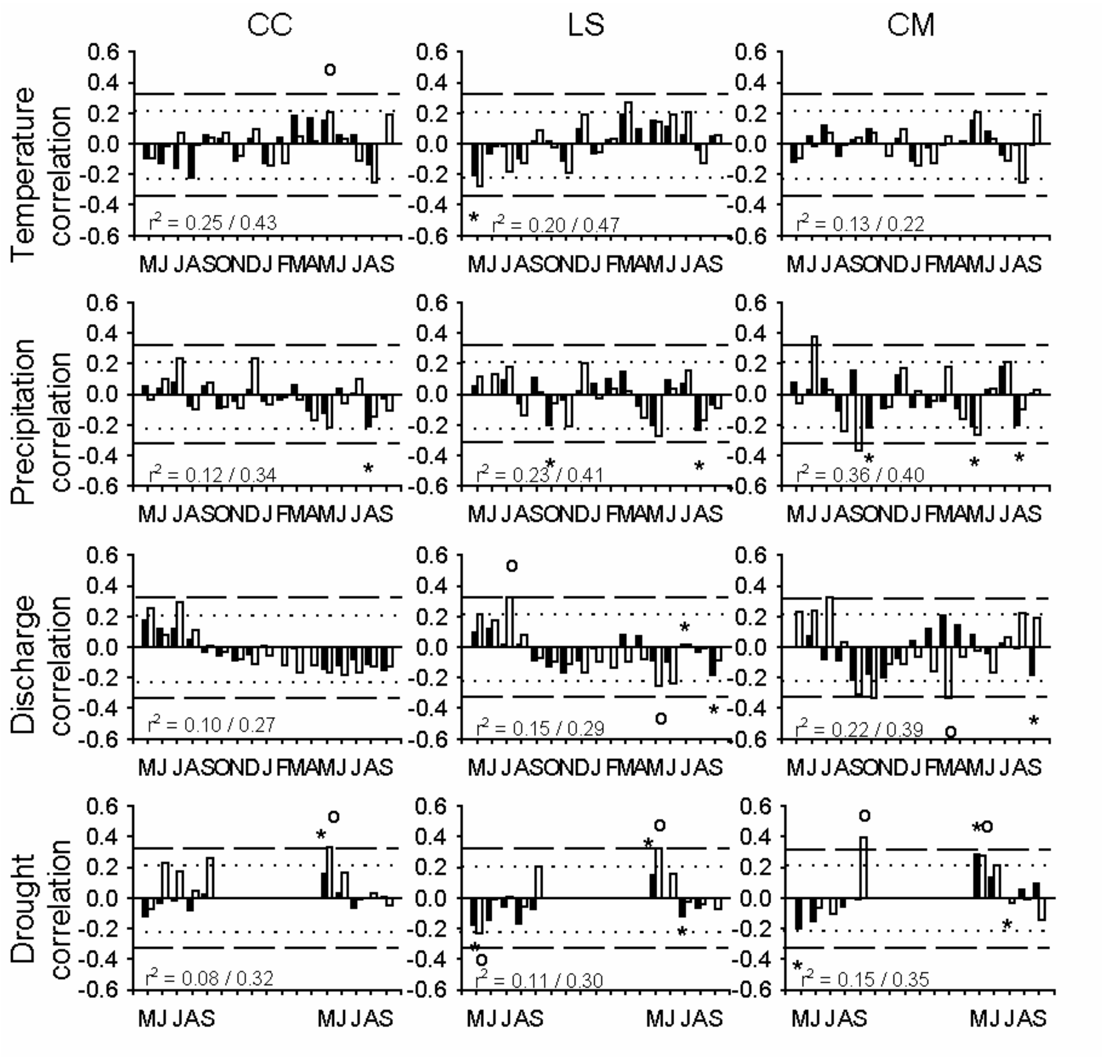

Figure 3.7b Pearson correlation coefficients between *Larix laricina* residual chronologies and temperature, precipitation, Harricana River discharge and drought index for the 1915 to 1996 (solid bars) and 1962 to 1996 intervals (empty bars). The sites shown are CC, LS and CM. The dotted lines and the dashed lines indicate a significant relationship at $p < 0.05$ (non-corrected significant level) for the 1915-1996 and 1962-1996 analyses, respectively. Significant variables ($p < 0.05$) tested separately with the response function analyses are shown by an asterisk (1915-1996) and a circle (1962-1996). First and second response function models r^2's are also indicated in order of analyses. Note that the increase of the r^2 from the first models to the second ones is only attributed to a decrease in the degrees of freedom (this is due to a decrease in the time interval studied).

ARTICLE III: DYNAMIQUE DES PEUPLEMENTS DE MÉLÈZE EN RELATION AVEC LES ÉPIDÉMIES DE LA TENTHRÈDE DU MÉLÈZE

Girardin, M.P., Tardif, J. et Bergeron, Y. soumis. Dynamics of eastern larch stands in relation to larch sawfly outbreaks in the Northern Clay Belt of Quebec. Canadian Journal of Forest Research 0: 00-00.

4.1 ABSTRACT

Climate change, fires and insects outbreaks can affect larch (*Larix laricina* (Du Roi) K. Koch) stand dynamics. In order to determine which of these factors had the greatest influence on stand dynamics, we sampled four wetlands dominated by larch near Lake Duparquet in northwestern Quebec. The ages of saplings, seedlings and trees were determined in 12-400m^2 plots. Increment cores were taken at breast height to determine past disturbance episodes related, among other factors, to larch sawfly (*Pristiphora erichsonii*) activity. Stem analysis was also conducted using tamarack and black spruce for identification of post-disturbance releases in height growth. At the multiple stand level, a discontinuous age-class distribution formed by four recruitment cohorts was observed. Analyses at stand and plot levels tend to show age structures formed by one or two recruitment cohorts. Analyses of the disturbance events identified using tree-ring and stem analysis related larch recruitment with the 1895-1912 and 1955-1962 larch sawfly outbreak episodes. Our results suggest that the larch sawfly might create canopy gaps within the stands instead of inducing tree mortality in the entire larch population. Our results also suggest that periodic spring floods contribute to maintain larch in the lowest part of the elevation gradient by inhibiting establishment of *Picea mariana* and *Thuja occidentalis* which are less tolerant to flooding. However, in the most elevated part of this gradient, larch is presently being excluded because of its inability to compete with the other two tree species. Further studies should be conducted in these stands to determine whether the gaps created by sawfly outbreaks are associated to factors such as tree age, tree density, topography, water table, community type or needle chemistry, as well as to determine their relative size.

Key words: *Larix laricina*; boreal forest; climate; flood exposure; dendrochronology; regeneration; Lake Duparquet (Quebec, Canada); *Pristiphora erichsonii*; *Thuja occidentalis*; *Picea mariana*.

4.2 RÉSUMÉ

Quatre tourbières entourant le Lac Duparquet au Nord-Ouest Québec, ont été échantillonnées avec l'objectif d'identifier les facteurs (changements climatiques, feux et/ou épidémies d'insectes) influençant le plus fortement la dynamique des peuplements de mélèze laricin (*Larix laricina* (Du Roi) K. Koch). L'âge des semis, des gaulis et des arbres a été estimé dans 12 quadrats de 400m^2. Des carottes ont été récoltées à 1.3 m du sol afin d'identifier les périodes de perturbation associées à la tenthrède du mélèze (*Pristiphora erichsonii*). Une analyse de tiges a également été réalisée sur le mélèze et l'épinette noire afin d'identifier les périodes de reprise de croissance en hauteur associées aux perturbations. À l'échelle de tous les peuplements, une distribution discontinue formée de quatre cohortes de recrutement a été observée. À l'échelle des sites et des quadrats, les structures d'âge sont plutôt formées d'une ou de deux cohortes de recrutement. L'analyse des perturbations observées dans la croissance radiale et dans l'analyse de tige a mis en relation les périodes de recrutement du mélèze pour le 20^e siècle avec les épidémies de la tenthrède de 1895-1912 et 1955-1962. Nos résultats suggèrent que la tenthrède peut induire la formation de trouées à l'intérieur des peuplements plutôt que d'induire la mortalité des arbres à l'échelle de la population. Nos résultats suggèrent également que les inondations printanières périodiques peuvent contribuer au maintien des mélèzes établis dans la partie la plus basse du gradient d'élévation, en empêchant l'établissement de *Picea mariana* et de *Thuja occidentalis*, qui sont moins tolérants aux inondations. Toutefois, dans la partie la plus élevée du gradient d'élévation, le mélèze serait éventuellement exclus en raison de son incapacité à compétitionner avec les deux autres espèces d'arbres. Des études plus approfondies devraient être réalisées dans ces peuplements afin de déterminer si la formation des trouées par les épidémies de la tenthrède est reliée à des facteurs tel que l'âge des arbres, la topographie, la densité des arbres, la nappe phréatique, le type de communauté végétale et la composition chimique des aiguilles, et aussi afin de déterminer la taille des trouées.

Mots-clés: *Larix laricina*; forêt boréale; climat; exposition aux inondations; dendrochronologie; régénération; Lac Duparquet (Québec, Canada); *Pristiphora erichsonii*; *Thuja occidentalis*; *Picea mariana*.

4.3 INTRODUCTION

Eastern larch (*Larix laricina* (Du Roi) K. Koch) is a tree species characteristic of many North American wetlands (Nairn et al. 1962; Schooley and Pardy 1981; Bergeron et al. 1982; Martineau 1985; Johnston 1990). Because it can tolerate high soil moisture and acidity, as well as low soil temperature, larch is generally most abundant in wetlands although scattered trees may occur in surrounding uplands (Bergeron et al. 1982; Johnston 1990; Girardin et. al. 2001*a*). Larch forms pure stands in many parts of the boreal zone but also forms mixed stands with eastern white cedar and black spruce (Johnston 1990; Girardin et al. 2001*a*). As with most stress-tolerant species, larch is not a good competitor and may be successionally replaced on sites where it grows with more shade tolerant species (Johnston 1990; Jardon 1994*a*). Thus, like many tree species, disturbance is important for the persistence of larch on most sites. Although fire is an important agent of disturbance controlling the structure and dynamics of many forests in the boreal zone, on wetland sites, where larch is most often abundant, it is likely to be less important (Curtis 1959; Rowe and Scotter 1973; Vitt and Bayley 1984; Johnston 1990). Disturbances caused by insect outbreaks or changes to site hydrology may therefore have more important effects on the dynamics of larch stands (Harper 1913; Lejeune 1955; Denyer and Riley 1964; Rose and Lindquist 1980; Bonkoungou et al. 1983; Martineau 1985).

