UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉTUDE DENDROÉCOLOGIQUE DES PEUPLEMENTS RIVERAINS DE CÈDRE BLANC (*THUJA OCCIDENTALIS* L.) DANS LA RÉGION DE LA FORÊT BORÉALE MIXTE DE L'OUEST DU QUÉBEC

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RÉSUMÉ

Plusieurs études dendroécologiques et dendroclimatiques effectuées dans la région boréale méridionale du Québec indiquent une augmentation des précipitations et, par conséquent, une diminution des périodes de sécheresse comme effet principal du réchauffement atmosphérique observé depuis la fin du «Petit Âge Glaciaire» au milieu du XIXe siècle. Ce changement climatique aurait été causé par le recul du front polaire permettant aux masses d'air chaud et humide d'avancer vers des latitudes plus nordiques. Les conditions climatiques altérées ont modifié le régime hydrologique du lac Duparquet, un grand lac naturel au nord-ouest du Québec, en causant une augmentation de la fréquence des crues printanières de grande amplitude. Celles-ci ont eu des conséquences, surtout au niveau de l'accroissement radial et du recrutement, pour les peuplements lacustres de frêne noir.

La présence de nombreux individus de cèdre blanc (*Thuja occidentalis* L.), âgés jusqu'à environ 500 ans, sur les rives du lac Duparquet a laissé supposer que l'analyse des peuplements riverains de cette espèce pourrait fournir des informations précieuses sur le changement du régime hydrologique à long terme de ce lac. L'objectif général de cette thèse doctorale fut donc d'analyser les effets des changements hydrologiques du lac Duparquet sur la frange riveraine de cèdre blanc. Nous sommes partis de l'hypothèse que les peuplements riverains de cèdre blanc se trouvent dans un déséquilibre démographique causé par la hausse du niveau d'eau du lac depuis le milieu du XIXe siècle. Les objectifs envisagés par cette étude sont i) la caractérisation des espèces arborescentes riveraines en relation avec leur environnement abiotique, particulièrement par rapport à l'exposition aux perturbations riveraines, ii) l'évaluation de l'influence des inondations sur l'accroissement radial du cèdre blanc, iii) l'évaluation de l'effet des feux de forêt et des perturbations riveraines sur la dynamique des populations de cèdre et iv) la reconstitution des variations à long terme du niveau du lac Duparquet.

L'importance des facteurs environnementaux pouvant régir la distribution des espèces arborescentes fut évaluée pour les forêts ripariennes entourant le lac Duparquet. La présence et la surface terrière relative de 10 espèces arborescentes ont été mesurées le long de 95 transects établis à partir du bord du lac jusqu'à 200 cm au-dessus du niveau d'eau moyen. Des régressions logistiques et des analyses canoniques des correspondances ont été effectuées sur l'ensemble des données et pour les cinq types géomorphologiques de berges pris séparément (plaines d'accumulation, plaines d'inondation, plages, terrasses et escarpements rocheux). Le gradient d'élévation, reflétant les inondations saisonnières, s'est révélé le facteur principal expliquant la distribution des espèces. Le type de dépôt de surface, la topographie, l'orientation et le temps écoulé depuis le dernier feu de forêt expliquent, du moins partiellement, les changements de composition observés pour chacun des types géomorphologiques selon un gradient d'élévation. L'exposition aux perturbations riveraines, par contre, semble surtout exercer un effet indirect en déterminant la différenciation morphologique du périmètre lacustre. L'extraordinaire taille moyenne des cèdres occupant la zone riveraine pourrait indiquer un état de

déséquilibre démographique relié aux changements du régime hydrologique du lac Duparquet.

Deux parties de cette étude furent consacrées à l'analyse de l'influence des inondations sur l'accroissement radial intra- et interannuel, respectivement, du cèdre blanc. L'activité cambiale de cette espèce fut suivie par des dendromètres manuels afin de i) retracer la période d'activité cambiale, ii) évaluer les effets de l'inondation sur la croissance radiale, et iii) analyser les relations avec des facteurs météorologiques et hydrologiques. Les changements quotidiens de la circonférence de quatre arbres dans chacun des deux sites, l'un à l'intérieur et l'autre au-dessus de la zone riveraine, ont été enregistrés pendant la saison de croissance de 1996, une année caractérisée par une crue printanière extrême. Le bois initial s'est développé de début juin jusqu'à la mi-juillet tel qu'indiqué par l'expansion nette et durable du tronc des arbres. Les changements synchrones et parallèles de la surface terrière aux deux sites montrent que l'inondation n'a pas retardé l'initiation de la croissance et n'a pas eu d'effet négatif ni sur la dimension ni sur la durée de la formation du bois initial chez les arbres riverains. Cette observation est expliquée par le retrait rapide des eaux juste avant le début de l'activité cambiale en juin. La période de mi-juillet à la mi-août fut caractérisée par des fluctuations distinctes à court terme, causées par des périodes alternées de pluie et de sécheresse, et une légère baisse de la surface terrière de tous les arbres sauf chez les deux individus les plus proches du lac pour lesquels les dendromètres enregistrèrent la formation du bois final. Le calcul de corrélations de Pearson avec les données météorologiques révèle que les changements quotidiens de la surface terrière des arbres sont positivement associés aux précipitations à l'exception de la période de la formation du bois initial, pendant laquelle les arbres ont probablement bénéficiés d'un taux d'humidité élevé dans le sol après la fonte des neiges. L'humidité moyenne et minimale de l'air corrèlent positivement et la température maximale de l'air négativement avec les variations quotidiennes de la surface terrière, démontrant ainsi l'importance des changements du flux de sève sur la circonférence du tronc des arbres.

Puisque les études déjà effectuées au lac Duparquet ont indiqué une augmentation du plan d'eau suite au changement climatique depuis le milieu du XIXe siècle, on a voulu évaluer indépendamment de ce lac naturel les réponses principales des cèdres blancs riverains à une augmentation du niveau d'eau. À cette fin on s'est tourné vers le lac Abitibi, un grand lac naturel situé à une quinzaine de kilomètres au nord du lac Duparquet qui fut transformé en réservoir après la construction consécutive de deux barrages sur la Rivière Abitibi. Le premier barrage a rehaussé le niveau d'eau d'environ 1,2 m en 1915 tandis que le deuxième barrage a changé le régime hydrologique sans rehaussement additionnel du niveau d'eau en 1922. L'avantage d'un réservoir est de connaître le moment précis et l'amplitude de l'augmentation du niveau d'eau. Quoiqu'un rehaussement artificiel dépasse la vitesse et l'amplitude d'une augmentation naturelle du niveau d'eau, il peut quand même servir comme modèle pour évaluer les réponses principales des arbres riverains à une augmentation du niveau d'eau. Si un tel événement ne cause pas de réaction de la croissance radiale, on ne peut pas non plus s'attendre à une réponse quand le niveau d'eau monte lentement en permettant aux arbres de s'adapter à l'environnement changeant. L'objectif principal fut donc d'évaluer les réponses du cèdre blanc au stress physiologique des inondations (croissance radiale) ainsi qu'au régime modifié des perturbations riveraines (mortalité des arbres, cicatrices glacielles, bois de compression, mort partielle du cambium). Les effets primaires du rehaussement des eaux en 1915 ont été i) la mort instantanée des arbres qui ont formé l'ancienne lisière de la forêt et qui furent sévèrement affectés par la fréquence et l'intensité accrues des perturbations riveraines et ii) la blessure et l'inclinaison des cèdres survivants qui forment la marge forestière actuelle. Aucun de ces indicateurs n'a enregistré le changement du régime hydrologique sept ans plus tard. L'absence d'anomalies de la croissance radiale des cèdres riverains suite aux deux événements hydrologiques indique que les inondations n'ont pas eu d'effet significatif sur le métabolisme des arbres. Il semble donc que les paramètres de croissance reliés aux perturbations, tels le bois de compression et les cicatrices glacielles, sont les meilleurs indicateurs pour la reconstitution d'une augmentation à long terme du niveau d'eau des lacs naturels dont les berges sont fortement exposées aux vagues.

La dynamique des populations de cèdre blanc et de frêne noir (*Fraxinus nigra* Marsh.) a été analysée pour déterminer l'impact des deux principales perturbations naturelles, feux de forêt et inondations, dont l'influence se chevauche à l'intérieur de la zone riveraine. La structure d'âge fut établie dans huit sites lacustres et terrestres au lac Duparquet caractérisés par une topographie en forme de terrasse et un degré variable d'exposition à l'activité des vagues et des glaces. Nous avons émis l'hypothèse que les peuplements riverains de cèdre blanc i) sont en déséquilibre démographique causé par les niveaux d'eau montants depuis la fin du 'Petit Âge Glaciaire' (ca. 1850) et ii) sont protégés des incendies au contraire des peuplements des hautes terres.

Les résultats montrent que le frêne noir n'occupe que la zone riveraine (< 200 cm d'élévation) alors que le cèdre blanc ne s'approche pas à moins d'un mètre (vertical) du lac à l'exception de quelques semis. La structure d'âge du cèdre le long du gradient d'élévation montre que les arbres qui s'étaient établis avant le dernier feu de forêt sont presque complètement restreints aux basses terres (< 175 cm) où la survie de cette espèce susceptible aux feux bénéficie probablement de la proximité du lac. La distribution composée cumulative d'âge du cèdre blanc suit une fonction négative exponentielle typique pour des peuplements inéquiens avec un apport continu de graines. Cependant, la structure d'âge des peuplements exposés aux perturbations riveraines indique un manque de recrutement après feu alors que celle des peuplements plus protégés indique une reproduction plutôt continue. Le frêne noir, plus tolérant aux inondations et aux poussées glacielles que le cèdre, a commencé à envahir les terrasses riveraines autour de 1850, c'est-à-dire à la fin du 'Petit Âge Glaciaire'. Il semble donc que les parties exposées de la frange de cèdre autour du lac Duparquet sont en train de se désintégrer, particulièrement à cause du faible taux de survie des semis et que cette espèce y est graduellement remplacée par le frêne noir. Ce développement est supposé continuer vu que le réchauffement atmosphérique sous l'influence de l'effet de serre devrait encore s'accentuer jusqu'au moins à la fin de ce siècle à peine commencé. Au fur et à mesure que les niveaux d'eau se stabiliseront, une nouvelle lisière de cèdre blanc pourrait s'établir sur la terre plus élevée.

Finalement, les changements de la limite inférieure du cèdre blanc témoignent des fluctuations à long terme du niveau d'eau dans le passé et indiquent trois périodes hydrologiques distinguées au Lac Duparquet: les niveaux relativement élevés d'avant ~ 1500 furent suivis par une baisse du niveaux des eaux d'environ 20 cm pendant le 'Petit Âge Glaciaire' (~ 1500 – 1850), une période relativement froide et sèche, qui fut suivie par une augmentation graduelle du niveau d'eau de 20 à 40 cm jusqu'à la fin du XXe siècle. Ces variations à long terme du niveau d'eau confirment les résultats d'autres études effectuées au Québec boréal et subarctique.

INTRODUCTION GÉNÉRALE

0.1 Les perturbations naturelles sous l'influence du climat

Depuis les années 1970, on reconnaît que les perturbations naturelles jouent un rôle prépondérant dans la dynamique des populations forestières (White 1979, Pickett 1980, Pickett et White 1985, White 1987). Le type de perturbation dominant varie selon le climat régional, la composition et la structure de la végétation, la topographie et bien d'autres facteurs. Dans la région de la forêt boréale, les feux constituent la principale perturbation naturelle (Carleton et Maycock 1978, Johnson 1992, Payette 1992, Bergeron et al. 1998). Une haute fréquence et intensité des feux mène généralement à une mosaïque de cohortes équiennes alors qu'un régime de feu plus modéré favorise le développement de peuplements inéquiens par des processus liés à la succession (Johnson 1992, Frelich et Reich 1995, Bergeron et al. 2001).

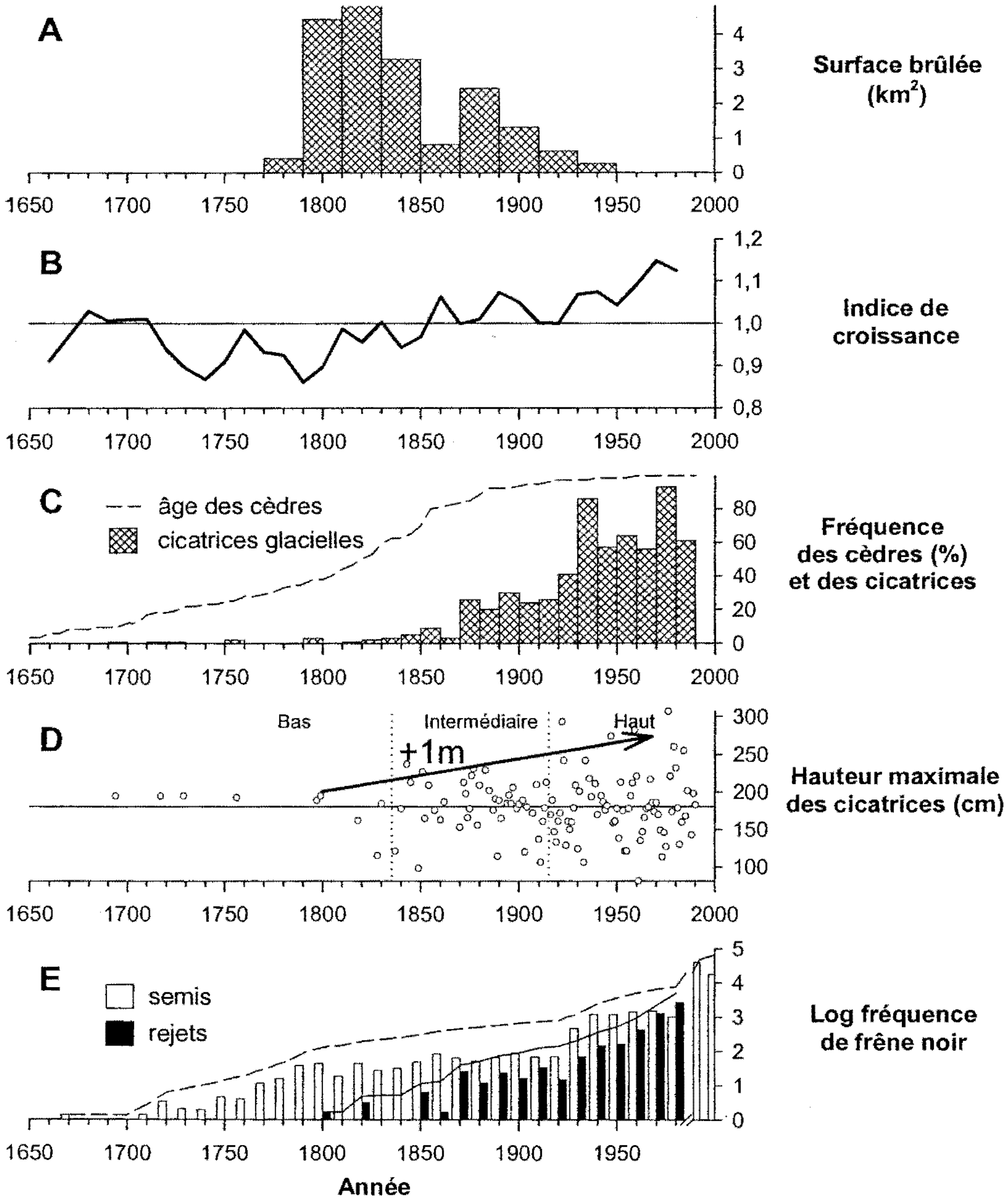
Comme la dynamique des populations est contrôlée par les perturbations, il devient très important de bien identifier les changements temporels du régime des perturbations. Le régime de plusieurs types de perturbations importantes tels les feux de forêt, les chablis et les inondations sont contrôlés par le climat et ses fluctuations. Ceci est important dans le contexte de la discussion actuelle sur les conséquences du réchauffement atmosphérique que l'on observe depuis une centaine d'années et qui est, selon toute vraisemblance, causé par l'émission excessive des gaz à effet de serre. Cette augmentation de la température planétaire s'élève en moyenne à 0,6 ±0,2 °C pour le XXe siècle (Houghton et al. 2001). Les scénarios les plus récents du *Groupe intergouvernemental d'experts sur l'évolution du climat* prévoient même un réchauffement additionnel entre 1,4 et 5,8 °C au XXIe siècle (Houghton et al. 2001). Plusieurs études laissent supposer que les effets directs de ce réchauffement atmosphérique (une possible augmentation de la production primaire) sont moins importants que les effets indirects reliés à une altération du régime des perturbations naturelles (Warrick et al. 1986, Clark 1988, Overpeck et al. 1990, Schindler et al. 1990, Flannigan et Van Wagner 1991, Apps et al. 1995, Bergeron et al. 1998, Flannigan et al. 1998). Il faut donc essayer de comprendre les interactions dans ce système complexe formé par le climat, les perturbations naturelles et la dynamique forestière si on veut évaluer les conséquences du changement climatique dans l'avenir.