In the late 19th and the early 20th century, larch forests were seriously threatened by a severe outbreak of the larch sawfly (*Pristiphora erichsonii*) that destroyed most mature stands in eastern North America (Muldrew 1955; Ives and Nairn 1966; Turnock 1972; Marie-Victorin 1995). In the late 20th century, numerous dendrochronological studies have been conducted to reconstruct past outbreaks (Arquillère et al. 1990; Jardon et al. 1994*a*; 1994*b*; Case 2000; Girardin et al. 2001*b*). Although sawfly populations are currently at endemic levels, outbreaks of this insect remain a potential threat to these forests (Arquillère et al. 1990; Cloutier and Filion 1991; Tailleux and Cloutier 1993; Jardon et al. 1994*a*; 1994*b*; Girardin et al. 2001*b*). While relationships between larch growth reductions, increasing mortality rates, and the occurrence of larch sawfly outbreaks are well known (Harper 1913; Beckwith and Drooz 1956; Ives and Nairn 1966), few studies have examined the impacts of sawfly outbreaks on stand dynamics (Turnock 1954; Bonkoungou et al. 1983). This lack of information is even more substantial when the dynamics of wetland stands of the Canadian boreal forest is considered.

Recent climate changes may also influence larch stand dynamics (Bonkoungou et al. 1983; Morin and Payette 1984). In North America, studies on forest dynamics and of various tree-ring data have provided considerable information about recent and past global climate changes (Jacoby and D'Arrigo 1989; Bergeron and Archambault 1993; Tardif and Bergeron 1997*a*; 1997*b*). Several authors report a trend of earlier spring snow melts and an increase in both temperature (about 0.5 to 0.7°C) and precipitation (greater than 17% since the 1950s) since the end of the Little Ice Age (~1850) (Bradley et al. 1987; Jacoby and D'Arrigo 1989; Jones and Briffa 1992; Karl et al. 1993; Groisman and Easterling 1994; Groisman et al. 1994; Brown and Goodison 1996). An increase in spring flood severity since the end of the "Little Ice Age" has also been observed in the boreal forest of southwestern Quebec (Tardif and Bergeron 1997*b*; 1999).

The objective of this study was to document the age structure and elucidate the dynamics of four larch stands in Quebec's southwestern boreal forest. We mainly wanted to assess the impacts of larch sawfly outbreaks and recent increases in spring flood severity on larch stand dynamics, notably on larch recruitment and age distribution. A previous study of larch radial growth in the Lake Duparquet area of northwestern Quebec indicated two severe larch sawfly outbreaks during the last hundred years (1895-1912 and 1955-1962)(Girardin et al. 2001*b*). These were inferred from the occurrences in larch of characteristic rings associated with larch sawfly outbreaks (missing and light latewood rings (Harper 1913). Growth comparison with a non-host species also indicated possibilities of less severe outbreaks for the early-1920s, late-1930s and late-1970s (Girardin et al. 2001*b*). However, only a few characteristic rings were observed for these periods, which made it difficult to confirm the evidences of an outbreak. Also, in the same study, an increase in the mean sensitivity of larch growth (since about 1960) was observed and might be related to an increase in the inter-annual variability of the flood level (Tardif and Bergeron 1997*b*; 1999). Therefore, we expected to find larch recruitment cohorts caused by the severe larch sawfly outbreaks of the early 1900s and mid-1950s. We also expected limited larch recruitment at relatively low elevations due to an increasing severity of spring flood~~s~~.

4.4 STUDY AREA

The study area is located at Lake Duparquet, 700 km north of Montreal in the Abitibi region of southwestern Quebec (48°28’N, 79°17’O, Fig. 4.1). Lake Duparquet covers a 50-km^2 area and drains northward from Duparquet River towards James Bay. Lake Duparquet is also one of the few lakes in the region that has not been regulated, which makes it a unique study site (Tardif and Bergeron 1997*b*).

The study area is part of the Northern Clay Belt of Quebec and Ontario, which resulted from the maximum extension of the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Mean annual temperature is 0.8°C and total precipitation varies from 800 to 900 mm (Environment Canada 1993). The mean frost-free period is 64 days but frost can occur at any time of the year (Anon.1982).

4.4.1 Sampling design

In the summer of 1999, three stands located on the shore of Lake Duparquet and one stand beside the Magusi river were sampled (Fig. 4.1). These stands were identified as BL1, BL2, CC and MAG. In each of them, 400m^2 plots (20m x 20m) were established along a transect perpendicular to the water bodies. We assumed that this placement of sample plots corresponded to a gradient in the length and severity of spring flooding (Girardin et al. 2001*b*). A total of twelve 400m^2 plots were established in the four stands.

In the first stand (BL1), four plots (BL1a, -b, -c, and -d) were sampled. These plots covered the inferior limit of larch distribution to the superior limit (Fig. 4.1). The second stand (BL2), which was characterised by the presence of both a lake and a river gradient, had one plot beside the lake (BL2a), one beside the river (BL2c) and one at the most elevated part of the gradient (BL2b). The third stand had one plot beside the lake (CCa), one in mid part of the wetland (CCb) and one at the elevated part (CCc). The forth stand (MAG) had only two plots, one located at the inferior limit (MAGa) and one at the superior limit of larch distribution (MAGb).

4.4.2 Vegetation description

Among the twelve sampled plots, six were considered pure larch stands (BL2a-b-c and CCa-b-c). In these, the understory vegetation was dominated by *Kalmia angustifolia*, *Andromeda glaucophylla*, *Myrica gale*, *Ledum groenlandicum*, *Cassandra calyculata*, *Smilacina trifolia* and a large proportion of the ground surface was covered by *Sphagnum* spp. Three plots (BL1a-b-c) were mixed larch and black spruce (*Picea mariana* Mill.) stands. In these, the understory was dominated by *Alnus rugosa*, *Ledum groenlandicum*, *Myrica gale* and *Betula pumila*, but the *Sphagnum* spp. cover was relatively low. Two other plots (BL1d and MAGa-b) were dominated by larch, black spruce and white cedar. The understory was mostly dominated by *Alnus rugosa*, *Ledum groenlandicum*, *Carex trisperma* and *Carex* spp. and *Sphagnum* spp. (a large percentage of the surface). Plots BL1d and MAGb where dominated by white cedar, although BL1d had relatively open tree canopy. For more details on stand vegetation, see Girardin et al. (2001*a*).

4.5 METHODS

4.5.1 Sampling

Diameter at breast height (DBH; 1.0 cm accuracy) and height (0.1 m accuracy) of all tree stems (> 5 cm DBH; live and recently dead [bark and branches well preserved]) were measured in each plot with a DBH measuring tape and a clinometer. Larch saplings (< 5 cm DBH) and seedlings (< 100 cm tall) diameter and height were also measured, whereas for cedar and black spruce, only height (1.0 cm class) was measured. To determine the age of all trees (larch, spruce and cedar), an increment core was taken as close as possible to the ground level (root collar) with a Pressler increment borer. If the wood was rotten at this height, a core was taken higher on the stem and its height was measured to allow for age correction by regression analysis (Bergeron and Gagnon 1987; Tardif and Bergeron 1999). All larch seedlings and saplings were collected for age determination. For black spruce and white cedar a subset was collected (at least ten individuals per 10 cm height class (0 to 1 m) when possible), as the two species were present at high densities.

In each plot, two to three cores were taken from dominant larch trees at DBH for construction of tree-ring chronologies that were used to identify stand disturbances (*sensu* Lorimer 1980; Holmes 1999; Tardif and Bergeron 1999). Furthermore, three dominant larch trees and three black spruce trees were felled and cross sections were taken at 0.0 m from ground, 0.5m, and at each following metre to determine height growth releases following stand disturbances (Zarnovican 1985; Bergeron 2000).

4.5.2 Age determination and development of larch chronologies

The cores and the cross sections (ground level and higher) from the saplings and the sampled trees were prepared following the standard procedures proposed by Stokes and Smiley (1968) and Swetnam et al. (1985). For these samples, visual cross-dating of tree ring growth patterns was done using the method described by Yamaguchi (1991). In addition, the cores taken at DBH were measured using a Velmex Uni Slide micrometer (0.001mm accuracy) and the cross-dating was validated using the COFECHA program (Holmes 1983).

For larch seedlings < 10 cm in height, age determination was made by counting all terminal bud scars from the apex to the root collar (Menes and Mohammed 1995). A number of larch trees were cut below the moss surface (~10 cm) to assess the possible underestimation of tree age compared with the samples collected at the moss level (Bergeron 2000). Also, to assess possible age underestimation of larch seedlings and saplings resulting from the cross-dating, a number of larch seedlings 10-20 cm tall were dated from both ring count and terminal bud scars count. From the results of these verifications, we estimated that the larch age determination error varied from 0 to 4 years. This process was repeated with black spruce and white cedar, where age underestimations were about seven and four years respectively. To account for possible dating errors, the age structures of larch are presented in frequency classes of 5-yr intervals (Bergeron and Gagnon 1987; Bergeron and Brisson 1990). For black spruce and white cedar, frequency classes of 10-yr intervals were used.

A multiple age-DBH-height regression analysis was used to estimate the age of recently dead trees and live larch trees with decayed centres. The regression was computed using the stems (seedlings, saplings and live trees) that could be aged via cross-dating and terminal bud scar counts. The large percentage of the variance explained by the regression model (adj R^2: 0.863, $P<0.001$, $n = 537$ individuals, $y_{(age)} = 10.834$ SQRT (DBH) + 24.352 SQRT (height) – 6.173) justified its use in age determination.

For some trees where the collection of cores at the ground level was impossible due to rotten wood, cores were taken higher on the trunk. For these, another regression model was used as a correction factor to adjust for the height of the cores (adj R^2: 0.838, $P<0.001$, $n =$ 537 individuals, $y_{(age)} = 32.553$ SQRT (height) – 6.157).

To estimate the age of the white cedar and black spruce stems (seedlings, saplings and trees) that were not cored, the process described for larch was repeated using an age-height regression model (white cedar: adj R^2: 0.596, $P<0.001$, $n = 88$ individuals, $y_{(age)} =$ 57.238 SQRT (height) –17.279; black spruce: adj R^2: 0.609, $P<0.001$, $n = 180$ individuals, $y_{(age)} = 31.796$ SQRT (height) + 2.615). For the cores collected higher on the trunk, the same equations were use to adjust for the height.

4.5.3 Data analysis

Three scales of analysis were conducted in this study, multiple stands, stand and plot levels, using age frequency distributions. The ages of both live and recently dead trees were included in the analyses. In all scales of analysis, stand dynamics were also studied using cumulative age distributions (Zar 1999). Similarities in age class distribution among plots were examined using complete clustering analysis (farthest neighbour) computed from the Chi-square distance matrix. This method of cluster analysis offers the advantage of excluding every pair of zeros in the quantification of the object descriptor relationships (Legendre and Legendre 1998). Following this analysis, the plots showing similarities in age frequency distributions were grouped together for further analyses. Throughout this paper, these groups of plots are identified as cluster types I, II, III and IV.

To examine the effects of disturbances on stand age structure, larch age frequency distributions were compared with the larch radial growth patterns. This helps to assess whether initial stem recruitment was related to past disturbance events, which were observed as tree growth releases and suppressions (*sensu* Lorimer 1980; Glitzenstein et al. 1986; Tardif and Bergeron 1999). After measuring and cross-dating larch cores taken at DBH height, a spline function (giving a 50% frequency response of 45 years) was applied to each measured series to produce standardized tree-ring series. The spline function mainly removes age/size-related trends in tree growth (Cook and Peters 1981). The standardized tree-ring series were grouped together based on the results of the cluster analysis conducted on the larch age frequency distribution. In order to combine the dendrochronological data for each cluster type, biweight means of the standard series were computed with ARSTAN (Holmes 1983; Cook 1985) to produce the standard chronologies. Therefore, one standard chronology will be shown per cluster type.

The growth release and the suppression periods were recorded for each measured tree-ring series following Holmes (1999). We considered trees to exhibit a release at a given year when ring width was at least 50% greater than the mean ring width of the 10 previous years (program parameters: jolt release factor of 1.5 and 10-year moving average (Holmes 1999)). This increase in ring width also had to be maintained for ten years. We considered trees to exhibit suppression at a given year when ring width was at least 50% lower than the mean ring width of the 10 previous years (program parameters: jolt suppression factor of 1.5 and 10-year moving average). This reduction in ring width also had to be maintained for ten years. The percentages of trees in growth releases and suppressions are presented for each cluster type. These analyses were conducted with the program JOLTS (Holmes 1999) on the raw measurement series.

4.6 RESULTS

As indicated by the R^2 of the regression models (Fig. 4.2), a high goodness of fit was observed between the square root transformed diameter and the age of larch ($p<0.01$)(Fig.

4.2a-b). Relationships between larch height and age, as well as larch height and radial growth, were also strong ($p<0.01$)(Fig. 4.2b,c).

4.6.1 Multiple stands and stand levels analyses

When data from all stands were combined, we found a wide distribution in the ages of larch trees with three distinct pulses of larch recruitment (Fig. 4.3). The first larch tree established in 1805. Afterward, relatively constant recruitment occurred from 1850 to 1885, ending with a decrease in ~1885. During the twentieth century, two episodes of moderate recruitment occurred from 1890 to 1915 and 1935 to 1950. Many seedlings were recruited from 1990 to 1999. This discontinuous age distribution is also illustrated by three breaks in the cumulative distribution curve (Fig. 4.3).

The frequency distribution of the tree ages estimated from regression analyses can also be observed in Figure 4.3. The distribution of these estimates is similar to the age frequency distribution of trees cored at ground level. Furthermore, the cross-dating of six dead trees from sites BL1 and CC indicated that these trees were killed in 1992 (N=2) and 1996 (N=3). One tree was killed in 1987. All of these trees were established around 1900.

A discontinuous larch age frequency distribution was also observed at the stand level. Among the four stands, two different types of age-distributions were observed, each one being characterised by two recruitment peaks (Fig. 4.4). The first was observed in stands BL1 and CC and was characterised by recruitment peaks for the periods 1840 to 1885 (mainly on CC) and 1935 to 1965 (Fig. 4.4). The first period was shorter in BL1 (1865 to 1885). Peaks were also found in BL1 from 1970 to 1975, and 1905 to 1910. In both stands, seedling recruitment was high between 1990 and 1999. The second type of age distribution was observed in stands BL2 and MAG and was characterised by a recruitment peak during 1860 to 1935. In both stands, the main recruitment peak was from 1880 to 1915. A recruitment peak was also found in both stands between 1975 and 1980.

4.6.2 Plot level analysis

Analysis of the plot data (Table 4.1) identified BL2b, CCb, BL1c, MAGb and BL1b as the plots with the highest tree densities; plots BL2b, CCb and BL1d had the highest larch density. However, the highest larch basal area was observed in plots BL2b, BL2c and CCa. High spruce density was found in BL1c, whereas high cedar densities were found in MAGb and BL1d. Larch tree density was low in these three plots.

The similarities between the plots were further examined using a cluster analysis conducted on the LOG_{10} transformed age-class frequency data of all twelve plots (Fig. 4.5). From this analysis, four larch age structures were observed. According to the results, larch age distribution is not related to position in the flood severity gradient (see Fig. 4.1). The twelve plots were grouped into four sets of data representing each type of age structure: Type I (BL1a-BL1b-CCb); Type II (BL1c-BL2b-MAGa); Type III (BL2c-CCa-CCc) and Type IV (BL1d-BL2a-MAGb) (Fig. 4.6 to 4.9).

One main cohort was observed in cluster Type I (BL1a-BL1b-CCb): 1935-1965 (Fig. 4.6a). Dates of major larch sawfly outbreaks during the 20th century at Lake Duparquet (from Girardin et al. 2001*b*) are also shown with the larch standard chronology (Fig 4.6b). The maximum recruitment peak occurred during 1940-1950, before the 1955-1960 outbreak. A second cohort was observed in BL1a and BL1b during 1910-1925, just after the 1895-1912 outbreak. In all three plots, the oldest tree established itself around 1890-1900. In addition, there was abundant recent recruitment in the CCb plot. The larch standard chronology (biweight mean of the four plots standard chronologies; see Table 4.2 for tree-ring statistics), indicated a significant period of growth suppression due to the larch sawfly outbreak that occurred from 1955-1965. This pattern of growth suppression was also observed in the growth suppression and release analyses where significant reductions in growth occurred during 1955-1962 (Fig. 4.6c). A much smaller decrease in growth was also observed from 1928 to 1932.

In contrast to cluster Type I, cluster Type II (BL1c-BL2b-MAGa) was characterised by an older tree cover, whose establishment mainly dated from 1870 to 1920 (Fig. 4.7a). For

BL2b, this period extended from 1870 to 1960. The oldest tree was found in BL1c (1805); whereas the oldest trees in BL2b and MAGa dated from 1865. Maximum recruitment occurred between 1875-1885 and 1905-1910 in BL1c, and 1900 to 1910 in BL2b and MAGb. Recruitment was generally low in MAGa with episodes of low recruitment occurring during the periods 1975-1990 and 1945-1950. Although the patterns of growth suppression during the late 1920s and late 1950s in these plots (Fig. 4.7b) were similar to those observed in cluster Type I, the late-1930s growth release was not observed in cluster Type II (Fig. 4.7c). However, an important growth release was observed from 1912 to the early 1920s.

Trees in cluster Type III (BL2c-CCa-CCc) dated mainly from the 1840s to 1920s, most of the stems being dated many years before the 1895-1912 outbreak (Fig. 4.8a). Maximum recruitment occurred in the 1840s, early 1850s to 1860s and 1880-1895. Plot CCa also had episodes of relatively low recruitment from 1945 to 1960, just before the 1955 sawfly outbreak (Fig. 4.8b). Observation of the measured tree-ring series (Fig. 4.8b) and analysis of the growth suppressions and releases (Fig. 4.8c) revealed that the recruitment peak observed from 1870 to 1875 in CCa (Fig. 4.8a) coincides with a growth release in 1873. Also, although the growth suppression observed in the late 1950s (Fig. 4.8c) was similar to the one observed in the other plot types (Fig 4.6c, 7c), little recruitment occurred, most of it being in CCa (fig 4.8a).

In cluster Type IV, we observed a recruitment episode from 1890 to 1930 in BL2a and MAGb and another from 1940 to 1970 in BL2a and BL1d (Fig. 4.9a). Most of the recruitment occurred after the 1895-1912 sawfly outbreak (Fig. 4.9b). The recruitment episode in the mid-20th century also coincides with a sawfly outbreak (1955-1962). In BL2a most recruitment occurred before the outbreak, whereas in BL1d it occurred afterwards (Fig. 4.9a). In all three plots, recruitment was high during the last two decades. Analysis of growth trends shows that the trees were seriously affected by the 1895-1912 and 1955-1962 sawfly outbreaks (Fig. 4.9b). This was confirmed by the growth release and suppression analyses, where growth suppression during the early 1900s was longer than in any other plot types (Fig. 4.9c).

Tree crown openings resulting from the early and mid century larch sawfly outbreaks can be observed from radial and height growth patterns. Analysis of the trends observed from the stem analysis indicates a height growth release in all plot types from 1905 to 1915, after the 1895-1912 sawfly outbreak (Fig. 4.6d, 4.7d, 4.8d and 4.9d). In most cases, we observed height growth of more than 10 metres in less than 50 years during 1900 to 1950. This is in contrast to the initial growth trend (period of 1850 to 1900), which was less than 2 metres in 50 years. The rates of height growth for trees that became established from 1900 to 1950 were similar to those of older trees during the same time period, but faster than the initial growth (1850-1900) of the older trees. Since the 1950s, all trees showed an important growth reduction, with a yearly growth rate similar to that observed in the 1850-1900 period.