Des études effectuées au Québec boréal et subarctique ont mis en évidence un changement du régime des perturbations naturelles et de la dynamique forestière lié au réchauffement climatique depuis la fin du «Petit Âge Glaciaire» au milieu du XIXe siècle. Depuis, le niveau lacustre ainsi que la fréquence et l'amplitude des crues printanières de plusieurs cours d'eau dans la région de la Baie d'Hudson ont augmenté (Payette 1980, Bégin et Payette 1988, 1991, Payette et Delwaide 1991, Payette et Filion 1993, Lepage et Bégin 1996, Bégin 2000a, 2000b, 2001). Ces changements du régime hydrologique s'expliqueraient par une augmentation des précipitations hivernales reliée au réchauffement climatique. Ces changements climatiques seraient aussi responsables de l'expansion des populations d'épinette blanche à sa limite septentrionale (Payette et Filion 1985), du changement de la forme de croissance dominante chez l'épinette noire de «krummholz» à une physionomie arborescente (Payette et al. 1985, 1989, Lavoie et Payette 1992, 1994) et de la fréquence réduite des feux (Filion et al. 1991).

Dans la région de la forêt boréale mixte du Québec, plusieurs études écologiques ont analysé les effets du récent réchauffement climatique depuis la fin du «Petit Âge Glaciaire» sur le régime des perturbations naturelles et la composition forestière. La reconstitution de l'historique des feux de forêt dans l'est de l'Ontario ainsi que l'ouest et le centre du Québec montre que le cycle des feux, c'est-à-dire le temps qui s'écoule jusqu'à ce qu'une superficie égale à celle du territoire soit brûlée, a significativement allongé dans toutes ces régions (Bergeron 1991, Bergeron et Archambault 1993, Bergeron et al. 2001). Cette diminution de la fréquence des feux, particulièrement prononcée au cours du XXe siècle (Fig. 0.1A), fut responsable de l'abondance croissante d'espèces de fin de succession (sapin baumier, cèdre blanc) au détriment des espèces pionnières telles le pin gris et les feuillus intolérants (Bergeron et Dubuc 1989, Bergeron et Dansereau 1993, Bergeron 1998). Ces changements semblent avoir eu un équivalent à l'Holocène moyen, une période relativement chaude qui aurait été caractérisée par une activité plus faible des feux et une dominance du cèdre blanc (Richard 1980, Carcaillet et Richard 2000, Carcaillet et al. 2001, Flannigan et al. 2001).

Au lac Duparquet, l'observation d'une augmentation à long terme depuis le milieu du XIXe siècle de la croissance radiale des peuplements de cèdre blanc provenant de sites xériques s'expliquerait par des précipitations estivales plus abondantes et/ou plus régulières qui auraient réduit les périodes de sécheresse (Archambault et Bergeron 1992a; Fig. 0.1B). De plus, l'établissement d'une chronologie de cicatrices glacielles formées sur des troncs de cèdre blanc riverain, causées par l'abrasion de la glace flottante pendant la débâcle printanière, révèle une hausse et de la fréquence des crues printanières et de leur amplitude d'environ

Figure 0.1 (page suivante) Indicateurs du changement climatique dans la région du lac Duparquet depuis la fin du «Petit Âge Glaciaire» (~1850). (A) Superficie brûlée sur 43 îles dans le lac entre 1688 et 1988 en classes de 20 ans (données de Bergeron et Archambault 1993). Les valeurs ne représentent que des estimations minimales, particulièrement celles pour les vieux feux, parce qu'une partie de la superficie pourrait avoir brûlé plus d'une fois. (B) Courbes d'indices de croissance radiale du cèdre blanc (n = 38 arbres) de sites xériques bordant le lac (données de Archambault et Bergeron 1992a). (C) Nombre de cicatrices glacielles de 1661 à 1990 par classes de 10 ans (n = 615) et distribution cumulative en pourcentage de cèdres blancs riverains portant des cicatrices (n = 81) (données de Tardif et Bergeron 1997). (D) Évolution à long terme de la hauteur maximale des cicatrices glacielles au-dessus du niveau d'eau provenant de 81 cèdres blancs et couvrant les années 1660 à 1990 (n = 121) (données de Tardif et Bergeron 1997). (E) Présentation (échelle semi-logarithmique) de la distribution d'âge statique et cumulative du frêne noir en classe de 10 ans et différenciée selon l'origine des tiges (sexuée ou végétative). Les barres à droite de l'interruption de l'axe des abscisses montrent le nombre de semis plus petits que 10 cm et de semis de moins d'un an, respectivement (données de Tardif et Bergeron 1999).


A
Surface brûlée (km²)
0
1
2
3
4
B
Indice de croissance
0,8
0,9
1,0
1,1
1,2
C
âge des cèdres
cicatrices glacielles
Fréquence des cèdres (%) et des cicatrices
0
20
40
60
80
D
Bas
Intermédiaire
Haut
+1m
Hauteur maximale des cicatrices (cm)
100
150
200
250
300
E
semis
rejets
Log fréquence de frêne noir
0
1
2
3
4
5
1650
1700
1750
1800
1850
1900
1950
2000
Année

1 m au cours de la même période (Tardif et Bergeron 1997; Fig. 0.1C et D). Des analyses climatiques ont montré que les crues glacielles majeures coïncidèrent avec des basses températures automnales et des précipitations abondantes pendant l'hiver et le printemps (Tardif et Bergeron 1997). Les niveaux d'eau plus élevés depuis la fin du «Petit Âge Glaciaire» auraient aussi causé une modification du type de recrutement chez le frêne noir (Tardif et Bergeron 1992, 1999, Tardif et al. 1994; Fig. 0.1E). Dans les sites fortement exposés aux inondations, la régénération végétative par des rejets de souche domine de plus en plus permettant à cette espèce de persister malgré son taux de recrutement sexué faible. Les tiges d'origine sexuée prévalent dans les sites peu affectés par les hauts niveaux d'eau.

L'historique des feux, la composition changeante des forêts, la croissance du cèdre blanc, les crues glacielles et le comportement de reproduction du frêne noir indiquent donc tous une augmentation des précipitations comme effet principal du réchauffement atmosphérique dans la région du lac Duparquet depuis le milieu du XIXe siècle. Ce changement climatique pourrait être causé par la migration vers le nord de la circulation générale de l'atmosphère permettant la pénétration plus fréquente de masses d'air méridionales chaudes et humides dans cette région (Archambault et Bergeron 1992a, Bergeron et Archambault 1993, Bergeron 1998, Flannigan et al. 2001).

0.2 Le cèdre blanc

La région du lac Duparquet se situe presque au centre de l'habitat principal du cèdre blanc (*Thuja occidentalis* L.) qui s'étend du sud-est du Manitoba jusqu'aux provinces maritimes du Canada et de la pointe méridionale de la Baie James jusqu'au sud de la région des grands lacs (Johnston 1990). Cette espèce est habituellement associée aux zones humides (Bergeron et al. 1983, Bergeron et Bouchard 1983, Johnston 1990), mais pousse aussi sur des sites mésiques et xériques (Archambault 1989, Larson et Kelly 1991). Par conséquent, elle occupe une grande variété de sols organiques et minéraux (Collier et Boyer 1989, Johnston 1990). Le cèdre blanc est très susceptible à l'endommagement par les feux de forêt à cause de son écorce inflammable, d'où sa plus grande abondance dans les sites protégés tels les marais, les bords des lacs et rivières, ainsi que sur les îles dans les régions où les feux sont sévères (Heinselman 1973, Ericsson et Schimpf 1986, Johnston 1990). Dans les sites protégés des feux, cette espèce peut atteindre des âges considérables au-delà de 500 ans (Thompson 1963, Wells et al. 1983, Archambault et Bergeron 1992a, 1992b, Kelly et al. 1994).

Quoique des peuplements équiens peuvent se développer après une perturbation ou par la colonisation de terres agricoles abandonnées (Johnston 1990), les peuplements inéquiens sont plus communs dans la région boréale méridionale où le cèdre est plutôt associé aux stages avancés de la succession (Bergeron et Dubuc 1989, Bergeron 2000). Deux hypothèses sont avancées pour expliquer son apparition tardive. Sa taille plutôt petite comparativement au sapin baumier et à l'épinette blanche pourrait limiter sa capacité de disperser ses graines (Sims et al. 1990). Alternativement, le manque d'un lit adéquat de germination après feu pourrait limiter sa dispersion. Le cèdre blanc germe le mieux sur du bois mort en décomposition et sur la mousse, deux substrats de plus en plus répandus au fur et à mesure que la succession avance et la cohorte d'après feu se désintègre (Scott and Murphy 1987, Simard et al. 1998). L'abondance grandissante avec le temps depuis le dernier feu de forêt s'explique aussi par sa grande capacité de régénération végétative par marcottage, surtout dans les marécages où les sphaignes sont abondantes, ainsi que par sa compétitivité élevée grâce à la tolérance à l'ombre, une grande longévité et la résistance à la plupart des insectes et des pathogènes (Bergeron et Dubuc 1989, Johnston 1990, Sims et al. 1990, Bergeron 2000).

0.3 Objectifs

Bien qu'il existe des études écologiques sur les populations de cèdre blanc occupant les hautes terres et les tourbières (voir Johnston 1990), peu est connu sur les peuplements lacustres de cette espèce et cela malgré son omniprésence dans les milieux riverains de la région boréale méridionale. Ceci pourrait s'expliquer en partie par le faible intérêt commercial pour ces peuplements dû aux restrictions légales (protection de la végétation bordant les cours d'eau). Pourtant, la démographie et la dynamique des peuplements riverains de cèdre (structure d'âge, mortalité, régénération et croissance) peuvent fournir des informations précieuses sur leur environnement puisque les conditions environnementales régnant dans l'écotone riparien diffèrent considérablement de celles rencontrées dans d'autres habitats. Au plan des perturbations, par exemple, une diminution de l'influence du feu s'oppose aux effets grandissants des perturbations riveraines à mesure que l'on se rapproche de la rive d'un lac. La compréhension de l'influence qu'exercent les inondations, les poussées glacielles et l'érosion sur la dynamique des populations et la croissance du cèdre blanc devrait permettre d'évaluer les conséquences qu'avait le changement climatique dans le passé mais aussi d'estimer les suites qu'il pourrait avoir dans l'avenir sous l'effet de serre.

L'objectif principal de cette thèse est donc d'accroître les connaissances sur la distribution, la croissance et la dynamique des peuplements riverains de cèdre blanc bordant le lac Duparquet et de déterminer les facteurs environnementaux qui les déterminent. De plus, cette étude vise à préciser le statut dynamique des populations de cèdre blanc dans la zone riveraine du lac Duparquet en relation avec les fluctuations à long terme du plan d'eau au cours des derniers siècles. La recherche se base sur l'hypothèse que le réchauffement atmosphérique observé depuis la fin du «Petit Âge Glaciaire», et coïncidant avec une augmentation des précipitations estivales dans la région du lac Duparquet (voir Fig. 0.2), a causé une hausse du niveau des eaux du lac et un déséquilibre démographique de la frange riveraine de cèdres blancs. Les objectifs visés par cette étude sont de: i) caractériser la végétation arborescente riveraine du lac Duparquet en fonction de la géomorphologie des rivages, ii) évaluer l'influence des inondations sur la croissance radiale du cèdre blanc, iii) évaluer les réactions du cèdre blanc à un rehaussement artificiel du niveau d'eau, iv) évaluer l'effet des feux de forêt et des perturbations riveraines sur la dynamique des populations de cèdre blanc et v) reconstituer les variations à long terme du niveau du lac Duparquet.

L'étude des peuplements riverains de cèdre blanc au bord du lac Duparquet est prometteuse pour plusieurs raisons. D'abord, ce lac d'une quarantaine de kilomètres carrés n'a jamais été régularisé et a donc préservé son régime hydrologique naturel contrairement à la plupart des grands lacs de la région. De plus, les forêts riveraines sont restées intactes sur la plus grande partie de son périmètre parce qu'elles ne furent pas touchées par les coupes forestières à grande échelle qui ont débuté dans le bassin versant du lac Duparquet vers la fin des années 1970 (Harvey et Bergeron 1989). En plus, la présence de cèdres âgés de quelques centaines d'années (Archambault et Bergeron 1992a, 1992b) proches des rives du lac permet le suivi des populations et de la croissance radiale sur plusieurs siècles. Finalement, la localisation du lac Duparquet, proche de la limite méridionale de la forêt boréale, concorde avec la zone d'oscillation du front polaire (Bryson 1966, Dugas 1975). Un changement de celui-ci devrait donc influencer non seulement le climat régional mais aussi, principalement par les précipitations, les fluctuations du plan d'eau de ce lac (voir chap. 0.1). Le lac Duparquet réunit donc plusieurs facteurs propices à l'étude de la dynamique forestière riveraine sous l'influence du climat changeant.

Une étude des effets indirects du changement climatique sur les forêts riveraines doit affronter deux problèmes potentiels majeurs. Le premier est que les fluctuations saisonnières et les changements à long terme du niveau des eaux se chevauchent. Les variations saisonnières du lac Duparquet s'élèvent à environ 2 à 3 mètres et sont supposées être beaucoup plus importantes que les changements décennaux ou séculaires (voir Fig. 0.1), ce qui crée beaucoup de bruit de fond, et il peut être difficile d'isoler le signal à plus long terme. Le deuxième problème est que les changements à long terme du plan d'eau s'effectuent dans la plupart des cas lentement, ce qui permet aux arbres affectés de s'y adapter physiologiquement et physionomiquement, par exemple, par la formation d'un système secondaire de racines. Pour contourner ces problèmes, une approche prometteuse consiste à s'appuyer sur des événements distincts tel que l'analyse des cicatrices glacielles formées par les arbres exposés aux hauts niveaux d'eau après l'abrasion de l'écorce par les glaces flottantes. Tardif et Bergeron (1997) ont reconstitué avec succès les crues printanières du lac Duparquet et le changement temporel de leur amplitude à l'aide de cicatrices glacielles (Fig. 0.1C et D). Dans cette thèse nous poursuivons dans la même voie mais en nous appuyant sur la distribution, la croissance et la dynamique des populations de cèdre blanc dans le milieu riverain.