For black spruce, there was only a small increase in height growth at the end of the 19th century and during the early part of 20th century (Fig 4.6d, 4.7d and 4.9d). However, in contrast to larch growth releases, spruce releases were weaker (less than three metres per 50 yr). As with larch, a reduction in spruce growth was observed in the second half of the twentieth century.

Black spruce and white cedar age distributions (from both dated and estimated stems) showed that most of the individuals became established after 1930. Maximum establishment occurred from the 1950s to the 1970s for cedar and from the 1960s to the 1990s for spruce on the higher elevations of the stands (Fig. 4.10). The oldest tree among all twelve plots, a spruce, was found in BL1d; it was at least 240 years old. An increase in spruce density, most notably in the youngest age-classes, occurred in conjunction with an increase in the distance from the shore (BL1a, BL1b, BL1c and BL1d). Cedar was mostly confined to plots occurring in the most elevated parts of the stands (BL1d, MAGb).

4.7 DISCUSSION

4.7.1 Role of disturbances

Age-class distribution results support the hypothesis that larch dynamics is predominantly controlled by major stand disturbances. The cumulative age distribution curves observed in our study are unlike the classic inverted "J" shape curves that are found in stable populations and characterised by declining tree density with increasing age or size (Lorimer 1980; Oliver and Larson 1990; Tardif and Bergeron 1999). Moreover, we found many discontinuities in larch recruitment (Fig. 4.3), which is common among tree species whose regeneration depends on catastrophic events, which open the forest canopy (Bergeron and Gagnon 1987, Bergeron and Brisson 1990; Morin 1994).

Considering the severity of the 1895-1912 and 1955-1962 larch sawfly outbreaks (Girardin et al. 2001*b*) and the reported decline of larch populations following the outbreak in the early part of the 20th century (Muldrew 1955; Ives and Nairn 1966; Turnock 1972; and Marie-Victorin 1995), we expected that most larch populations surrounding Lake Duparquet would be equally affected by high larch mortality rates. This would have resulted in a series of single-cohorts distributed throughout the different stands. However, the age frequency distributions observed in the plot level analysis were different from those observed at the stand and at the multiple stand levels. This suggests that larch dynamics is dependent on stand level factors. Canopy gaps is one of such factors. Beckwith and Drooz (1956) found that the larch sawfly killed only a small fraction of the larch in their plots (i.e., <30%) during the outbreak in the middle of the 20th century. The effect of the sawfly on larch population dynamics may be similar to the impact that the spruce budworm has on the dynamics of *Abies balsamea* in stands surrounding Lake Duparquet; tree mortality resulting from the outbreaks is distributed in patches instead of being uniformly distributed over the entire landscape (Kneeshaw and Bergeron 1998; 1999). Although it remains unclear what factors contribute to the patchy distribution of larch mortality in this study, Beckwith and Drooz (1956) reported that larch mortality generally occurred along exposed edges of stands or on mineral soils. According to Ives and Nairn (1966), older trees would also be more affected by mortality, as immature larch would be able to withstand several years of severe defoliation before succumbing.

4.7.2 Effects of larch sawfly on recruitment and growth

Larch dynamics in our study area are dependent on larch sawfly outbreaks to initiate stand recruitment. The cohort of the early-20th century was mostly initiated during or at the end of the 1895-1912 outbreak. We suspect that this cohort was associated with increasing seed production during and after the outbreak. In contrast, the cohort associated with the 1950s outbreak was initiated before the 1955-1962 outbreak. We suspect that this cohort may be associated to the existence of a pre-established seedling bank. A more open canopy resulting from mortality of larch during an outbreak may stimulated the growth of seedlings from seed banks and/or a greater seed production among surviving trees (Nelson 1950; Johnston 1990).

Larch produces abundant seed crops every 3 to 6 years (Payette et al. 1982; Duncan 1954; Johnston 1990), with small amounts of seed produced during intervening years (Johnston 1990). Larch can bear viable seeds on trees as young as 12 years of age, although massive seed production occurs later, at the age of about 40 years (Johnston 1990). Optimum seed production occurs when trees are about 75 years old (Johnston 1990). According to Nelson (1950), the amount of light available for each tree would be an important factor in seed production. The amount of seeds produced would notably decrease in conjunction with the closure of the tree canopy (Nelson 1950). Also, although larch seedlings may tolerate shade for a few years, considerable larch seedling mortality may occur (usually before their sixth year, Logan 1966) if no canopy opening is made (Duncan 1954; Coppel and Leius 1955; Johnston 1973; 1990). High mortality of larch due to shade intolerance occurs in mixed cedar and spruce stands, but also in pure larch stands where individuals need to be in a dominant position to survive (Johnston 1990). In the Lake Duparquet area, mortality of mature larch trees due to the larch sawfly probably promotes the survival and growth of some of the pre-established juveniles by reducing competition for light (Johnston 1990). This was demonstrated in the stem analysis for the periods of the 1900s and the 1950s where high height growth releases were observed in juvenile stems. Similar height growth releases were also observed on surviving mature larch and spruce trees, indicating that a relatively important proportion of the tree crown died following each outbreak.

The probable causes responsible for the creation of different stand recruitment types (seedling bank or increase seed production) may relate to the length and severity of an outbreak. Survival of the larch stems during an outbreak period is directly associated with the length of this period (Nairn et al. 1962; Ives and Nairn 1966). When mature trees are severely defoliated for many years (1895-1912; Girardin et al. 2001b), the sawfly larvae might fall to the ground and consume all or most of the pre-established seedling bank (Duncan 1954; Nairn et al. 1962). Stand recruitment thus depends on the production of seeds from surviving trees. On the other hand, regeneration during a shorter outbreak (1955-1962) may not depend as much on seed production because of the increased survival rate observed in seedlings and saplings already present in the understory. The lack of post-outbreak recruitment may then result from the death of the newly germinated seedlings which relates to light insufficiency associated with their non-dominant position (see Johnston 1990).

4.7.3 Role of flooding

We expected to find larch seedling banks across the entire study area but five of the twelve sampled plots had no seedlings (age classes 1990-1999). The location of these plots did not correspond to the flooding gradient (i.e., distance from shore or another water body, or water table depth). However, perhaps abundant *Kalmia augustifolia*, *Spiraea alba* and *Sphagnum* spp. in these plots contributed to low larch recruitment (Girardin et al. 2001*a*). In these wetland communities, there is little substrate heterogeneity (less moisture variability) compared to other stands and soil pH, as well as soil nutrient availability, is low. These are not adequate conditions for larch seed germination and seedling establishment (Robertson et al. 1978: Bares and Wali 1979; Inderjit and Mallik 1996; Girardin et al. 2001*a*).

An important factor that may affect larch recruitment is the intrusion of other tree species in the stands, resulting in the closure of the canopy. Because larch is a shade intolerant species (Johnston 1990; Montague and Givnish 1996) it may be replaced by black spruce during succession, particularly after a sawfly outbreak where larch seedlings are incapable of surviving under the shade of spruce. On dry sites in northern Quebec, low larch recruitment is related to the lack of microsites for seedling establishment (due to high lichen cover) and the low frequency of disturbance events affecting spruce populations (Jardon et al. 1994*a*; Jardon, Y. personal communication). In our study, successional replacement of larch is likely to occur only in the most elevated part of the mixed wetland stands, where the spring flood severity and the lower water table are less critical to the survival of spruce and cedar (Heinselman 1970; Johnston 1990; Girardin et al. 2001*a*). Most larch trees observed in these environments were dominant canopy trees, although some juvenile trees were observed in gaps at the margin of the cedar and spruce forests. Although a relatively high number of larch seedlings were observed under dense cedar cover, we suggest that most of these will eventually die because of insufficient light. Severe flooding in the lower elevational parts of the stand (Girardin et al. 2001*a*) likely contributes to the persistence of larch (which tolerates floods) on these sites, as well as preventing the establishment of white cedar and black spruce trees. This is supported by the low number or absence of young white cedar and black spruce in the lower part of stands MAG and BL1.

4.8 CONCLUSION

We suspect that larch sawfly outbreaks are a major factor controlling the dynamics of larch stands in wetlands of the southeastern part of the boreal forest. Most of Lake Duparquet's larch recruitment was associated with the 1895-1912 and 1955-1962 sawfly outbreaks. The results of this study also support the hypothesis that the larch sawfly outbreaks, instead of inducing tree mortality across the entire larch population, operate at a smaller scale by creating small canopy gaps. This would lead to the discontinuous age-class distributions observed at the stand level and across all stands. Finally, our results suggest that periodic spring floods prevent the establishment of flood intolerant species, such as black spruce and cedar, and thus maintains larch (a flood tolerant but shade intolerant species) as a dominant on the lowest part of the elevation gradient. However, on the more elevated sites, larch will eventually become excluded because of its inability to compete with black spruce and white cedar for light. Further studies should be conducted in these stands to characterise the size of canopy gaps and to study their spatial distribution. It would also be interesting to determine what factors (e.g., tree age or density, topography, water table, plant species assemblage, needle chemistry, etc.) induce sawfly outbreaks to create these gaps in the Lake Duparquet area, as opposed to a more uniform pattern of mortality over the entire landscape.

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Table 4.1 Stand structures at four Lake Duparquet sites, Abitibi

	BL2a	**CCa**	**BL2c**	**CCc**	**BL2b**	**CCb**	**BL1a**	**BL1b**	**BL1c**	**MAGa**	**MAGb**	**BL1d**
Larch												
No. of living stems /ha	1550	2225	1600	725	3000	2800	775	750	775	675	1325	2500
No. of dead stems /ha	150	200	250	25	575	150	0	50	75	50	25	25
% of dead stems	9.7	9.0	15.6	3.4	19.2	5.4	0.0	6.7	9.7	7.4	1.9	1.0
Tree density (ha)	675	975	1125	600	2150	725	425	225	600	350	325	175
Tree basal area (m^2/ha)	22.0	74.0	68.0	45.0	55.8	11.7	23.3	12.3	39.2	29.7	29.7	4.0
White cedar												
No. of living stems /ha	-	-	-	-	-	-	-	-	-	175	4425	9775
% among all stems	-	-	-	-	-	-	-	-	-	12.1	61.0	69.3
Black spruce												
No. of living stems /ha	-	-	-	-	-	-	50	175	3275	600	1500	1825
% among all stems	-	-	-	-	-	-	6.1	18.9	80.9	41.4	20.7	12.9
Total no. of stems /ha	1550	2225	1600	725	3000	2800	825	925	4050	1450	7250	14100

Table 4.2 Larch tree-ring statistics for Lake Duparquet, Abitibi

Larch tree-ring statistics												
Chronology lenght (years)	87	142	118	128	106	90	84	82	91	101	138	-
No. of measured series	24	26	24	12	24	4	24	12	35	20	18	-
Mean sensitivity	0.35	0.34	0.29	0.42	0.37	0.37	0.43	0.36	0.32	0.28	0.34	-
Standard deviation	0.31	0.31	0.26	0.36	0.32	0.32	0.37	0.31	0.28	0.25	0.29	-
Autocorrelation 1st order	0.32	0.38	0.70	0.49	0.53	0.33	0.15	0.19	0.28	0.37	0.70	-
Interseries correlation	0.61	0.66	0.51	0.66	0.44	0.76	0.67	0.67	0.66	0.61	0.53	-
% of missing rings	0.67	0.53	1.93	0.68	0.83	0.29	1.07	0.69	0.33	0.26	1.24	-
Variance due to autoregression (%)	11.9	19.6	50.9	9.0	0.0	9.5	2.5	3.0	7.8	20.4	45.3	-

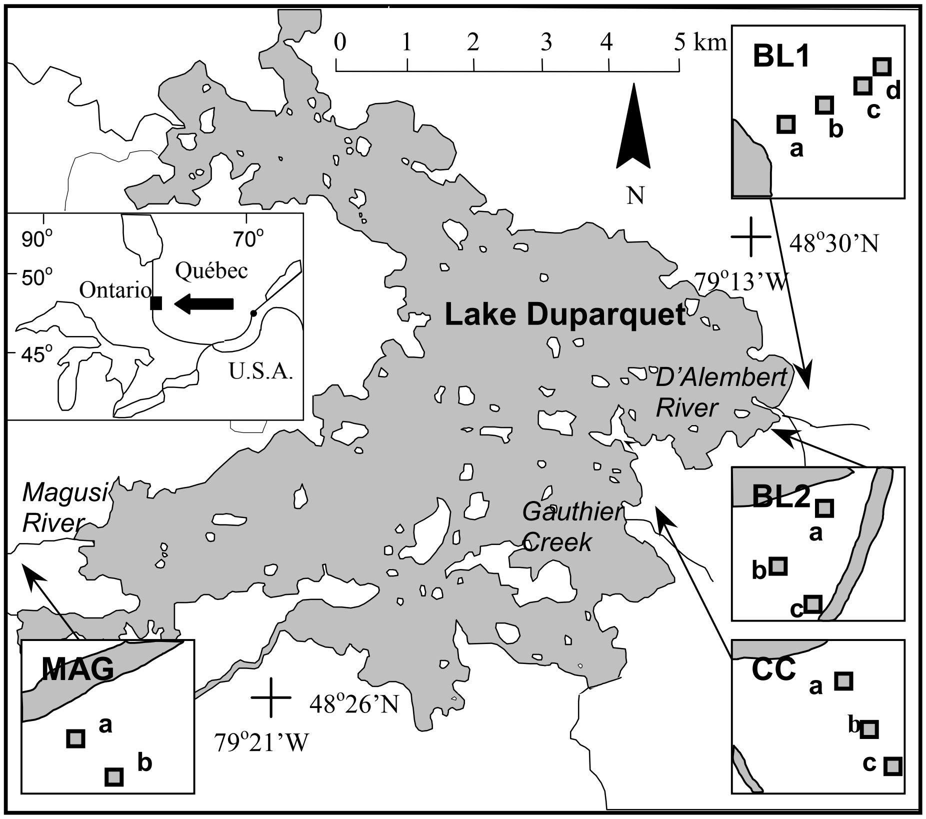

Figure 4.1 Map of Lake Duparquet showing the distribution of larch (*Larix laricina*) sample plots.

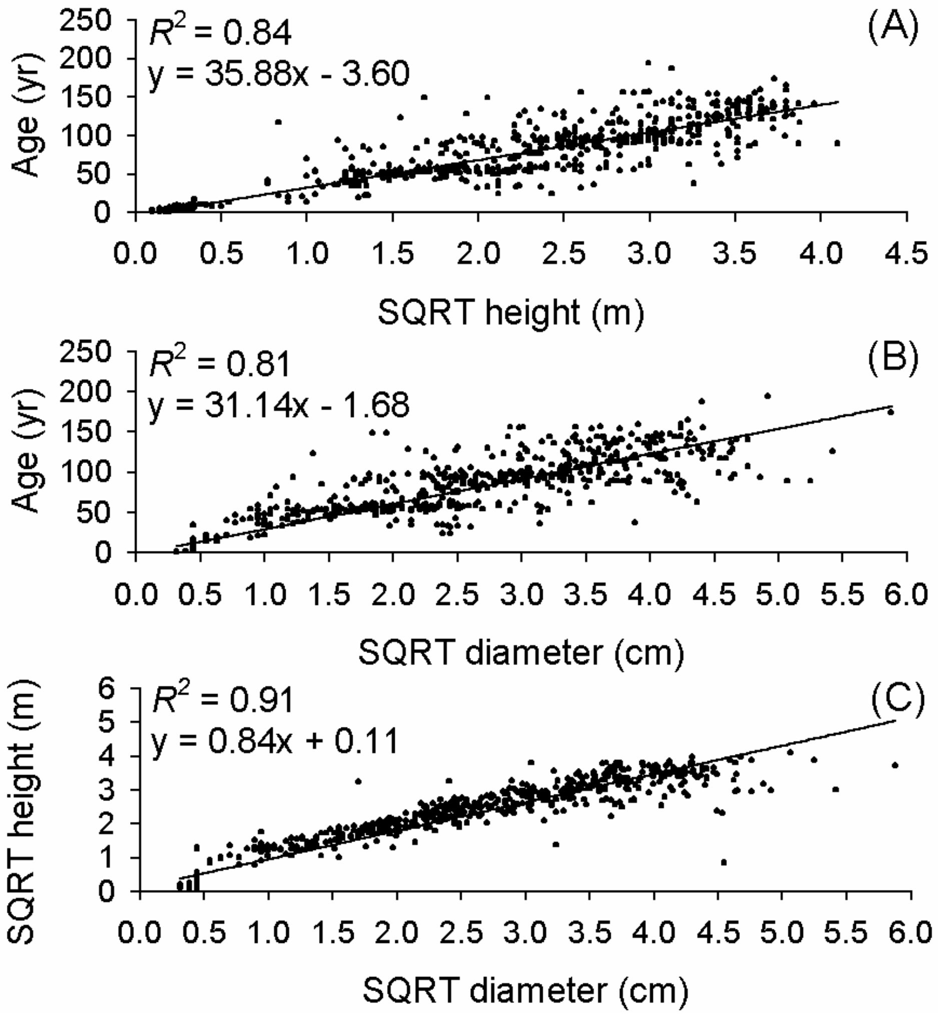

Figure 4.2 Age-height (A), age-diameter (B) and height-diameter (C) regressions for larch trees (DBH > 5 cm), saplings (DBH < 5 cm) and seedlings (height < 100 cm). DBH and height data were converted using a square root transformation.

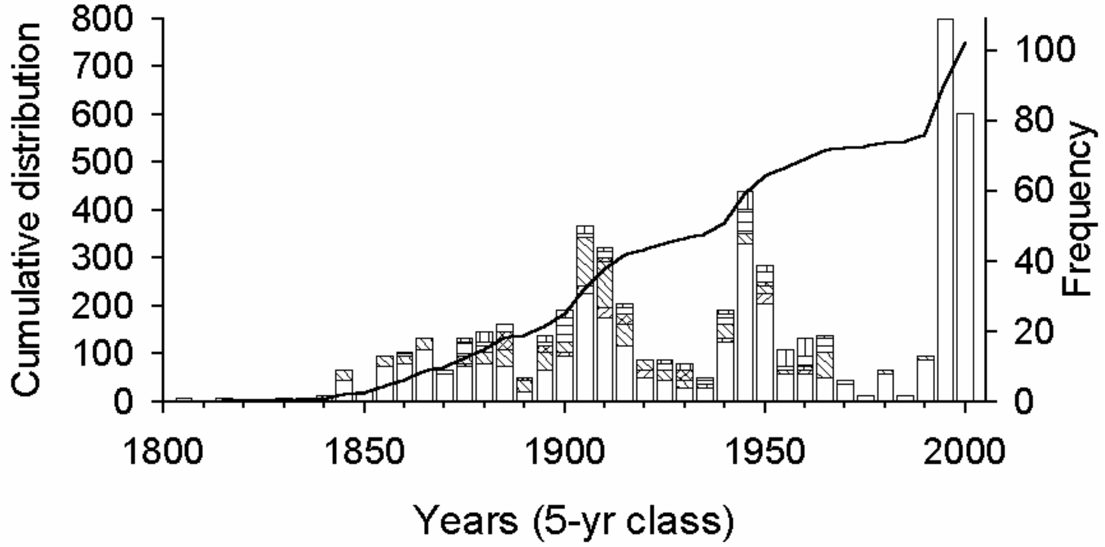

Figure 4.3 Frequency and cumulative age distributions of larch stems for Lake Duparquet. The empty vertical bar plot represents the age frequency of the living trees estimated from the cores taken at ground level. The bars with diagonal lines rising to the right represent the age frequency of the recently dead trees estimated from the cores taken at ground level. The bars with lines rising to the left (living trees) and diagonal crosshatches (dead trees) were estimated from the height regression whereas horizontal lines (living trees) and vertical lines (dead trees) were estimated from the height-DBH regression. The curve represents the cumulative distribution.