0.4 Structure de la thèse

Le premier chapitre vise à décrire la distribution des espèces arborescentes retrouvées dans les forêts riveraines du lac Duparquet et à identifier les facteurs environnementaux pertinents pouvant la régir. Puisque le périmètre lacustre montre d'importantes différences par rapport à la topographie, les sédiments et l'exposition aux perturbations riveraines, l'échantillonnage est structuré selon cinq types géomorphologiques de berges: plaines d'accumulation, plaines d'inondation, plages, terrasses et escarpements rocheux. La présence et la surface terrière relative de chaque espèce sont mesurées le long de 95 transects établis à partir du bord du lac jusqu'à 200 cm au-dessus du niveau d'eau moyen. Des régressions logistiques et des analyses multidimensionnelles d'ordination sont effectuées sur l'ensemble des données et pour les cinq types géomorphologiques de berges pris séparément. Les résultats permettent d'évaluer l'importance des perturbations riveraines et des hauts niveaux d'eau dans la distribution des espèces.

Le chapitre deux évalue les effets des inondations sur la formation du cerne de croissance du cèdre blanc, c'est-à-dire la réaction de cette espèce au stress physiologique exercé par un excès d'eau. À cette fin, la croissance intra-annuelle des troncs d'arbres est comparée entre deux sites; un site riverain où les arbres sont exposés aux inondations pendant les crues printanières, et un site supra-riverain où les arbres sont hors de l'influence des crues. Cette étude part de l'hypothèse que l'inondation printanière retarde l'initiation de l'activité cambiale et, par conséquent, la formation des premières trachéides par rapport aux arbres non-inondés. Les arbres riverains peuvent éventuellement rattraper ce retard au cours de l'été en profitant de l'humidité du sol plus élevée qui atténue la sécheresse estivale. L'activité radiale est suivie en utilisant des dendromètres à bande circonférentielle à lecture manuelle et les changements de longueur de la bande sont mesurés quotidiennement du mois de mai jusqu'à la fin d'août. Ces mesures, transformées en changements de la surface terrière, sont comparées avec des facteurs explicatifs (données météorologiques et hydrologiques) pour déterminer lesquels d'entre eux influencent la formation du xylème au cours de la saison de croissance. Les objectifs sont donc i) de délimiter la saison de croissance du cèdre blanc, ii) d'isoler l'effet d'inondation sur la formation du xylème, et iii) de déterminer les facteurs météorologiques qui influencent l'activité circonférentielle quotidienne.

L'analyse des effets du rehaussement artificiel du lac Abitibi sur les peuplements riverains du cèdre blanc après la construction de deux barrages sur la rivière Abitibi, l'un en 1914 et l'autre en 1921, constitue le troisième chapitre. L'objectif principal est d'évaluer les réactions du cèdre blanc au stress physiologique des inondations (croissance radiale) ainsi qu'au régime modifié des perturbations riveraines (mortalité des arbres, cicatrices glacielles, bois de compression, mort partielle du cambium). Il s'agit donc d'évaluer si cette espèce, particulièrement la largeur des cernes de croissance, est utile pour la reconstitution des fluctuations à long terme du niveau d'eau d'un lac naturel tel le lac Duparquet. Quoiqu'un rehaussement artificiel dépasse et la vitesse et l'amplitude d'une augmentation naturelle du niveau d'eau, il peut quand même servir comme modèle car, si un tel événement ne cause pas de réaction de la croissance radiale, on ne peut pas non plus s'attendre à une réaction quand le niveau d'eau monte lentement en laissant tout le temps aux arbres pour s'adapter à l'environnement changeant. Le deuxième objectif est d'évaluer si la limite inférieure de cette espèce vers le lac est contrôlée par un stress excessif d'inondation (limite physiologique) ou plutôt par un régime sévère de perturbations composé de l'activité des vagues, des poussées glacielles et de l'érosion (limite mécanique). L'aire d'étude se restreint à la rive sud de la partie québécoise du lac Abitibi entre la plage de Roquemaure et l'embouchure de la rivière Duparquet où tous les cèdres riverains, vivants et morts, assez vieux pour pouvoir témoigner du rehaussement artificiel du niveau d'eau, ont été échantillonnés.

Le dernier chapitre vise les populations riveraines de cèdre blanc et de frêne noir occupant les terrasses autour du lac Duparquet soumis au régime des feux de forêt et à celui des inondations. L'analyse de la structure d'âge, de la mortalité et de la régénération le long du gradient d'élévation dans huit sites différents permet d'évaluer l'importance des feux de forêt et des inondations dans la dynamique des populations de ces deux espèces. Cette analyse permet aussi de conclure sur la stabilité des populations riveraines en regard des changements hydrologiques à long terme. On a émis les hypothèses suivantes: La zone riveraine serait relativement bien protégée des feux de forêt de sorte que les grands cèdres s'y établirent avant le dernier feu tel que reconstitué pour les environs des sites d'échantillonnage. Aussi, la frange de cèdre blanc autour du lac Duparquet se trouverait actuellement dans un déséquilibre démographique causé par l'augmentation du niveau d'eau depuis la fin du «Petit Âge Glaciaire».

CHAPITRE I

AN ATTEMPT TO EXPLAIN THE DISTRIBUTION OF THE TREE SPECIES COMPOSING THE RIPARIAN FORESTS OF LAKE DUPARQUET, SOUTHERN BOREAL REGION OF QUEBEC, CANADA

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1.1 RÉSUMÉ

Nous avons évalué l'importance de différents facteurs environnementaux pouvant régir la distribution des espèces arborescentes retrouvées dans les forêts riveraines du lac Duparquet dans la région boréale méridionale du Québec, Canada. La présence et la surface terrière relative de 10 espèces arborescentes ont été mesurées le long de 95 transects établis à partir du bord du lac jusqu'à 200 cm au-dessus du niveau moyen d'eau. Des régressions logistiques et des analyses canoniques des correspondances ont été effectuées sur l'ensemble des données et pour les cinq types géomorphologiques de berges pris séparément (plaines d'accumulation, plaines d'inondation, plages, terrasses, et escarpements rocheux). Le gradient d'élévation, reflétant les inondations saisonnières, est le facteur principal expliquant la distribution des espèces. Le type de dépôt de surface, la topographie, l'orientation et les incendies de forêt expliquent, du moins partiellement, les changements de composition observés pour chacun des types géomorphologiques selon un gradient d'élévation. L'exposition aux vagues semble ne jouer qu'un rôle mineur. Cependant, étant donné que les vagues sont responsables de l'érosion et de la sédimentation, celles-ci déterminent largement la différenciation morphologique du périmètre lacustre. Des toposéquences présentant la distribution des espèces caractéristiques sont illustrées pour chacun des types géomorphologiques de berge.

1.2 ABSTRACT

The objective of this study was to evaluate the most important environmental factors determining the distribution of tree species within the riparian zone of Lake Duparquet, located in the southern boreal region of Quebec, Canada. Occurrence and relative basal area of 10 species were recorded within an altitudinal range of 200 cm above mean water level along 95 transects. Stepwise logistic regression and canonical correspondence analysis were performed on the overall data set as well as separately for the five geomorphological shore types distinguished (depositional flats, floodplains, beaches, terraces, and rock outcrops). The elevation gradient, representing seasonal flooding, is the main factor determining the distribution of the species. The differences between the geomorphological shore types with respect to composition and arrangement of the arborescent vegetation along the elevation gradient are at least partially explained by surficial substratum, topography, aspect, and fire. Exposure to wave activity seems to be of minor importance only. However, since they are the driving force of erosion and sedimentation, the waves are to a great part responsible for the morphological differentiation of the shoreline. The distribution of the tree species along a characteristic physiographic cross-section is illustrated for each geomorphological shore type.

1.3 INTRODUCTION

The riparian vegetation surrounding lakes is generally arranged into several parallel shoreline belts, each of them under the influence of different environmental factors. Thus, species of non-woody riparian vegetation belts proximal to the shoreline are arrayed mainly along gradients of increasing wave energy (exposure) and water depth (Keddy 1983, Wilson and Keddy 1985). However, zonation patterns within the riparian forests (distal from the shoreline) are mainly determined by the species' tolerances to frequency, duration and period of flooding (Sigafoos 1961, Beschel and Webber 1962, Bell 1974, Bell and del Moral 1977, Robertson et al. 1978, 1984, Metzler and Damman 1985, Tardif and Bergeron 1992, Nakamura et al. 1997). Soil texture, shore slope, and topography also play an important role as they modify drainage capacity and, hence, duration of flooding (Robertson et al. 1978, 1984, Frye and Quinn 1979, Buchholz 1981, Metzler and Damman 1985, Vincent et al. 1986, Tardif and Bergeron 1992). Some studies focus on the importance that flood-induced disturbances such as water and sediment flow, wave activity, ice push, erosion, and sedimentation have on the distribution of the shoreline species and the dynamics of the riparian forest (White 1979, Pickett 1980, Hupp 1982, Hupp and Osterkamp 1985, Harris 1987, Bégin and Lavoie 1988, Bégin and Payette 1989, Nakamura et al. 1997). Along the shore slope of rivers and lakes, these disturbances and the stress caused by seasonal immersion form a complex gradient that is represented by the elevation relative to the water level. However, hydrological (e.g., ice push) and geomorphological processes can modify this elevation gradient through the creation of landforms such as levees, beach ridges, and terraces (Frye and Quinn 1979, Buchholz 1981, Hupp and Osterkamp 1985, Harris 1987, Hupp 1988, Nakamura et al. 1997). Thus, vertical and lateral patterns of vegetation along the perimeter of the same body of water, be it river or lake, are a function of permanent shore characteristics and their multiple variations associated with shore dynamics (Hupp 1982, 1988, Nakamura et al. 1997).

In the domain of the southern boreal forest, the few studies that have focused on the composition of the woody vegetation adjoining lakes in relation to environmental factors were restricted to a subset of tree species only (Tardif and Bergeron 1992, Bergeron et al. 1997). The aim of the present study is to identify the most important environmental factors that determine the distribution of the shoreline tree species all around Lake Duparquet (Quebec). Unlike most of the bigger lakes in the southern boreal region of Quebec, the water level of this lake has never been regulated by man. This allows the examination of the influence of a natural regime of water level fluctuations on the riparian vegetation.

Our hypothesis was that the species composition of the riparian forests around Lake Duparquet reflects the complex structure of its shoreline with regard to topography, surficial substratum, and disturbance regime. Therefore the distribution of the tree species was analyzed not only in its entirety, but also separately for the several geomorphological shore types distinguished for this purpose. In addition, most of the tree species encountered in the riparian zone of Lake Duparquet are not restricted to the land-water interface, and their distributions also react to terrestrial environmental factors. Therefore, fire was included in the analyses as an independent variable, as it is the most important terrestrial disturbance type in the area (Bergeron 1991).

1.4 METHODS

1.4.1 Study area

The study area is part of the Lake Duparquet Research and Teaching Forest, located approximately 550 km northwest of Montreal in western Quebec, Canada (Fig. 1.1). Landscape depressions are mainly covered by clay deposits that are remnants of the proglacial Lakes Barlow and Ojibway (Veillette 1994) whereas the higher elevations are mostly characterized by the presence of glacial till and rocky outcrops (Bergeron et al. 1983). Climate is continental with cold winters and warm summers. The mean annual temperature and precipitation between 1961 and 1990 (measured at La Sarre, 42 km to the north) are 0.8 °C and 856.8 mm, respectively (Environment Canada 1993). The Lake Duparquet region is situated in the southern part of the boreal forest within the domain of the balsam fir - white birch mixedwood forest (Grandtner 1966, Rowe 1972). Balsam fir (*Abies balsamea*[1]), in association with white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*), characterize the mesic sites (Bergeron and Bouchard 1983). Tamarack (*Larix laricina*), black spruce (*Picea mariana*), eastern white-cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) dominate the hydric sites around Lake Duparquet (Bergeron et al. 1983). Black ash, and sporadically balsam poplar (*Populus balsamifera*), occupy the floodplains of the lake (Tardif and Bergeron 1992).

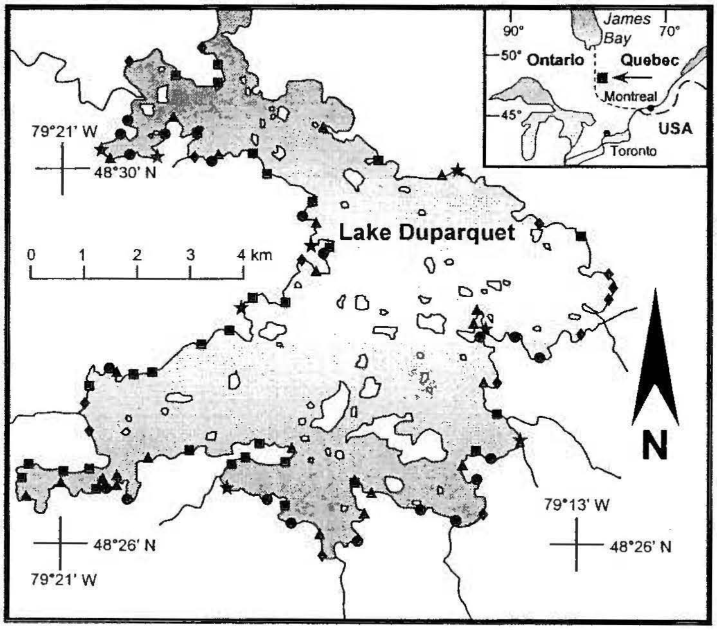

Figure 1.1 Location of the Lake Duparquet study area and the 95 transects analyzed. Each of them belongs to one of five geomorphological shore types: depositional flats (diamonds), floodplains (stars), beaches (circles), terraces (squares), and rock outcrops (triangles).

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[1] Nomenclature of the species names follows that of Burns and Honkala (1990).

The main disturbance type in the area is forest fire (Bergeron 1991, 1998). The reconstruction of fire history for the lakeshore area and the islands in Lake Duparquet, however, shows a considerable decrease of both frequency and extent of fires since about 1850, which is explained by an increase of precipitation (Bergeron and Archambault 1993). Fire influences the composition of the forests by favoring monospecific stands either of jack pine (*Pinus banksiana*), white birch, or trembling aspen. These fire-adapted pioneer species are later replaced by others such as balsam fir, black spruce, white spruce, and eastern white-cedar, which are more shade tolerant and able to reproduce under a closed canopy (Bergeron 1998). This species replacement strongly influences the gap disturbance regime. Early successional forests are characterized by individual or small-group tree mortality, whereas forests of later successional stages are particularly affected by spruce budworm (*Choristoneura fumiferana*) outbreaks, killing whole stands of balsam fir and thus creating larger gaps (Bergeron et al. 1995, Kneeshaw and Bergeron 1998). Three outbreaks have been reconstructed for the 20th century, occurring at intervals of 25 - 30 years (Morin et al. 1993).