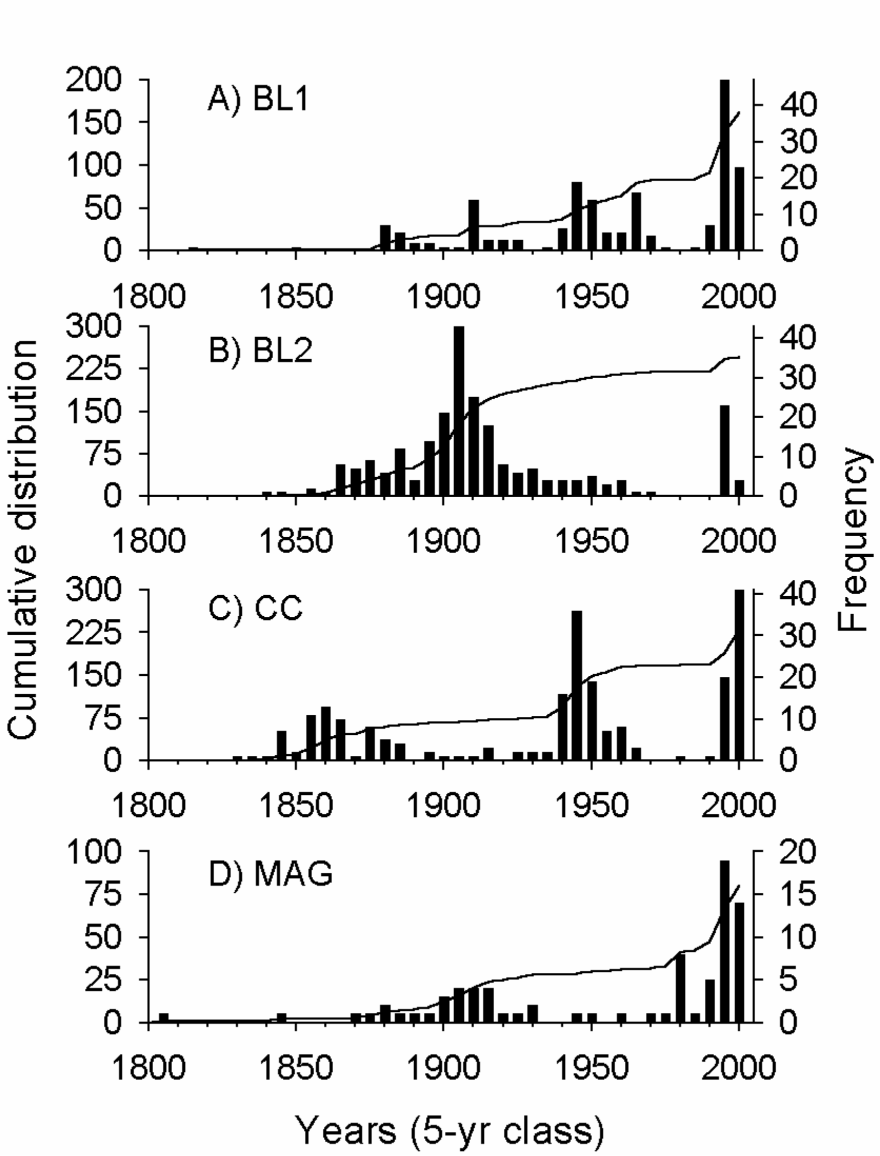

Figure 4.4 Frequency (vertical bars) and cumulative age distribution (solid lines) of larch stems (both live and recently dead) for each studied stand.

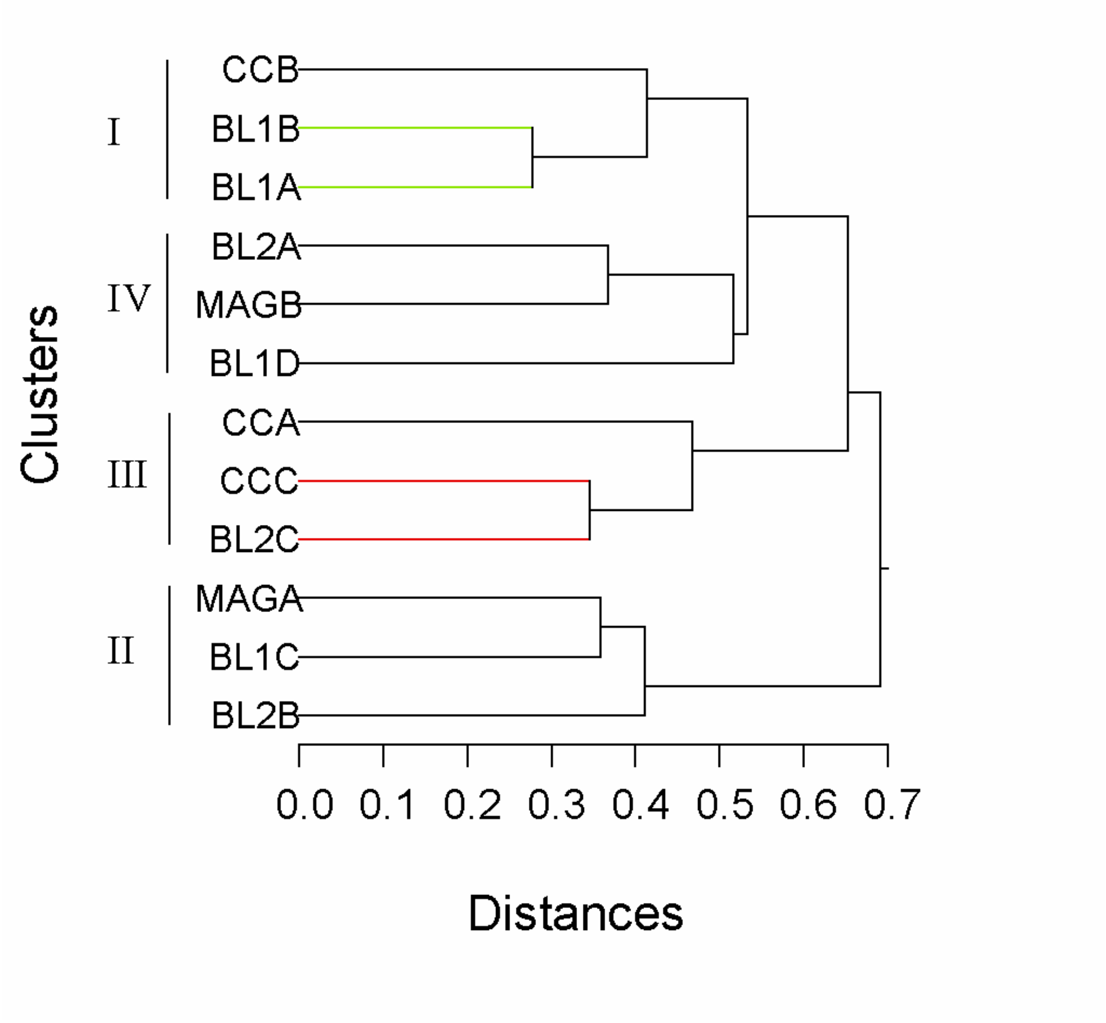

Figure 4.5 Results of the complete clustering analysis conducted on the LOG_{10} transformed larch age-class frequency distribution. As the distance increases in the linkage process (X-axis), the similarities between the two linked plots (or groups of plots) decrease.

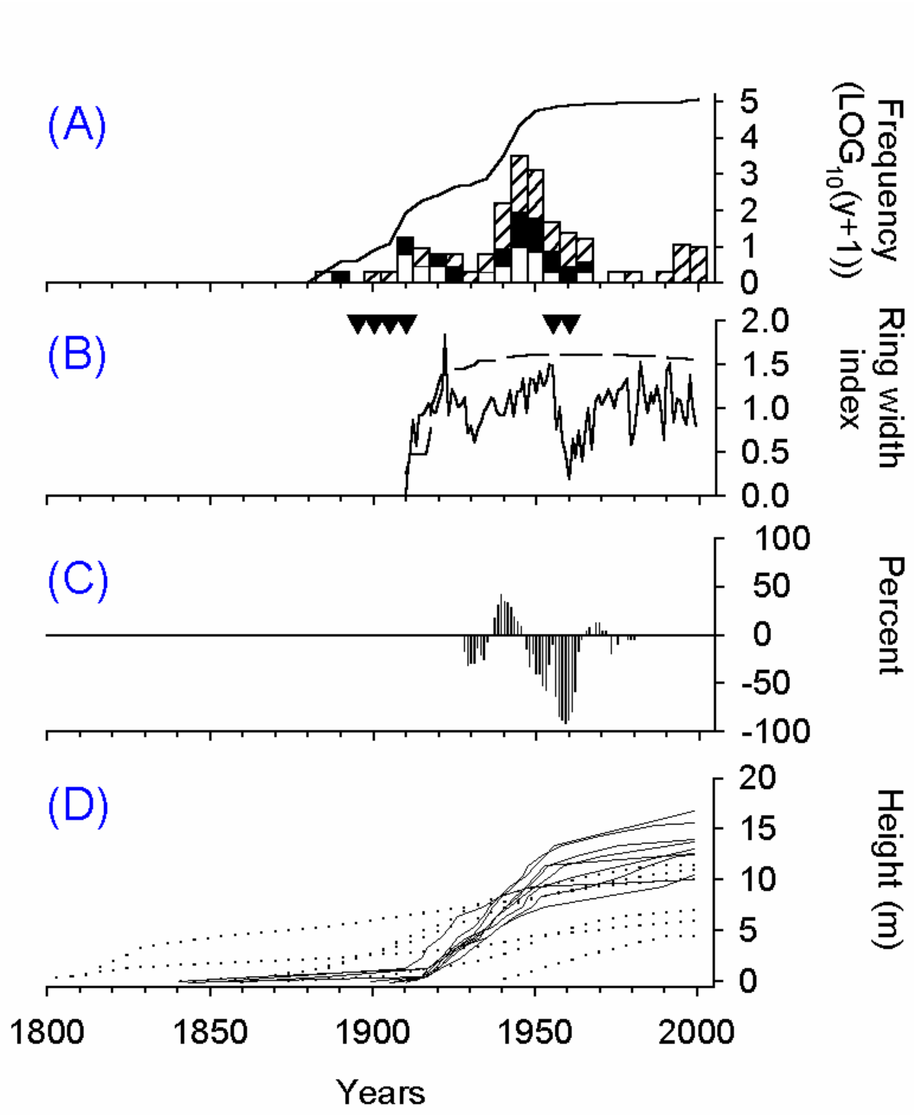

Figure 4.6 Relationships between larch recruitment and radial growth in cluster Type I. (A) Frequency (stacked vertical bars) and cumulative age distribution (solid lines) of larch stems (live and recently dead) for plots BL1a (empty bars), BL1b (filled bars) and CCb (rising right lines). The age data were previously transformed using a LOG$_{10}$(y+1) function. (B) Standard chronology (solid line) computed from the mean of the standardized tree-ring series. The dashed line shows the number of measured rings (data transformed using a LOG$_{10}$(y+1) function) at a given year. Periods of severe larch sawfly outbreaks (Girardin et al. 2001*b*) are shown by the black triangles. (C) Growth suppression and growth release analysis. Each bar represents the relative frequency of trees in either a growth release (positive values) or growth suppression (negative values) at a given year. (D) Results of the larch (solid lines) and black spruce (dotted lines) stem analysis. On the “Y” scale is obtained any value of height for a given tree at a given year.

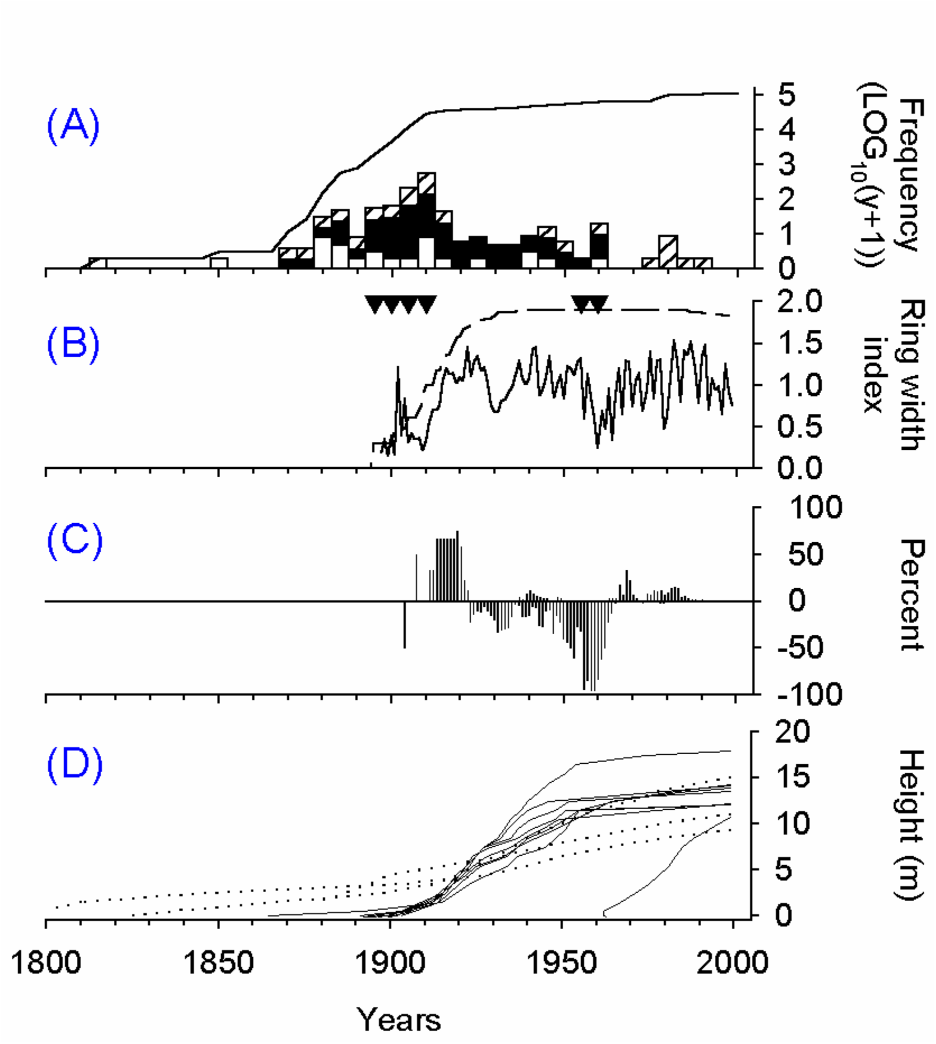

Figure 4.7 Relationships between larch recruitment and radial growth in cluster Type II (plots BL1c (empty bars), BL2b (filled bars) and MAGa (rising right lines). Definitions are as in Figure 4.6.

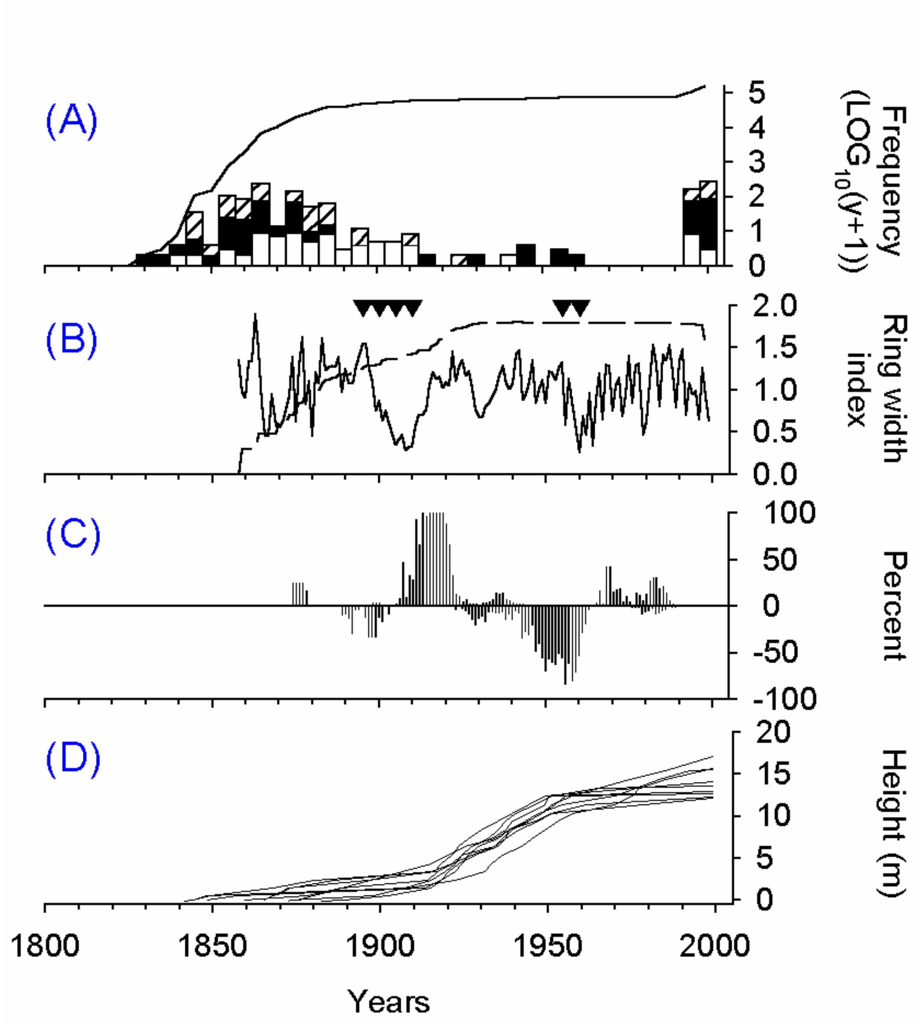

Figure 4.8 Relationships between larch recruitment and radial growth in cluster Type III (plots BL2c (empty bars), CCa (filled bars) and CCc (rising right lines). Definitions are as in Figure 4.6.

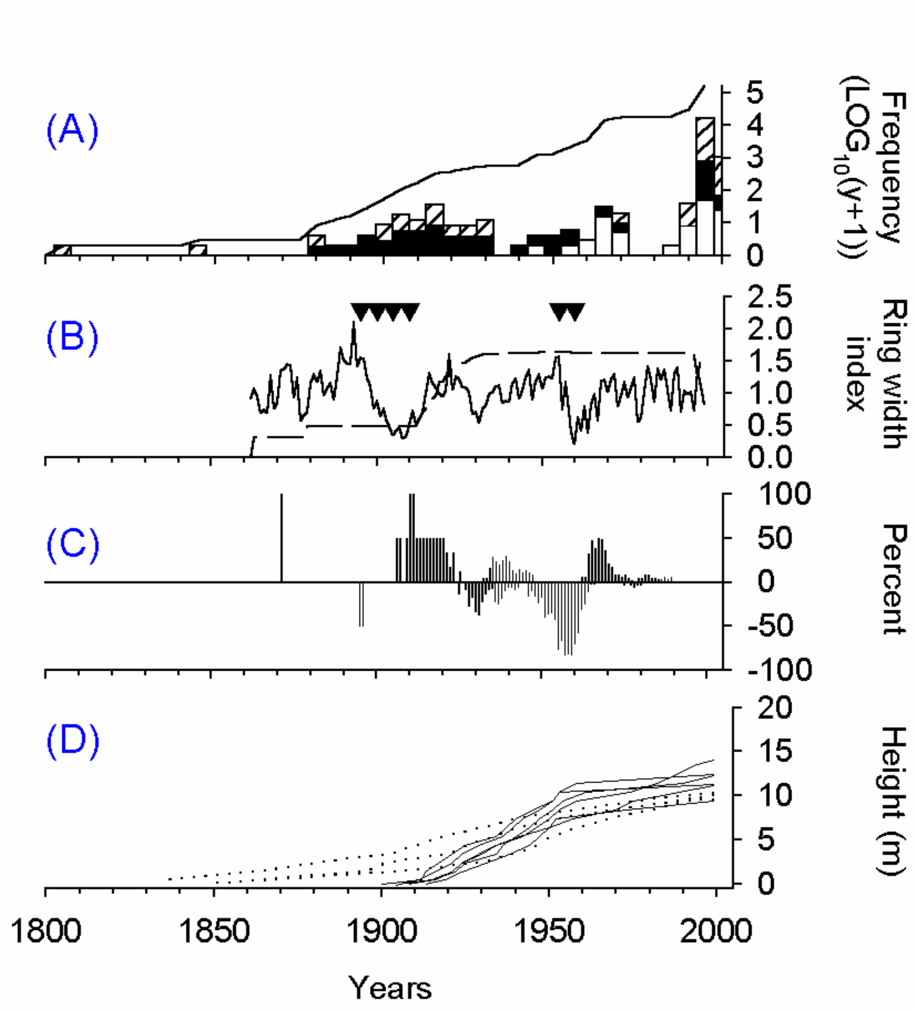

Figure 4.9 Relationships between larch recruitment and radial growth in cluster Type IV (plots BL1d (empty bars), BL2a (filled bars) and MAGb (rising right lines). Definitions are as in Figure 4.6.