Lake Duparquet is a medium-sized lake (about 40 km^2) with a perimeter characterized by deep embayments separated by long ledges. This highly structured shoreline and the extensive number of islands (over 150) emphasize the low depth of the basin. Seasonal water level fluctuations can exceed 3 m. Long-term variations show an upward trend since the mid-19th century, the maximal spring high water levels having approximately increased by 1 m (Tardif and Bergeron 1997). The riparian forests have not been affected by the extensive forestry activities in the catchment area of Lake Duparquet, which began in the late 1970s (Harvey and Bergeron 1989). However, in earlier times there might have been some cutting along lakeshores, the timber being floated on the Duparquet River and Lake Abitibi down to Iroquois Falls in Ontario where a large paper-mill was built in 1913 (Perron 1989, Asselin and Gourd 1995). Potential indirect effects of logging on runoff, sedimentation, and erosion are supposed to be negligible because of the relatively few clearcuts in the vicinity of the lake, and because most of the rivers flowing into Lake Duparquet pass through small lakes acting as sediment traps. Mining and building activities destroyed the natural vegetation of a part of the lake perimeter, particularly on the north shore. Nevertheless, the bulk of the shoreline of Lake Duparquet remains almost untouched.

1.4.2 Data collection

The first step consisted in the establishment of a classification system of the shores based on several criteria that included form of the shoreline (bay, ledge), substratum, topography, and predominant geomorphological processes (erosion, sedimentation). This resulted in the distinction of five geomorphological shore types: depositional flats, floodplains, beaches, terraces, and rock outcrops. Depositional flats are large, flat areas created by the hydrodynamic redistribution of fine mineral sediments over the preexisting surface. High groundwater levels favor the accumulation of thick peat layers. In some cases, wave activity heaped up beach ridges parallel to the shoreline. Floodplains are large, flat areas inundated during periods of high water but without considerable sedimentation in comparison with the depositional flats. Beaches are narrow edges of fine sediment in embayments with moderate slopes. Strong erosion can cause a retrogression of the shoreline creating pocket beaches flanked by rocky ledges. Terraces are raised flats delimited on the landside by a talus of erosion and on the lakeside by a boulder-bordered slope originating from wave breaking. Rock outcrops are mostly steep shores with less than 25 cm sediment over bedrock.

The entire perimeter of Lake Duparquet (without islands) was mapped with the object of associating one of these shore types to each homogeneous section of the shoreline with a minimal length of 50 m. Next, 106 shoreline points were chosen as locations for the establishment of transects in the unaltered parts of the lake perimeter (Fig. 1.1). One hundred points were selected randomly, the number of points per shore type corresponding approximately with the relative length of its total shoreline section[2]. To cover all of the rare tamarack stands, six additional transects were drawn through them.

The starting point of all transects was positioned relative to a reference water level of 266 m above sea level, which roughly represents the mean level of Lake Duparquet. From each shoreline point, a transect perpendicular to the topographic contours was drawn to analyze the composition of the tree layer of the riparian forest within a 3-m wide strip. An exception was made for the sparse tamarack forests where a 10-m width was used in order to reach a sufficient number of trees. Transects ended at 2 m above mean lake level. The geomorphological situation indicated that it was about the position of high water levels. However, some transects could not be completed up to this height, because the topographic divide between the lake and adjacent water bodies did not exceed 2 m in elevation. In this case, data collection ended approximately at the culminating point. The length of the transects varied between 2 m and almost 400 m. The elevation gradient of each transect was divided into four equal parts, all of these plots covering thus a vertical interval of 50 cm. Very long plots were further subdivided until their length did not exceed 20 m in order to get a better resolution of the horizontal distance to the lakeshore. Within each plot, the stem diameter at breast height (dbh) of all living trees larger than 5 cm was measured.

1.4.3 Environmental variables

The environmental data comprise the following factors, recorded for all shoreline points: geomorphological shore type, inclination and aspect of the slope, fetch to the opposite shore of the lake, exposure to wave activity, and year of the last

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[2] All sections of a particular shore type were numbered consecutively, and random numbers were used to select the shoreline sections within which the transects should be placed. To get a somewhat regular distribution of the transects all around the lake, three times as many random numbers were determined, and after arrangement in ascending order, only each third number was retained.

forest fire. Type of substratum, elevation, and horizontal distance to the lakeshore, however, were determined for each plot.

Inclination and aspect of the slope

The inclination of the slope is defined as the angle, measured with a clinometer, between the horizontal at mean water level and the highest point of the transect. The aspect of the slope is represented by the closest of the eight main cardinal points (N, NE, ..., W, NW).

Fetch and exposure

The energy of the waves arriving at the shore is related to wave height, which is in turn a function of speed and duration of winds, fetch, and water depth (Pond and Pickard 1978). In this study, a modification of the method of Keddy (1982, 1984) was applied using fetch measurements, wind data, and shore slope to calculate exposure measurements.

Direct fetch: A map of Lake Duparquet at a scale of 1 : 20 000 was fixed on a drawing board to measure, for each of the 106 shoreline points, the distance to the opposite shore of the lake (mainland or island) in 36 different directions (i.e., at 10° intervals). Directions from which waves cannot arrive have a zero value. The mean of this so-called direct fetch for each shoreline point was used as a separate environmental variable (Table 1.1).

Effective fetch: Narrow embayments and long ledges, but also the many small islands of Lake Duparquet, can result in extreme and less meaningful values for direct fetch (Keddy 1982). Therefore, a correction was performed by taking into account the adjacent fetch measurements: each effective fetch value is composed of the weighted direct fetch values of all adjacent directions that are less than 45° away (for calculations see Keddy 1982).

Wind exceedance: Presuming the shoreline trees are mainly disturbed by severe events, particular importance must be attached to strong winds. Thus, the exceedance value, calculated separately for each of the 36 compass bearings, represents the proportion of strong wind measurements (≥20 km/h) in relation to all wind measurements of the same direction based on hourly readings for the time period ranging from 1971 to 1997. The wind data that was used came from the weather station of Rouyn-Noranda, about 50 km southeast of Lake Duparquet. Exceedance was calculated for three different time periods: May, the growing season, and the ice-free period. During May, the ice of Lake Duparquet breaks up and ice scouring increases the effect of wave activity; during the growing season, from June to September, the trees might be particularly vulnerable to wave damage; and during the ice-free period, from May to November, the waves can affect shoreline vegetation.

Slope: Waves approaching the shore lose a part of their energy depending on the inclination of the lakebed. To consider this topographical effect, the exposure value was multiplied by the sine of the slope, assuming that the slope above the waterline is the same as that in the near offshore zone. Thus, the exposure value for a flat shore where the waves are broken by the gently rising lake bottom decreases considerably (e.g., sin(1°) = 0.017 as the multiplier) whereas it doesn't change much for a steep slope (e.g., sin(60°) = 0.866).

By using fetch (direct, effective) and wind exceedance (May, growing season, ice-free period) in combination with or without the correction by the inclination of the lakeshore, 12 (2 x 3 x 2) different exposure values were received for each shoreline point. Six values were calculated by multiplying fetch with wind exceedance and the consecutive summation over all 36 directions:

$$[1] \qquad E = \sum_{i=1}^{36} (\text{fetch}_{10°i} \times \text{exceedance}_{10°i})$$

The resulting exposure values (E) were in turn multiplied by the sine of the angle of the slope (α) to get a second set of six exposure values (E_S):

$$[2] \qquad E_S = E \times \sin(\alpha)$$

Forest fire

At some shoreline points, trunks and stumps bearing fire scars were found indicating that forest fires have reached the lakeshore. Thus, the year of the last forest fire was determined for each transect using the stand initiation map of Bergeron et al. (1995), which is based on the fire history reconstruction of Bergeron (1991), and Dansereau and Bergeron (1993). Since the northeastern part of the lake perimeter was not mapped by these authors, nine transects with 35 plots have missing values. Showing only 11 different dates, fire was registered on ordinal scale with 1 for the oldest fire (A.D. 1717) and 11 for the youngest (A.D. 1944).

Substratum

At the center of each plot, a sample of the surficial substratum was taken with a tube sampler down to maximally 50 cm. The following five types were distinguished: bedrock, no sediment over the acid basaltic rock outcrop; glacial till, morainic deposition composed of all granulometric fractions from clay up to boulders; glaciolacustrine clay, almost pure clay deposited in the proglacial lakes Barlow and Ojibway; fine mineral sediment, a mixture of clay, silt, and (normally dominating) sand, eroded and redeposited by the wave activity; peat, accumulation of at least 40 cm of organic matter.

Elevation and horizontal distance to the lake

As already mentioned, the elevation of the plots corresponds with one of the four classes of 50 cm between zero and 2 m above mean lake level. The distance between the lakeshore and the center of each plot was measured at a precision of 0.5 m, and, for steep slopes (≥10°), corrected by the cosine of the angle to get a better value for the horizontal distance.

1.4.4 Data analyses

Only those species present in more than three transects were included in the analyses. Thus, *Pinus banksiana*, *Pinus strobus*, and *Pinus resinosa* were not considered. The major habitat of these three pine species seems to be on the islands of Lake Duparquet rather than on the mainland (Bergeron and Brisson 1990, Bergeron et al. 1997). Since the four encountered species of *Salix* (S. *discolor*, S. *lucida*, S. *petiolaris*, and S. *rigida*) were not present in more than three transects and because all of them can be associated with humid habitats (Marie-Victorin 1995), their analysis was limited to the genus level.

Of the 106 transects, 11 had to be omitted mainly because no living individual of the selected tree species was recorded within the 2-m vertical interval or, if some were present, they were too small to be considered (dbh < 5cm). Plots without any living trees, quite often encountered at the lowest vertical interval (0-50 cm) where bare sediment or rock, herbs and shrubs predominate, were not included in the analyses. Hence, the overall data comprise 241 plots from 95 transects (Table 1.1). Twenty environmental variables were used as predictors to try to explain the distribution of the 10 common tree species occurring in the riparian zone of Lake Duparquet. In statistical calculations, the three nominal environmental variables, namely shore type, substratum, and aspect, were transformed into dummy variables.

Stepwise logistic regression (SPSS Inc. 1997) was applied to help identify the combinations of factors that explain the occurrence of each species on the lakeshore. For this purpose, each plot was described in terms of presence or absence of every tree species. Environmental variables were entered in the model if their scores were significant at a level of 0.05, corrected by the method of Bonferroni (Sokal and Rohlf 1995). To deal with the problem of missing values for the fire variable, a first run was performed. If fire was not retained by the forward selection procedure, the calculations were redone without this variable, which allowed all observations to be included.

To identify relationships between the various environmental factors and the relative abundance of the species, a direct gradient analysis was performed using stepwise canonical correspondence analysis (CCA; Ter Braak 1987) with the CANOCO software package. To do this, the relative basal area of each species was calculated as percentage of the basal area of all species present in the same plot. The forward selection is based on a Monte Carlo permutation test with 999 permutations; environmental variables were retained at a significance level of 0.001. To test if the selected variables play a significant role in determining the relative abundance of the species, an unconstrained analysis of the species data by correspondence analysis (CA) was performed. The resulting sample scores were compared with those obtained by CCA through the calculation of a correlation coefficient for each of the four ordination axes.

Logistic regression and the gradient analyses were performed for the complete data set and for each geomorphological shore type separately. In the latter case, only those species present in at least 10 plots of the corresponding shore type were considered.

Table 1.1 Some descriptive statistics of the study sites for all plots and the five shore types

		Geomorphological shore type				
Parameter	Overall	Depositional flats	Floodplains	Beaches	Terraces	Rock outcrops
Lake perimeter[*] (km)	85.7 (100.0%)	8.5 (9.9%)	1.9 (2.2%)	11.6 (13.5%)	29.8 (34.8%)	27.2 (31.7%)
No. of transects	95	14	8	20	31	22
No. of plots	241	69	33	45	66	28
Substratum (% of all plots)						
Bedrock	4.1	—	—	—	—	35.7
Glacial till	25.7	8.7	—	2.2	66.7	39.3
Glaciolacustrine clay	45.2	10.1	97.0	97.8	28.8	25.0
Fine mineral sediment	8.3	23.2	3.0	—	4.5	—
Peat	16.6	58.0	—	—	—	—
Slope[†] (°)	11.8±11.814	0.9±0.539	2.5±1.324	10.6±5.725	9.7±3.336	26.1±15.621
Horizontal distance[‡] of the plots (m) and number of plots (in parentheses)						
0-50 cm[§]	2.7 (21)	57.2 (6)	6.0 (4)	1.3 (5)	2.2 (5)	1.2 (1)
50-100 cm	15.1 (74)	88.0 (35)	14.1 (10)	5.3 (11)	5.0 (16)	3.3 (2)
100-150 cm	14.5 (78)	53.6 (23)	37.5 (13)	8.3 (15)	7.8 (21)	4.6 (6)
150-200 cm	10.5 (68)	76.9 (5)	39.5 (6)	11.6 (14)	10.8 (24)	3.9 (19)
Direct fetch[†] (km)	0.429±0.247	0.424±0.201	0.320±0.185	0.244±0.159	0.525±0.226	0.478±0.287
Exposure[†] (E_S_DG)["]	0.363±0.461	0.025±0.017	0.059±0.058	0.185±0.133	0.360±0.219	0.853±0.687

[*] The shoreline sections modified by man (6.4 km = 7.5 %) and an esker (0.3 km = 0.4 %) were not considered for the selection of the transects.

[†] Mean ± SD.

[‡] Median.

[§] The four height intervals of the variable elevation.

["] Calculated with direct fetch (D) and wind exceedance during growing season (G).

1.5 RESULTS

The highly structured shoreline of Lake Duparquet was reflected in the considerable length of its total perimeter of 85.7 km (Table 1.1). Terraces and rock outcrops each contributed to about one third of the total shore length, whereas the proportions of the three other shore types were much smaller. Beaches and floodplains were almost completely composed of glaciolacustrine clay (Table 1.1). Less than one fourth of all plots in the depositional flats revealed fine mineral sediments as substratum, because those are often covered by a thick layer of peat. In the terrace plots, two out of three borings contained glacial till. Finally, the rock outcrops were often overlain by thin layers of either clay or till.

Depositional flats and floodplains had very gentle slopes, whereas the rock outcrops fell precipitously to the lake (Table 1.1). However, the standard deviations of mean slope for all five shore types were high. The medians of the horizontal distance roughly reflected the slopes: the steeper the shore, the closer the plots were to the lake. But the values for the different elevations are not consistent, mainly because plots without living trees were excluded. Thus, relatively few plots lay in the lowest, and therefore most exposed, elevation class. Some of the more elevated plots had to be omitted either because they were in gaps created by a recent spruce budworm outbreak, or because elevation of the terrain did not reach 2 m. The flat terrain of the flood- and depositional plains resulted in a relatively high number of plots in the two middle elevation intervals because of the multiple subdivision of the very long parts of some transects. This led also to a high value of the median horizontal distance for the alluvial plains. The resulting unbalanced sampling design is not a problem, because this study aimed principally at the description of the species' distribution along an ecological gradient and not at the precise prediction of their abundance as function of the ecological variables. Therefore, it was important to cover the whole gradient but not to represent proportionally each part of it.

Terraces and beaches, respectively, showed the longest and shortest mean direct fetch (Table 1.1). The three other shore types presented the extreme values for exposure to wave activity. Slope was undoubtedly responsible for the infinitely small values for the very flat shoreline sections and the greatest index for the steep rock outcrops.

For all tree species, mean diameter at breast height did not vary significantly between the four elevation classes (Table 1.2). However, several species showed a slight trend towards higher values with increasing elevation from the lake up to about 1.5 m. Eastern white-cedar had a considerably high value for the second elevation interval, indicating a concentration of large and probably old individuals. Relative basal area revealed that white-cedar, tamarack, and black ash were dominant in the plots where they occur, whereas black spruce, willow, balsam fir, and white birch were generally of minor importance (Table 1.2).