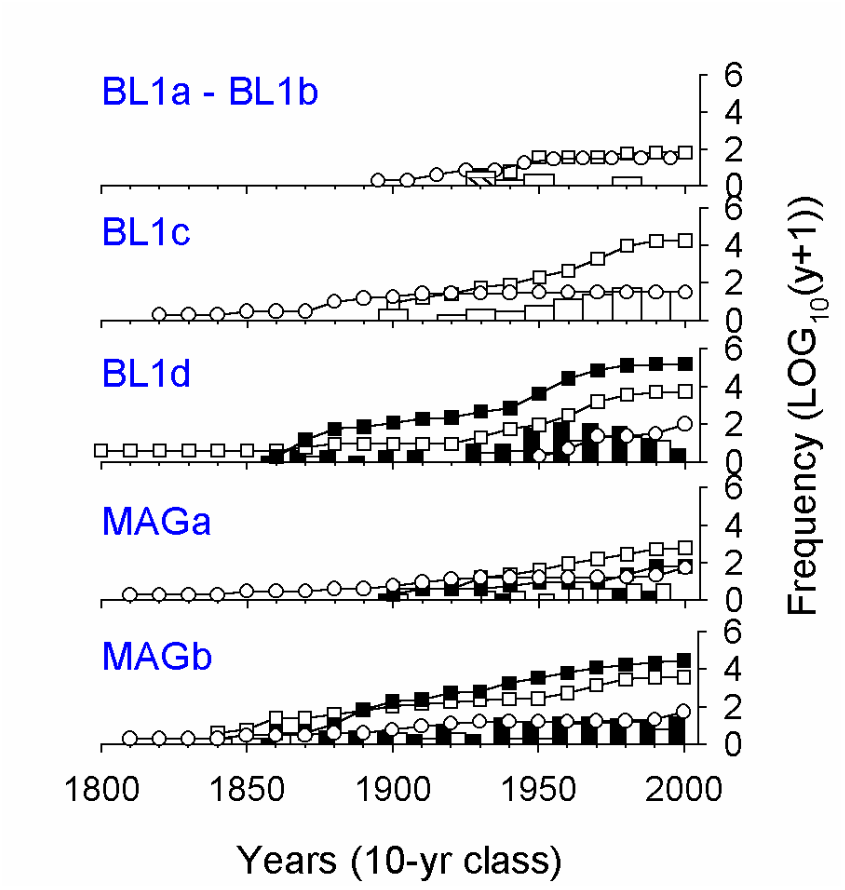

Figure 4.10 Age class frequencies of black spruce (A – empty bars) and white cedar (B – filled bars), and cumulative age frequency distributions of black spruce (A - empty squares) and white cedar (B - filled squares) for mixed plots (contains both live and recently dead trees). Note that for Figure A, plots BL1a (empty bars) and BL1b (rising left lines) are both shown by stacked bars and that the cumulative spruce frequency only accounts for BL1b. The cumulative frequency distribution curves of larch stems (live and recently dead) are also shown by the empty circles. The age-class data were previously transformed using a LOG$_{10}$(y+1) function.

CONCLUSION GÉNÉRALE

5.1 ANALYSE DES GRADIENTS ÉCOLOGIQUES

Les résultats indiquent que, outre l'effet de distance de la rive (en relation avec les dommages physiques subis par les inondations (Denneler *et al.*, 1999), le gradient lié à la concentration en nitrates du substrat serait particulièrement important dans l'explication de la distribution des communautés dans les tourbières bordant le Lac Duparquet. Ceci appuie donc ce qui avait été observé par Jeglum et He (1995). De même, des relations significatives ont été établies entre les concentrations de nitrate (NO_3) de la tourbe et la présence d'*Alnus rugosa* et de *Kalmia angustifolia*. Bien que la capacité d'enrichissement des sols par *A. rugosa* soit bien documentée (Ringius et Sims, 1997; Schwintzer et Tjepkema, 1997), la relation établie entre *K. angustifolia* et les conditions nutritives faibles des sols demeure toujours débattue (Facelli et Pickett, 1991; Zhu et Mallik, 1994; Inderjit et Mallik, 1996; Inderjit et Mallik, 1999). Certaines études ont conclu que *Kalmia* n'est pas responsable de la chute des concentrations en éléments nutritifs mais que ces conditions étaient déjà existantes avant son établissement. D'autres études ont conclu qu'il y a une perte importante en éléments nutritifs lorsqu'il y a présence de *K. angustifolia*, par processus de chélation ou de lessivage, perte pouvant avoir des conséquences sur la croissance d'autres espèces (Inderjit et Mallik, 1996 ; Inderjit et Mallik, 1999).

En plus de montrer l'existence d'une relation significative avec les conditions nutritives du substrat, l'étude de la distribution des espèces indique également des relations significatives avec la distance de la rive (gradient de tolérance des espèces à l'inondation), le pH et la conductivité du substrat, ainsi que le pH, la conductivité, la profondeur et la concentration en carbone de la nappe phréatique. L'interférence lumineuse s'est également révélée un facteur important, notamment sous le couvert de *Thuja occidentalis*. L'étude de la dynamique du mélèze tend à montrer que cette espèce, très intolérante à l'ombre, pourrait être amenée à disparaître aux endroits où s'est installé le *T. occidentalis* (niveau supérieur du gradient d'élévation). Par contre, cette même étude indique que le mélèze sera maintenu au niveau inférieur du gradient d'élévation en raison de la plus grande intolérance de *T.*

occidentalis aux crues printanières prolongées et ce, contrairement au mélèze qui leur est relativement tolérant (Johnston 1990).

5.2 ÉTUDE DE LA CROISSANCE RADIALE DU MÉLÈZE

Bien que le mélèze soit relativement bien adapté aux crues printanières, sa croissance radiale est affectée. D'abord, l'étude dendroclimatique a montré une augmentation de la sensitivité (ou variabilité interannuelle) dans la réponse du mélèze au facteur climatique. Cette augmentation coïncide principalement avec un changement dans la réponse des arbres au climat depuis 1960. Dans la première moitié du XXe siècle, les températures du mois d'avril expliquait une grande part de la variabilité dans la croissance (données non-publiées). Vers 1960, nous avons observé une diminution de l'importance de ce facteur climatique, alors que les niveaux d'eau du mois de mai devenaient le facteur explicatif. Ceci concorderait avec l'hypothèse d'une augmentation de la sévérité des crues printanières rapportée par Tardif et Bergeron (1997) sur le Lac Duparquet.

Nos résultats tendent à démontrer que la tenthrède aurait un impact important sur la croissance du mélèze et la dynamique des forêts des milieux tourbeux. L'étude des cernes de croissance a démontré au moins trois périodes d'épidémie au cours du siècle passé: 1895-1912, 1937-1942, 1955-1962. L'analyse statistique entre espèces hôte et non-hôte a non-seulement permis de confirmer ces périodes, mais également de spéculer sur la possibilité qu'il y ait eu plusieurs autres périodes (début 1920, fin 1970 et début 1980) moins sévère. Ces périodes correspondent à des fréquences faibles de cernes manquants et de cernes à bois terminal pâle.

5.3 DYNAMIQUE DU MÉLÈZE

La tenthrède du mélèze est l'une des forces majeures régularisant la dynamique des forêts tourbeuses de la région du Lac Duparquet. Elle exerce un impact important à l'échelle des peuplements de mélèze (purs et mixtes) lorsque la densité de l'insecte atteint des niveaux épidémiques tel qu'observé au cours des années 1955-1962 (voir rapports annuels 1937-1982 du Ministère de l'énergie et des ressources, Québec). Le mélèze étant très intolérant à l'ombre (Johnston, 1990), l'ouverture du couvert suite à la mortalité des arbres matures lors d'une épidémie permettrait d'une part la survie des semis préétablis. D'autre part, les arbres ayant survécus a une épidémie pourraient aussi contribuer à rétablir le peuplement par une augmentation de la production de graines. Selon la durée et de la sévérité de l'épidémie, l'un ou l'autre de ces deux processus serait dominant (voir Duncan (1954) et Nairn *et al.* (1962)).

Contrairement à nos attentes initiales (mortalité à l'échelle du peuplement avec survie de quelques tiges), cette étude a démontré que les épidémies de la tenthrède n'affecteraient pas les mélèzaies à l'échelle du peuplement, mais plutôt de façon localisée à l'intérieur de ceux-ci, d'où une dynamique se rapprochant beaucoup plus de celle des trouées. À l'échelle du peuplement et du paysage, ce type de dynamique résulterait en une distribution inéquienne de deux ou plusieurs cohortes. Ce phénomène est entre autres observé dans les peuplements de sapin baumier (*Abies balsamea*) avec les épidémies de la tordeuse des bourgeons de l'épinette (Kneeshaw et Bergeron, 1999). Il serait intéressant d'étudier les peuplements de mélèzes du Lac Duparquet d'une façon plus approfondie afin de déterminer la taille des trouées observées et plus précisément les facteurs induisant leur formation (qualité nutritive des sites, topographie, proximité d'une source d'eau, etc).

Enfin, en raison du difficile recrutement du mélèze sous un couvert dense (Johnston, 1990), certaines évidences laisse croire que la tenthrède pourrait induire un changement important dans la composition des peuplements mixtes de mélèze, de cèdre et d'épinette noire. Bien que ceci soit relativement spéculatif, la tenthrède pourrait être responsable de la disparition du mélèze dans ces sites et ce faisant elle occuperait une place de premier plan dans le processus de succession de ce type de forêt. Cette inquiétude avait notamment déjà été soulevée par Jardon *et al.* (1994b) concernant des peuplements beaucoup plus nordiques. Des études de la tourbe et de son contenu, notamment en cônes et pollens, pourrait en indiquer beaucoup plus sur cet aspect.

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