Logistic regression over all 241 plots selected elevation as the most significant factor explaining the presence of balsam fir, white birch, and white spruce (Table 1.3). The same variable also was retained for black ash, but with a negative partial correlation coefficient. Balsam fir was also associated to low exposure and the beach shore type. Black ash occurred mainly in floodplains and depositional flats, but the variation in the occurrence of this broadleaf species appeared to be affected by many of the environmental factors. Exposure was the prime predictor of the occurrence of tamarack. The only factor retained for black spruce was horizontal distance to the lakeshore, which indicates the presence of this species in large alluvial plains. Balsam poplar was the only species for which the variable forest fire was retained. In addition to southeastern and western aspect, beaches and floodplains were positively related to the occurrence of trembling aspen. For eastern white-cedar, logistic regression selected slope followed by till, which was the principal substratum of the shore terraces (see Table 1.1). None of the analyzed environmental variables were significant predictors for the presence of the willows. This could indicate that the ecological range of the included species of *Salix* is too large to be analyzed at the level of the genus.

Table 1.2 Number of plots, diameters at breast height differentiated for the four elevation classes, and relative basal area of the 10 tree species

		Diameter at breast height (mean±SD) of the four elevation classes				
Species name (abbr.)	Occurrences (plots)	0–50 cm (cm)	50–100 cm (cm)	100–150 cm (cm)	150–200 cm (cm)	Relative basal area[*] (%)
Abies balsamea (ABA)	61	—	7.8±2.360	11.3±4.650	9.9±3.949	37.0 (0.7-100.0)
Betula papyrifera (BPA)	24	—	8.5[†]	15.3±6.165	19.8±9.334	38.4 (2.1-100.0)
Fraxinus nigra (FNI)	79	11.9±7.758	12.6±7.352	14.3±9.174	9.5±4.928	63.5 (0.5-100.0)
Larix laricina (LLA)	26	10.3±3.830	14.4±6.038	17.7±6.944	—	72.6 (7.5-100.0)
Picea glauca (PGL)	13	—	—	24.9±11.919	19.5±8.246	56.6(11.7-100.0)
Picea mariana (PMA)	12	—	10.2±4.264	13.0±3.599	12.0[†]	25.0 (2.1-65.4)
Populus balsamifera (POB)	25	15.5±8.846	20.1±9.628	15.5±9.423	21.9±11.588	48.2 (0.3-100.0)
Populus tremuloides (POT)	21	—	20.5±9.000	24.4±9.897	27.7±8.598	55.1 (1.2-100.0)
Salix spp. (SAL)	21	12.0[†]	11.0±5.492	11.3±5.128	8.0±0.866	25.5 (0.5-100.0)
Thuja occidentalis (TOC)	126	23.7±13.662	42.0±13.928	23.2±13.974	18.8±14.128	80.0 (2.5-100.0)

[*] Mean and range (in parentheses) of the relative basal area, using only plots where the corresponding species was present.

[†] Only one individual.

Table 1.3 Variables retained by the forward selection procedure of the logistic regression and their explicative power (partial *r*) for each species* ($P \leq 0.004$)

Species	Variable	Partial *r*
Abies balsamea	1. Elevation	0.390
	2. Exposure (E_S_DG)†	-0.186
	3. Beaches	0.171
Betula papyrifera	1. Elevation	0.259
Fraxinus nigra	1. Fine sediment	0.221
	2. Floodplains	0.333
	3. Depositional flats	0.275
	4. Aspect SE	0.258
	5. Exposure (*E*_DG)†	-0.212
	6. Elevation	-0.210
	7. Aspect S	0.204
	8. Aspect NE	0.201
Larix laricina	1. Exposure (*E*_DG)†	0.420
Picea glauca	1. Elevation	0.265
Picea mariana	1. Horizontal distance	0.505
Populus balsamifera	1. Forest fire	0.232
Populus tremuloides	1. Aspect SE	0.318
	2. Beaches	0.308
	3. Floodplains	0.301
	4. Aspect W	0.223
Thuja occidentalis	1. Slope	0.242
	2. Glacial till	0.160

Note: The variables are in the order they were selected by the forward procedure.

*No variable was retained for *Salix* spp.

†Calculated with direct fetch (D) and wind exceedance during growing season (G).

The forward selection of the stepwise canonical correspondence analysis (CCA) retained seven environmental variables as significant (Fig. 1.2). The first two canonical axes were strongly related to the selected environmental variables (species-environment correlation: R_1 = 0.79, R_2 = 0.74), and together accounted for 78.8 % of the variance of the species-environment relationship as well as 16.8 % of the variance of the species data. From the biplot, it can be seen that the first axis represents an elevation/slope gradient that separates the three shore types retained in the analysis. Species on the left, such as white spruce, balsam fir, and white birch, had high relative basal area values on elevated sites, whereas tamarack, black spruce, black ash, and willow dominated on the low sites. A third group, composed of balsam poplar, trembling aspen, and white-cedar, took an intermediate position on the elevation gradient. Five species dominated the beaches, whereas black ash, willow, and balsam poplar were important in the floodplains. No species was close to the depositional flat shore type, because its two major substrata were strongly separated by the second axis. This means that the dominant species of fine mineral sediments (black ash) were different from those observed on peat (tamarack and black spruce).

The correlations of the sample scores from direct and indirect gradient analyses were significant for all four axes (Table 1.4A). Whereas the coefficients for the first and fourth axes took positive values, those for the two other axes were negative. The eigenvalues of the axes were quite different between the two ordination models. The eigenvalues of the third and fourth canonical axes of the CCA were low, and not very important. The strongly correlated sample scores showed that the environmental variables entered in the analysis partially predicted the distribution of the species data. However, the considerable differences in the respective eigenvalues of the CA and CCA indicate the presence of other important environmental factors that were not measured.

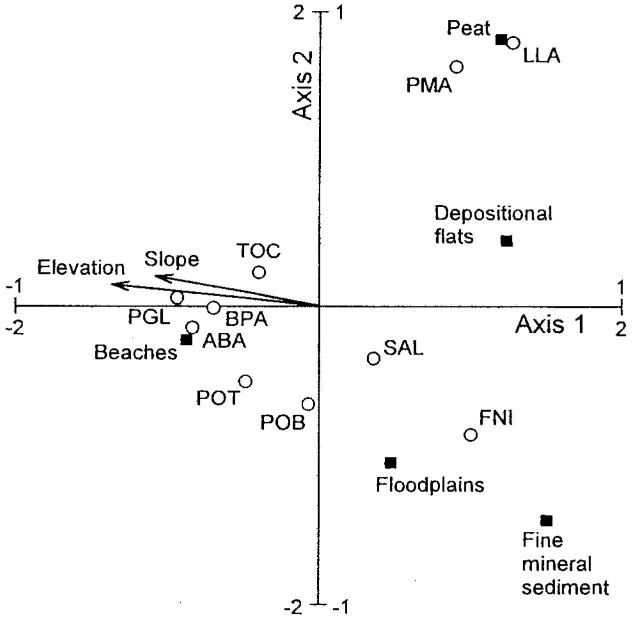

Figure 1.2 Results of the stepwise canonical correspondence analysis of the Lake Duparquet data. Ordination diagram representing species scores (open circles), biplot scores of the environmental variables (arrows), and centroids of the nominal variables (filled squares) for the first two canonical axes. Those span from –1 to +1 for the biplot scores and from –2 to +2 for the species scores and the centroids. See Table 1.2 for the abbreviations of the species names.

1.5.1 Analyses of species distribution according to geomorphological shore types

The results of the logistic regression for each shore type, which included only those species occurring in at least 10 plots, are presented in Table 1.5. Given that within the considered height interval of 2 m tamarack and black spruce were almost completely restricted to the depositional flats, the stepwise procedure for this shore type alone retained the same variables for them as in the overall analysis (see Table 1.3). Exposure was selected for black ash and southeastern aspect for the willows. The presence of white-cedar was predicted by peaty soil and high elevations. In the floodplains too, this species tended to occupy the higher sites. The only species with significant predictors for the beach shore type was balsam fir for which logistic regression retained elevation as the prime factor and (negative) exposure as the second factor (Table 1.5). On the lacustrine terraces, the occurrence of balsam fir and white birch increased with rising elevation and distance to the lake, respectively. Black ash, however, colonized the lower parts of the terraces. White-cedar remained without any retained variable. The case is the same for the rock outcrops where this species was the only one present in more than 10 plots.

Table 1.4 Comparison of indirect (CA) and direct (CCA) gradient analyses

	1st Axis	2nd Axis	3rd Axis	4th Axis
A. Correlation coefficients and eigenvalues for all transects				
Pearson's *r*	0.2164	-0.2278	-0.7742	0.8174
(Prob.)	(0.001)	(0.000)	(0.000)	(0.000)
Eigenvalues				
CA	0.923	0.872	0.792	0.765
CCA	0.539	0.500	0.192	0.063
B. Eigenvalues for the geomorphological shore types				
Depositional flats				
CA	0.969	0.826	0.409	0.330
CCA	0.722	0.141	0.116	0.033
Floodplains				
CA	0.725	0.000	0.000	0.000
CCA	0.468	0.257	0.000	0.000
Beaches				
CA	0.877	0.828	0.000	0.000
CCA	0.432	0.079	0.749	0.445
Terraces				
CA	0.859	0.812	0.684	0.000
CCA	0.400	0.116	0.062	0.748

Note: Pearson's product-moment correlation coefficient (*r*) for the sample scores obtained by CA and CCA of the whole data set (A), and the eigenvalues of both gradient analysis techniques for the first four ordination axes, for all plots (A) and for each shore type (B), respectively. Rock outcrops were not considered because no CCA could be calculated for this shore type (only one species).

Table 1.5 Number of plots, relative basal area, and the results of the stepwise logistic regression with forward selection procedure for each geomorphological shore type including only those species that were present in at least 10 plots

Shore type			Step #1		Step #2	
Species	Plots	rBA* (%)	Variable	Partial $r^{\dagger}$	Variable	Partial $r^{\dagger}$
Depositional flats	69					
Fraxinus nigra	37	71.7	Exposure (E_DG)‡	-0.429	—	
Larix laricina	26	72.6	Exposure (E_DG)‡	0.457	—	
Picea mariana	11	22.8	Horizontal distance	0.448	—	
Salix spp.	10	22.7	Aspect SE	0.357	—	
Thuja occidentalis	20	69.7	Peat	0.334	Elevation	0.285
Floodplains	33					
Fraxinus nigra	25	63.3	—		—	
Thuja occidentalis	10	49.8	Elevation	0.348	—	
Beaches	45					
Abies balsamea	21	47.8	Elevation	0.338	Exposure (E_FI)‡	-0.279
Populus balsamifera	10	61.7	—		—	
Thuja occidentalis	22	81.7	—		—	
Terraces	66				—	
Abies balsamea	18	39.5	Elevation	0.372	—	
Betula papyrifera	11	49.1	Horizontal distance	0.357	—	
Fraxinus nigra	11	58.1	Elevation	-0.387	—	
Thuja occidentalis	50	83.1	—		—	
Rock outcrops	28					
Thuja occidentalis	24	93.1	—		—	

*Mean of the relative basal area, using only plots where the corresponding species was present.

$^{\dagger}P \leq 0.009$.

‡Calculated with direct (D) or effective (F) fetch and wind exceedance during the growing season (G) or the ice-free period (I), respectively.

The comparison of the eigenvalues of the CA and CCA for each shore type (Table 1.4B) shows that the first canonical axis explained most of the variation in the species data, and thus the ordination diagrams of Fig. 1.3 must be particularly interpreted with regard to this axis. In the depositional flats, eastern white-cedar, tamarack, and black spruce had high relative basal areas in plots with peaty soil (Fig. 1.3A). The latter two species were mostly associated with west- and northwest-facing alluvial plains. Black ash and willow, however, dominated those with a southeastern aspect. Stepwise CCA for the floodplain data retained elevation and distance as significant predictors, and both lie on the first axis (Fig. 1.3B). The two species included in the analyses, black ash and white-cedar, occupy opposite positions on this elevation/distance gradient. In the beach shore type, balsam fir dominated the elevated plots, whereas balsam poplar and white-cedar had high relative basal area values in the lower plots (Fig. 1.3C). On the terraces, balsam fir, white birch, cedar, and black ash are arrayed along a high-to-low elevation gradient (Fig. 1.3D). The second axis represents an age-of-fire gradient. Paper birch had high relative basal areas on those sites where the last fire passed recently. For the rock outcrops, CCA could not be performed, because only white-cedar was present in more than 10 plots.

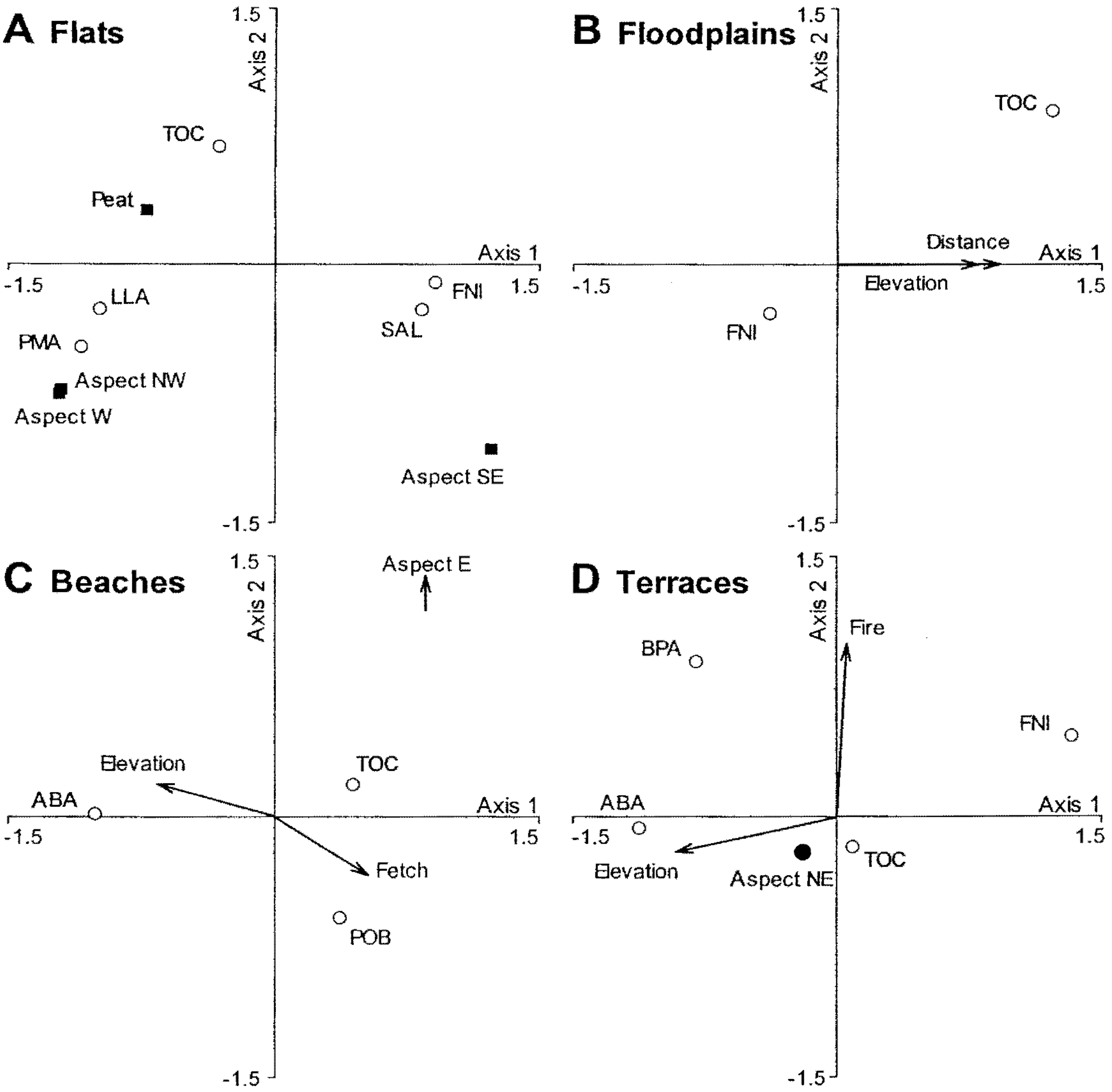

Figure 1.3 Results of the stepwise canonical correspondence analyses for four of the shore types: depositional flats (A), floodplains (B), beaches (C), and terraces (D). No CCA was performed for the rock outcrops because there was only one species in more than 10 plots. See Fig. 1.2 for the symbols and Table 1.2 for the abbreviations of the species names.

1.6 DISCUSSION

All five geomorphological shore types distinguished in this study are the product of several factors that include surficial substratum (partly inherited from postglacial deposits), topography, and the long-term activity of the waves (shore breaking and littoral drift). Consequently, each of them has its own characteristic physiographic cross-section of tree species in the shore immersion zone (Fig. 1.4).

1.6.1 Depositional flats

The dominant tree species in the fens of the depositional flats is tamarack (Fig. 1.4, illustrations Aa and Ab). This species occurs exclusively on peaty soil where it often forms pure and sparse stands. Most of the tamarack forests are situated in the large bays on the east side of the lake. These bays face west or northwest and have long fetches to the opposite shore, which results in high exposure. The exposure measure retained by logistic regression (*E*_DG; Table 1.5) seems to indicate that the gently sloping lakebed does not play a major role. This suggests that exposure during periods of high water maintains the large, treeless belt of shrubby vegetation fronting the tamarack forests (Fig. 1.4, illustration Aa). But this also signifies that high exposure merely explains the absence rather than the presence of tamarack. This is emphasized by the situation observed in the only larch population in an east-facing bay (Fig. 1.4, illustration Ab). Instead of a shrub belt, there is a beach ridge that is colonized by black ash and, on the top, eastern white-cedar. As in the other bays, tamarack occupies the low, peaty sites and is not found on the ridge. Thus, it is assumed that the principal reasons for the presence of tamarack are (i) its tolerance of prolonged flooding, (ii) a habitat relatively protected from wave activity either by a beach ridge or a large shrub belt associated with a gently sloped lakebed, and (iii) the capacity to reproduce on a thick layer of organic matter.

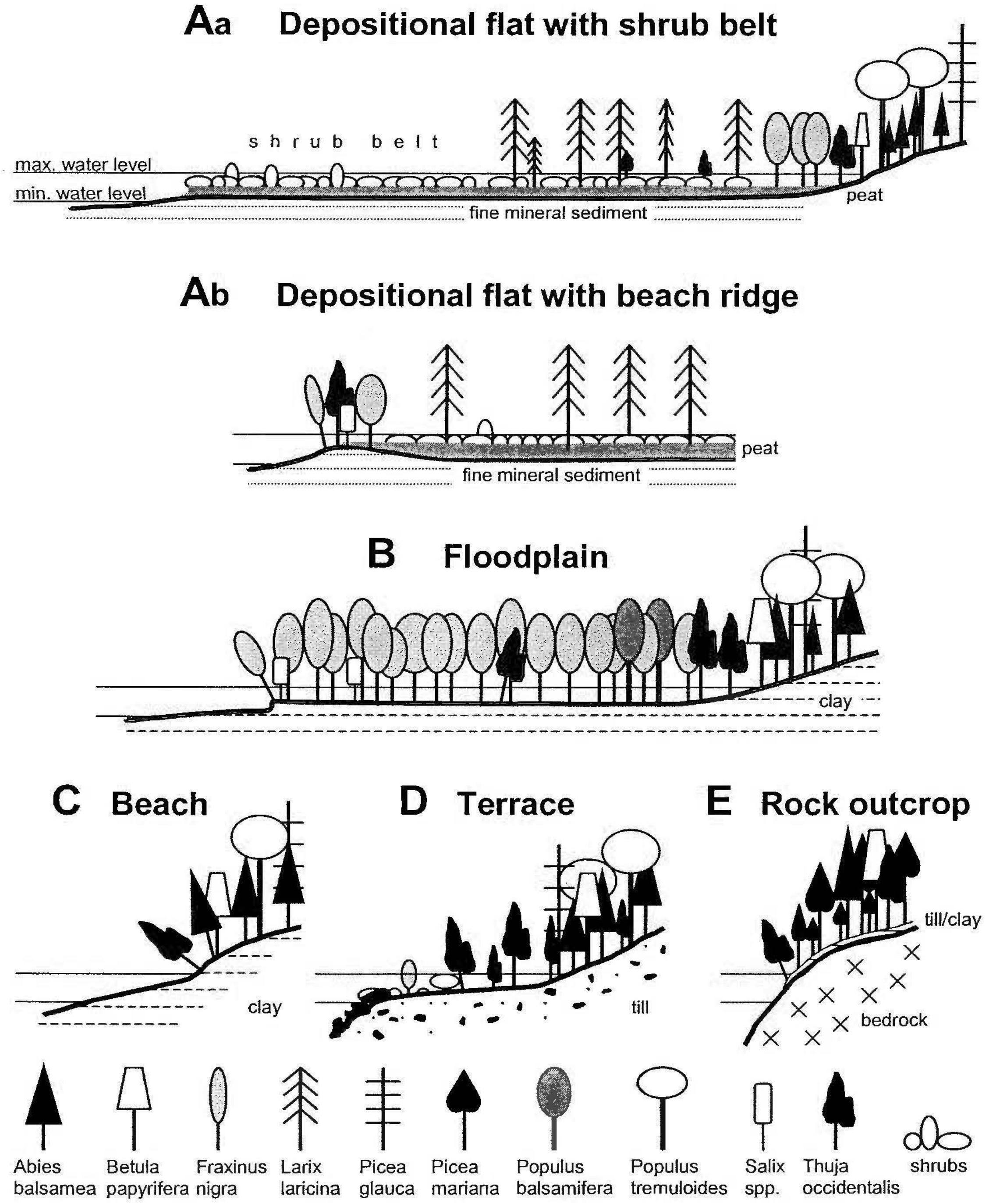

Figure 1.4 Schematic illustration of the distribution of the tree species along characteristic physiographic cross-sections for the five geomorphological shore types. Explanations are in the text.

The absence of tamarack on the beach ridges and in the other shore types might be explained by both, its intolerance to shade (Burns and Honkala 1990) resulting in a low competition capability, and the necessity to recolonize after fire out of preserved zones like the humid riparian fens. Black spruce and especially eastern white-cedar accompany tamarack in some alluvial plains. Black ash and, to a lesser degree, arborescent willows can also be found in the depositional flats where their occurrence is explained by the presence of mineral soil. Thus, they occupy either the marginal zones around the alluvial fens or the beach ridges. Similar habitats along the rivers that discharge into Lake Duparquet are mainly colonized by black ash (Bergeron et al. 1983).

1.6.2 Floodplains

The floodplains of Lake Duparquet are composed of glaciolacustrine clay, which is in some rare cases overtopped by a thin layer of sandy material deposited there by the waves (Table 1.1). They are the domain of black ash, a species well adapted to prolonged seasonal inundation (Fig. 1.4, illustration B). Balsam fir, white-cedar, willow, trembling aspen, and especially balsam poplar may accompany it. Pure stands of the latter species, however, are rare and relatively small. Eastern white-cedar sometimes forms a narrow, monospecific fringe between the black ash stands and the mesic forests above the riparian zone.

1.6.3 Beaches

Almost pure glaciolacustrine clay and a considerable slope (see Table 1.1) facilitate the erosive activity of the waves in the embayments, which leads to a retrogression of the shoreline. This morphological instability of the shore hinders almost completely the development of riparian vegetation (Fig. 1.4, illustration C).

Balsam poplar and eastern white-cedar can dominate the low sites in some bays less affected by the waves.

1.6.4 Terraces

The heterogeneous composition of glacial till, the principal substratum of the terraces (see Table 1.1), could be the reason for the existence, or at least the persistence, of this shore type. Selective erosion of the small particles leaves rocks and boulders on the lakeside slope of the terraces that protect them from being eroded despite generally long fetches and high exposure to waves. Where it was not disturbed by fire, the vegetation shows a distinct physiographic cross-section (Fig. 1.4, illustration D). Black ash occupies the lowest elevations. In contrast with what is observed on the floodplains, the trees on the terraces are often relatively small, and stump sprouting is common. This is the consequence of high exposure to wave activity and ice push. Black ash is followed by eastern white-cedar, which dominates the main part of the terraces, often accompanied by some individuals of balsam fir, white birch, white spruce, or trembling aspen. However, these species are more common in the upper part of the riparian zone.

1.6.5 Rock outcrops

Although rocky outcrops constitute nearly a third of the whole lake perimeter (see Table 1.1), only few trees were recorded within the riparian zone, because these sites are unfavorable to tree establishment and growth. This might be the reason why logistic regression did not select this shore type as a significant predictor of the occurrence of black spruce (see Table 1.3) although this species is very common on xeric bedrock. Protection from fire due to the proximity of the water in combination with a relative longevity on xeric sites (Archambault 1989) might be the reasons why eastern white-cedar was more frequently recorded than other species (Fig. 1.4, illustration E).

1.6.6 Overall data

If all study sites are taken together, one can distinguish three different groups of species with respect to the occupied habitat. The first group includes tamarack, black spruce, black ash, balsam poplar, and willow. These species occupy the low sites that are heavily affected by high water levels, and thus are most common in depositional flats and floodplains. Their occurrence and relative basal area differ according to shore type, surficial substratum, topography, elevation, and aspect. The second group of species is composed of balsam fir, white birch, white spruce, and trembling aspen. Although occasionally found on low sites, they mainly occupy the higher elevations where they are rarely reached by the floods. Thus, they have been recorded in all shore types. However, in floodplains and depositional flats they are restricted to the foot of the slope as it corresponds with the transition to a mesic forest not affected by the seasonal floods of Lake Duparquet. Eastern white-cedar, finally, forms its own group because it is omnipresent on hydric, mesic, and xeric sites. Its presence in almost 85 % of all transects, in all geomorphological shore types, and on all substrata emphasizes its wide ecological range. In general, white-cedar has the highest relative basal area on moderately elevated sites.

1.6.7 Environmental factors

Frequency and duration of seasonal flooding, as reflected in the importance of the variable elevation, emerge as the principal environmental factors determining the distribution of the tree species around Lake Duparquet. In other words, specific differences with respect to tolerance of temporary inundation are of prime importance for the occurrence and relative dominance of the species. However, flooding is not the only environmental factor influencing the distribution of tree species. Substratum, slope, and geomorphological landform also play a role in structuring the riparian vegetation. These conclusions correspond with those from the literature (e.g., Robertson et al. 1978, 1984, Metzler and Damman 1985, Tardif and Bergeron 1992). But focusing exclusively on aquatic disturbances such as flooding, wave activity, ice push, erosion, and sedimentation as done by most studies dealing with riparian forest dynamics (e.g., Hupp 1982, Hupp and Osterkamp 1985, Bégin and Lavoie 1988, Nakamura et al. 1997) is not sufficient for regions with a dominant fire regime. The results of this study show clearly that fire, as a terrestrial disturbance type, may also influence the composition of the riparian forests and the relative importance of the tree species present. The occurrence of balsam poplar at Lake Duparquet, for example, was predicted by the time elapsed since the last fire (Table 1.3), indicating that it is a pioneer species after fire on hydric sites and confirming the observations made by Bergeron and Bouchard (1983). Also, the canonical correspondence analysis for the terrace transects alone (Fig. 1.3D) shows the influence of the forest fire dynamic on the relative abundance of some species. White birch, another pioneer tree after fire (Burns and Honkala 1990), dominates in plots where the last fire passed recently, whereas balsam fir and eastern white-cedar, species that are typical of later successional stages, are more common where fire occurred a long time ago.

Unlike the nonwoody vegetation (e.g., Keddy 1983), and with the exception of tamarack on depositional flats without protecting beach ridge, the direct disturbance effect of the waves seems to be of minor importance for the distribution of the riparian tree species. The influence of the waves is rather indirect. Since they are the driving force of erosion and sedimentation, their activity is responsible, together with substratum and topography, for differentiation and modification of the shoreline, creating the geomorphological shore types.

The comparison between direct and indirect gradient analysis (Table 1.4) showed that the chosen environmental variables explain only a part of the observed variance in the vegetation data. Other factors, such as competitive interactions and reproductive behavior, may play a major role, as it has been shown for nonwoody riparian vegetation (Grace and Wetzel 1981, Keddy and Ellis 1985, Wilson and Keddy 1985, 1986). Herbivory might be of prime importance for the distribution of certain species at Lake Duparquet. As already mentioned, balsam fir is periodically attacked by spruce budworm outbreaks. In addition, it has been observed that beaver (*Castor canadensis*) has cut many trees of trembling aspen close to the shoreline, particularly on the terraces, whereas stands more distant from the shore were unaffected. Thus, this diligent rodent, for which trembling aspen is the preferred resource (Bordage and Filion 1988), considerably influences the relative abundance of trembling aspen.

Since the analyses suggest flooding as the main environmental factor structuring the shore vegetation, it can be asked whether the supposed long-term rise of the water level of Lake Duparquet since the mid-19th century (Tardif et al. 1994, Tardif and Bergeron 1997) manifests itself in the distribution of the tree species. The lowest white-cedar stands are, in contrast with the upper part of the riparian zone, dominated by thick and therefore probably old individuals. This observation is supported by the extremely high mean dbh of 42 cm in the second elevation class (see Table 1.2). This supposed skewed age structure leads us to assume that cedar exhibits a lack of reproduction on the low sites that could signify a landward shift of its realized ecological niche. On the terraces, black ash occupies exclusively the lowest sites (negative partial *r* for elevation in Table 1.5), and is normally of small size. This could suggest a recent colonization, because the terraces became increasingly favorable for this hydric species on the course of the water level rise. The analysis of the age structure along the elevation gradient could be a promising approach to elucidate the effects of a long-term rise of the water level on the distribution of the tree species.

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CHAPITRE II

FLOODING EFFECT ON TREE-RING FORMATION OF RIPARIAN EASTERN WHITE-CEDAR (*THUJA OCCIDENTALIS* L.), NORTHWESTERN QUEBEC

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2.1 RÉSUMÉ

La formation du cerne de croissance du cèdre blanc (*Thuja occidentalis* L.) au bord d'un lac au nord-ouest du Québec, Canada, fut suivie à l'aide de dendromètres manuels afin de i) retracer la période d'activité cambiale, ii) évaluer les effets de l'inondation sur la croissance radiale, et iii) analyser l'influence de facteurs météorologiques. L'activité circonférentielle quotidienne de quatre arbres sur deux sites, l'un à l'intérieur et l'autre au-dessus de la zone riveraine, fut enregistrée pendant la saison de croissance de 1996 afin d'isoler l'effet du haut niveau d'eau printanier relativement extrême. Le bois initial s'est développé de début juin jusqu'à la mi-juillet tel qu'indiqué par l'expansion nette et durable du tronc des arbres. Les changements synchrones et parallèles de la surface terrière aux deux sites montrent que l'inondation n'avait pas d'effets négatifs sur la croissance des arbres riverains, ce qui s'explique par le retrait rapide des eaux juste avant le début de la croissance en juin. La période de mi-juillet à la mi-août fut caractérisée par des fluctuations distinctes à court terme, causées par des périodes alternées de pluie et de sécheresse, et une légère baisse de la surface terrière de tous les arbres sauf chez les deux individus les plus près du lac pour lesquels les dendromètres enregistrèrent la formation du bois final. Le calcul de corrélations de Pearson avec les données météorologiques révèle que les changements quotidiens de la surface terrière des arbres sont positivement associés aux précipitations à l'exception de la période de la formation du bois initial, pendant laquelle les arbres ont probablement bénéficiés d'un taux d'humidité élevé dans le sol après la fonte des neiges. L'humidité moyenne et minimale de l'air corrélèrent positivement et la température maximale de l'air négativement avec les variations quotidiennes de la surface terrière, démontrant ainsi l'importance des changements du flux de sève sur la circonférence du tronc des arbres.

2.2 ABSTRACT

Tree-ring formation of eastern white-cedar (*Thuja occidentalis* L.) at a lake in northwestern Quebec, Canada, was monitored using manual band dendrometers to i) retrace cambial activity phases, ii) evaluate the effects of flooding on radial growth, and iii) analyze relationship with meteorological factors. The daily circumferential activity of four trees at each of two sites, a riparian and an upland site, was recorded during the growing season of 1996, a year with an extreme spring flood. First cambium cell divisions occurred near June 9, followed by a distinct and sustained upward trend in the stem basal area until mid-July that reflected the earlywood formation. The strongly synchronous circumferential activity at both sites suggests no adverse flooding effect on growth of the riparian trees, which is explained by the rapid retreat of the water just before growth initiation in early June. The period from mid-July to mid-August was characterized by strong short-term fluctuations due to alternating drought and rain periods and a slight downward trend of the basal area for six of the eight banded white-cedars. The dendrometers of the two trees closest to the shore, however, showed a slight upward trend probably reflecting the latewood formation. Pearson correlation with meteorological data indicated that precipitation was positively related to the daily changes in basal area of all trees except during the period of earlywood formation, which was probably due to the high soil moisture after spring snow-melting. Mean and minimum air humidity were positively and maximum temperature negatively related to the daily variations in stem circumference during the whole monitoring period emphasizing the importance of the internal water status on stem size.

2.3 INTRODUCTION

Flooding usually represents a severe stress to trees, which results in reduced annual radial growth and, if inundation is prolonged or chronic, in death for almost all tree species (Broadfoot and Williston 1973; Tang and Kozlowski 1982; Kozlowski et al. 1991). However, the growth response depends highly on flood characteristics, species tolerance and tree size (Kozlowski 1984). Temporary inundation can have no effect at all on growth (Green 1947; Johnson and Bell 1976; Mitsch and Rust 1984) or even increase radial increment if flooding is of short duration or occurs during the dormant period (Broadfoot and Williston 1973; Teskey and Hinckley 1977; Kozlowski et al. 1991). Nevertheless, growth response of riparian trees to flooding was successfully used to reconstruct historical changes in lake levels (Stockton and Fritts 1973; Bégin and Payette 1988; Bégin 2000).

Studies focusing on the effects of flooding on the intra-annual radial growth, i.e. on tree-ring formation, are rare. Conner et al. (1981) and Conner and Day (1992) detected distinct growth reduction due to inundation stress in swamp trees growing under different flooding regimes. In contrast, Langdon et al. (1978) found that diameter increment of a typical swamp species was positively related to higher water levels. However, these studies were done in the southern USA with a much more temperate climate relative to the higher latitudes of the boreal forests where the flooding effects on the tree-ring formation might differ.

In this study, we monitored the circumferential activity of eastern white-cedar (*Thuja occidentalis* L.) bordering a natural lake in the southwestern boreal area of Quebec, Canada. Spring of 1996 was characterized by extremely high water levels, which inundated the riparian trees up to 1 m, enabling us to analyze the effect of flooding on the intra-annual tree-ring formation of white-cedar with the perspective of using flood-induced changes in ring width of this common species for the reconstruction of past floods. We compared the daily circumferential activity of shoreline trees flooded in spring 1996 to that of nearby upland trees not affected by flooding. We hypothesized that spring flooding would delay the initiation of the cambial activity and, hence, the formation of the first tracheids relative to the upland trees. In summer, however, the riparian trees could eventually make up for the later start of the growth period by benefiting from elevated soil moisture that prevented drought-caused slowdown or even cessation of cambial growth. As a consequence, flooding and drought may induce changes in both total secondary growth or changes in early- to latewood ratios. We focused on three objectives that were to i) delimit the growing period of white-cedar, ii) isolate an eventual flooding effect by comparison of the circumferential activity between the two sites, and iii) determine the meteorological factors influencing the daily circumferential activity.

2.4 METHODS

2.4.1 Study site

Lake Duparquet (48°28'N; 79°17'W) is a large (~ 40km^2) water body located about 600 km northwest of Montreal, Quebec. The slopes of the surrounding rolling, rocky hills are mainly covered by glacial tills, which are often overlain by proglacial lacustrine clay deposits in the landscape depressions (Bergeron et al. 1983; Veillette 1994). Lake Duparquet has never been regulated and, hence, has a natural hydrological regime. Records of the fluctuations in spring and summer water levels of this lake exist only for 1989 to 1991 and 1996 to 1998 (Fig. 2.1). The spring flood of 1996 was by far the most extreme and represented an extraordinary event as revealed by the partial inundation of several buildings close to the lakeshore.

Cold winters and warm summers characterize the continental climate of the region. From 1971 to 2000, mean annual temperature and precipitation at La Sarre, the closest meteorological station (about 40 km to the north), were 0.7 °C and 890 mm (Environment Canada: http://climate.weatheroffice.ec.gc.ca/climate_normals/). Mean monthly temperatures vary between –18.2 °C (January) and 16.9 °C (July), and snowfall amounts for 28 % of the total annual precipitation. It is not unusual for snowpacks to reach 1 m in depth and to persist into early May. Mixedwood forests dominate the area of Lake Duparquet, the late successional stages being mainly composed of balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.), which are accompanied by white spruce (*Picea glauca* (Moench) Voss) and eastern white-cedar (Bergeron and Bouchard 1983). The latter species occurs over a wide range of soil moisture contents (Collier and Boyer 1989) and develops a shallow, wide-spread root system (Johnston 1990). At the shores of Lake Duparquet, the fire-sensitive white-cedar is very common and can attain ages up to about 900 years (Archambault and Bergeron 1992; Denneler et al. 1999).

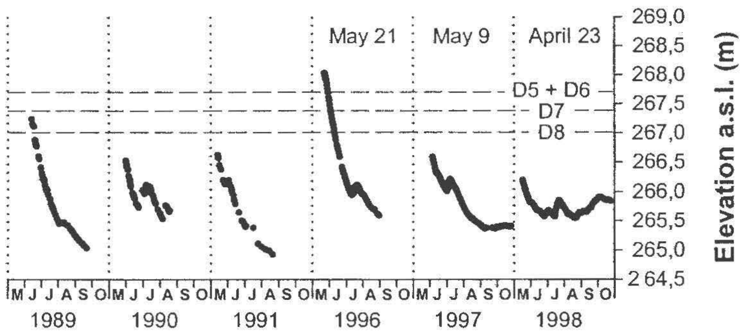

Figure 2.1 Seasonal water level fluctuations of Lake Duparquet between May and October of 1989 to 1991 (data from Tardif and Bergeron, 1997) and 1996 to 1998. The first four years are manual records, whereas 1997 and 1998 represent daily means of a hydrograph placed on the bottom of the lake. The dashed lines indicate the position of the four banded eastern white-cedars from the riparian site (D5 – D8). The date of the first ice-free day is given for 1996 to 1998.

The monitoring site was selected at a part of the northern shore of Lake Duparquet that was unaffected by human impacts and where several healthy eastern white-cedar trees of at least 15 cm diameter at breast height (DBH) were found within and above the riparian zone to minimize differences in environmental factors such as surface sediment type and aspect to better isolate the flooding effect. The topography of the monitoring site forms a slight terrace within the riparian zone whose slope falls relatively steeply down to the lake (Fig. 2.2). The forest established after the last fire dating from 1760 (Bergeron 1991; Dansereau and Bergeron 1993) and the species found surrounding the site were trembling aspen (*Populus tremuloides* Michx.), white birch, and white spruce in the open upper canopy with white-cedar and balsam fir in the sub-canopy.

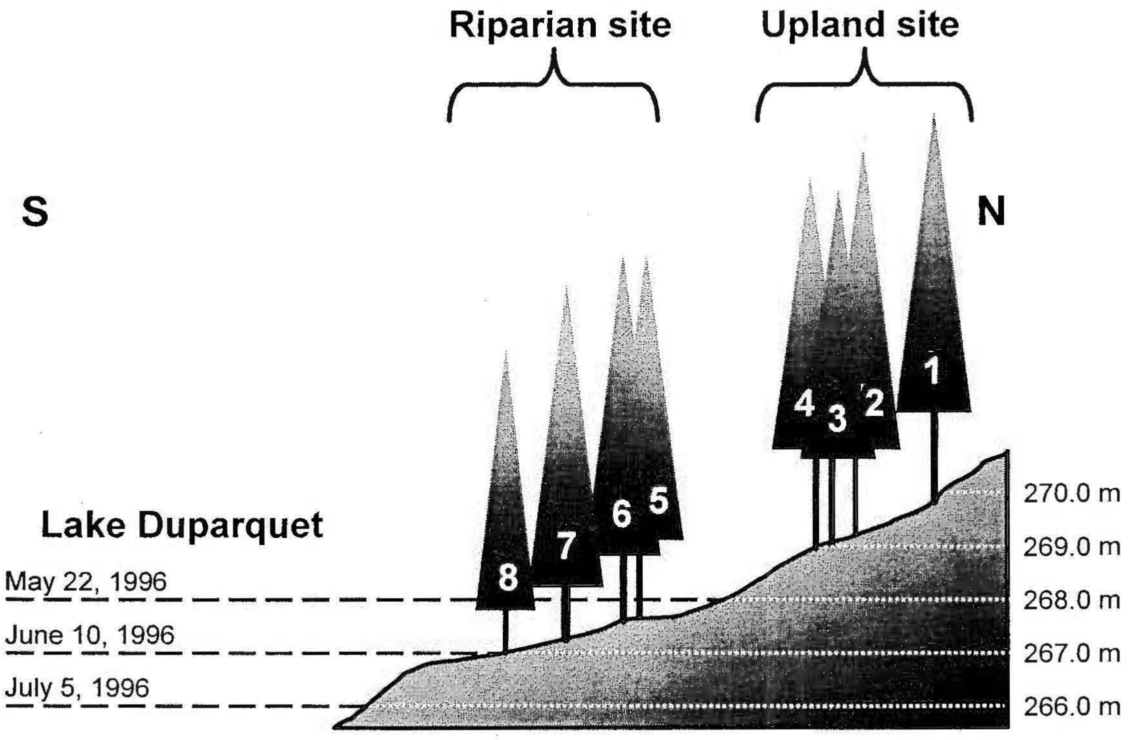

Figure 2.2 Design of the intra-annual circumferential activity monitoring by manual band dendrometers on eastern white-cedar. Four upright trees were chosen at each of two sites, the upland site at least 1 m above the maximum high water level (numbers 1 to 4), and the riparian site at the immediate shore (numbers 5 to 8), respectively. The water level of Lake Duparquet is indicated for three dates (in meters above sea level).

2.4.2 Dendrometer and environmental data

Monitoring the stem radial activity by band dendrometers is non-invasive and furnishes data with high temporal resolution (Kozlowski 1971; Telewski and Lynch 1991; Schweingruber 1996). In spring 1996, we thus installed manual band dendrometers at breast height on the smoothed stems of four upright eastern white-cedars (D5 – D8) within the riparian zone close to the shore (subsequently called the riparian site; see Fig. 2.2) and on the same number of trees that were a few meters uphill and at least 1 m above the maximum high water limit (D1 – D4; subsequently called the upland site). Elevation above the water level and distance from the shoreline in early July 1996 were < 170 cm and ≤ 10 m for the first group of trees, but > 300 cm and ≥ 16.5 m for the latter group (Table 2.1). The stem diameters ranged from 15.6 to 38.0 cm DBH and the approximate establishment date of the trees from ~ 1730 to ~ 1890, both mean size and mean age being slightly higher at the riparian site. The sapwood width varied between 9.0 and 18.3 mm and was composed of 15 to 24 tree rings (Table 2.1).

We used the well type band dendrometer from the *Agricultural Electronics Corporation* (AEC 1990). This device consists of a brass tube attached to the stem and a second brass tube that is inserted within the first one and held back by a spring. An Invar steel band is fixed at the end of the outer tube, wrapped around the trunk, and attached to the inner, movable tube. Changes in stem circumference make move the inner tube back and forth within the outer tube and can thus be determined by measuring the distance between the ends of the two tubes using a micrometer. The resolution of the readings was 10 µm and, to increase reliability, measurements were repeated three times for each tree and consecutively averaged. The daily measurements were always done at approximately the same time, between 16 and 19h (EDT), to minimize the influence of diurnal stem shrinkage and swelling of the tree stems due to transpiration water loss and water uptake (Daubenmire 1949; Kozlowski and Winget 1964; Kozlowski 1971; Herzog et al. 1995). Since the dendrometer readings were done in the late afternoon, i.e., at the minimum of the diurnal cycle of the circumferential fluctuations, those might show a

Table 2.1 Descriptive statistics of the dendrometer trees at the riparian and upland site (see Fig. 2.2 also)

Statistic	Dendrometer trees									
	Upland site					Riparian site				
	D1	D2	D3	D4	Mean ±SD	Mean ±SD	D5	D6	D7	D8
Elevation (cm)[a]	394	317	310	306	331.8 ±41.7	136.8 ±32.8	163	161	130	93
Distance (m)[a]	21.0	18.0	17.0	16.5	18.1 ±2.0	8.0 ±2.3	10.0	9.5	7.5	5.0
DBH (cm)	23.1	16.5	19.2	18.4	19.3 ±2.8	23.6 ±9.9	19.9	20.9	38.0	15.6
Establishment year	~1890	~1825	~1820	~1820	1839 ±34.2	1835 ±71.9	~1870	~1850	~1730	~1890
Sapwood width (mm)	18.3	11.9	10.0	9.0	12.3 ±4.2	14.5 ±1.3	14.1	15.9	15.1	13.0
Sapwood rings (*n*)	17	15	18	21	17.8 ±2.5	20.8 ±3.2	18	23	24	18
Flooding depth (cm)[b]	—	—	—	—	—	—	~30	~30	~70	~100
Flooding end	—	—	—	—	—	—	May 30	May 30	June 4	June 10

[a] with respect to the water level of July 5, 1996 (266.08 m a.s.l.)

[b] at May 22, 1996

higher variability than if the readings would have done in early morning when cell turgor normally is at its maximum.

The daily circumference increment data were compared to both hydrological and meteorological variables. From spring to autumn 1996, the daily water level fluctuations of Lake Duparquet (see Fig. 2.1) were measured manually using a stick driven in the lake bottom. To determine depth of the groundwater table at the two monitoring sites, we dug a hole close to the dendrometer trees D6 (riparian site) and D3 (upland site) and installed a 1-m long piece of a drainage tube of 10 cm diameter in a vertical position. The depth was measured daily by inserting slowly and evenly a narrow plastic tube of the same length into the drainage tube, on which points every centimeter were drawn with non-permanent ink. By this way, depth of the groundwater table was determined by the last point not washed off by the water. Before installing the drainage tubes, we measured the lower limit of the main root horizon at ~ 15 cm (upland site) and ~ 20 cm (riparian site), respectively, i.e., restricted to the organic layer of the soil. Some roots, however, were observed down to 60 cm. The soil at both sites consisted of glacial till, but that at the riparian site contained more clay. Elevation above the lake level of the dendrometer trees and the upper end of the two drainage tubes was surveyed with a WILD-T2 theodolite (WILD, Heerbrugg, Switzerland), and these data as well as the lake level and groundwater table data were transformed into elevation above sea level using the reference point 78L235 of Canada's vertical control data set (Geodetic Survey of Canada 1986). Hourly data of air temperature and air humidity were taken in 1996 from a weather station on Heron Island in Lake Duparquet, ~ 7.5 km southeast of the dendrometer sites. Since the precipitation gauge did not work correctly in that year, we acquired the precipitation data from another weather station located at Rapide-Danseur, ~ 6.5 km to the north.

2.4.3 Data treatment and analysis

Stem circumferences, water level of Lake Duparquet, and depth to groundwater were recorded daily from mid-May to mid-August 1996 (except during four days in June) and sporadically during the second half of August (5 measurements in 2 weeks). The dendrometer data were corrected for thermal expansion and contraction of the Invar band (1 µm m^{-1} °C^{-1}) and the brass tube (3 µm °C^{-1}) (AEC 1990). All dendrometer, hydrological, and meteorological data were checked for outliers caused by lightning, animals, or other, unknown reasons, but no aberrant value was detected. Since each dendrometer band needed some time after installation to adjust before it could reflect changes in tree circumference, the measurements of the first eight days, during which the circumference decreased almost continually, were dropped. Thus, the analyzed measurement series start at May 31.

We transformed the daily circumference increments into basal area (BA) changes to allow comparison between the uneven sized trees (Conner et al. 1981; Conner and Day 1992) and set the value of June 9, the day for which seven of the eight monitored trees reached their early season minimum, to zero (Fig. 2.3A). Furthermore, we transformed the tree BA increment curves into percentage to minimize the effect of age, vigor, and competition (Fig. 2.3B; Daubenmire and Deters 1947; Tardif et al. 2001) and calculated the daily mean percentages for the two monitoring sites (Fig. 2.3C).

Before assessing relationship between the trees' circumferential changes and the meteorological factors, we removed the intrinsic growth trend of the cumulative BAI curves using first-order differencing (Chatfield 1989), which simply consists in calculating the difference between successive values to obtain daily BA changes (Bormann and Kozlowski 1962; Tardif et al. 2001). However, the resulting first-order differences normally have unstable mean and variance with time due to changes of both growth rates and swelling/shrinkage conditions during the growing season (Tardif et al. 2001). Also, biological response to the same environmental variable can

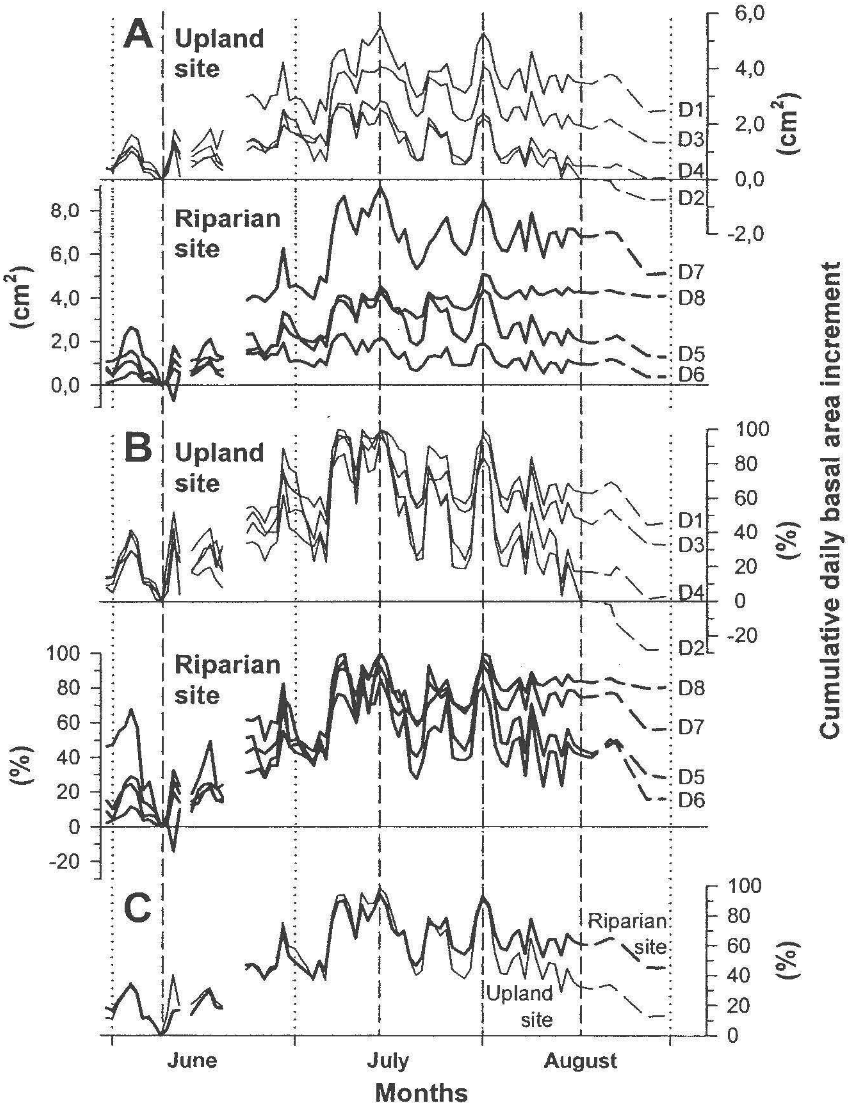

Figure 2.3 Daily basal area (BA) increment curves for the 4 eastern white-cedar trees at the upland (thin lines) and the riparian site (bold lines) from May 31 to August 31, 1996. Absolute (A) and relative (B) cumulative daily BA increment are presented for each tree separately but grouped by site. Mean cumulative daily BA increment in percentage (C) is given for each of the two sites. The dashed parts of the graphs indicate interpolated data for the second half of August. The vertical dashed lines delimit the three periods of cambial activity discussed in the text (June 9 to July 15, July 16 to August 1, and August 2 to 17, respectively).

change during the year as revealed by separate dendroclimatic analyses of early- and latewood chronologies (e.g., Tardif 1996). We divided therefore the daily BA change series of the eight trees into three relatively homogeneous periods covering June 9 to July 15, July 16 to August 1, and August 2 – 17, respectively. For each period, Pearson's correlation coefficients were calculated between the tree's daily BA changes and the meteorological variables air temperature, air humidity (for both: first-order differences of the daily maxima, means, and minima), and rainfall (daily sums). To better highlight the main meteorological factors associated with the daily BA changes, the resulting correlation matrices were joined and submitted to a principal component analysis (PCA), calculated on a covariance matrix using the program CANOCO 4.02 (ter Braak and Smilauer 1998). The meteorological variables entering the ordination were restricted to those with at least six significant correlation coefficients.

2.4.4 Ring-width analysis

To better evaluate if flooding in 1996 influenced radial growth of riparian eastern white-cedar, ring-widths of the monitored trees from the two sites were compared. Therefore, each dendrometer tree was cored twice at breast height and the cores were mounted on wooden supports and sanded. The ring widths were measured to the closest 0.001 mm with a Velmex UniSlide micrometer. Correct dating of the tree rings was verified by visual and statistical crossdating applying the programs ITRVIEW (Grissino-Mayer et al. 1996) and COFECHA (Grissino-Mayer 2001). The software ARSTAN (Cook and Holmes 1986) was used to eliminate the low-frequency variations in the measurement series by 32-year spline detrending and to build tree chronologies by averaging the two index series of each tree. Pearson's correlation coefficients were calculated between each pair of tree chronologies using the routine MAT of the Dendrochronology Program Library (Grissino-Mayer et al. 1996).

Response in annual growth to flooding was analyzed for eight years with extreme spring high water levels of Lake Duparquet. Beside 1996, the years 1922, 1934, 1947, 1959, 1976, 1979, and 1984 were considered. In these years, Lake Duparquet attained the highest spring water levels in the 20th century as evidenced by an ice-scar chronology (Tardif and Bergeron 1997), and it was supposed that the banded riparian trees were flooded as in 1996. The individual ring-width index of the year preceding the spring flood was subtracted from that of the flooding year and the resulting differences were subsequently averaged over all trees from the same site. The between-site differences of this mean growth response to flooding were then tested for significance using the GLM Repeated Measures procedure of SPSS 11.5 (SPSS Inc., Chicago, Illinois).

2.5 RESULTS

2.5.1 Basal area increment

The short-term fluctuations of the cumulative daily BA increment curves of the eight eastern white-cedars were very similar, but, their seasonal trends differed (Fig. 2.3A). For the upland site until August, the rank order of the cumulated BA increase corresponded to the tree's diameter (see Table 2.1); D1 had the greatest increase and D2 the least. But at the riparian site, D8, the smallest tree, accumulated more basal area than the larger trees D5 and D6. As the growing season progressed, the curves of the two trees that were most flooded (D7 and D8) diverged from the falling curves of the less flooded trees D5 and D6 (Fig. 2.3A, B).

Several distinct periods of BA increment were common to both sites (Fig. 2.3C). An initial BA increase was observed during the first few monitoring days followed by a decrease to values less than those noted on May 31, the designated starting point. The period from June 9 to July 15 was characterized by fluctuating but increasing BA values at both sites, suggesting a similar growth rate. During the second half of July, both curves, but particularly that of the upland trees, decreased dramatically, recovered, decreased again, and recovered once more to values near those of July 15. Afterwards, the mean cumulative BA increment curves for the two sites started to diverge. By end of August, mean BA of the upland white-cedars had decreased to only 13 % of the maximum values, whereas mean BA of the riparian trees varied around 60 % before dropping to 45 % in the last days of August (Fig. 2.3C).

2.5.2 Relationship with hydrological and meteorological data

The day after the ice on Lake Duparquet had disappeared in 1996 (May 21), all banded eastern white-cedars of the riparian site were flooded up to ~ 30 cm (D5 and D6), ~ 70 cm (D7), and ~ 100 cm (D8), and the stems remained flooded until May 30 (D5 and D6), June 4 (D7), and June 10 (D8), respectively (Table 2.1, Fig. 2.4D). The groundwater table at the riparian site was 36 cm below the surface (267.17 m a.s.l.) when measured for the first time on June 8 (Fig. 2.4D). Thus, the upper 20 centimeters, representing the main root horizon, were already aerated for tree D6. If we assume for the other three trees the same span of time between the end of flooding and the aeration of the upper root horizon as for D6, i.e., about 5 days, the adverse effect of flooding should end around June 4 (D5 and D6), June 9 (D7), and June 15 (D8) for the four riparian trees. Both lake and groundwater levels had a small secondary peak in mid-July after a period of abundant rainfall (Fig. 2.4C, D). On August 7, the groundwater level for the riparian site decreased below 1 m. At the upland site, the groundwater table was never within the 1-m deep drainage tube over the whole measurement period.

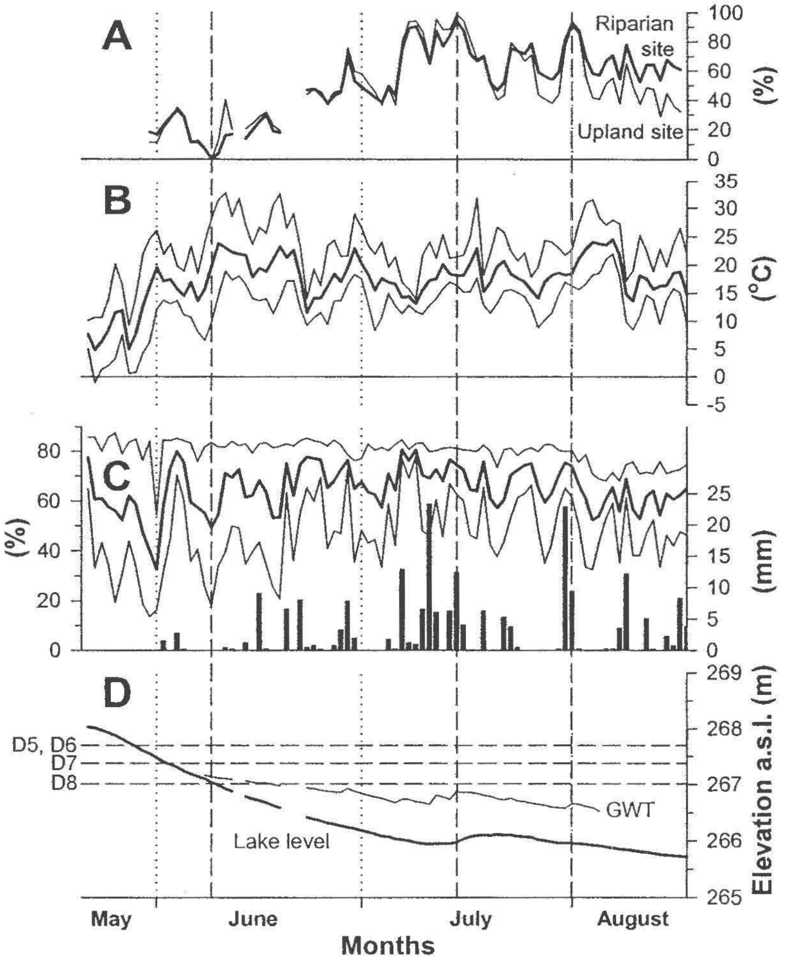

Figure 2.4 Comparison of the 1996 mean daily basal area (BA) increment with selected meteorological and hydrological factors. (A) Mean cumulative daily BA increment in percentage for the riparian (bold line) and the upland site (thin line). (B) Maximum, mean, and minimum air temperature. (C) Maximum, mean, and minimum air humidity (line graphs) as well as rainfall (vertical bars). (D) Water level of Lake Duparquet and depth of the groundwater table (GWT) at the riparian site, both transformed into elevation above sea level. After August 6, the groundwater level remained below 1 m (266.53 m a.s.l.). Elevation of the banded trees at the riparian site (D5 – D8) is indicated. The period covered is from May 22, the second day after disappearance of the ice cover on the lake, to August 17. The vertical dashed lines delimit the three periods of cambial activity discussed in the text (June 9 to July 15, July 16 to August 1, and August 2 to 17, respectively).

Figure 2.4 opposes the mean cumulative daily BA increment to the meteorological and hydrological data. The initial swelling of the stems in early June was preceded by a distinct increase in air temperature of about 10 °C from 5 – 10 °C to 15 – 20 °C (Fig. 2.4B) and paralleled an increase in air humidity and some rainfall (Fig. 2.4C). This was followed by an abrupt decrease in BA during a short dry and cool period. The initiation of a period of generally increasing basal area at both sites coincided with the longest hot period of the whole summer with maximum temperatures above 30 °C (Fig. 2.4B). Towards the end of June, minimum humidity as well as precipitation started to increase. The 37 days from June 9 to July 15 were a wet period with 114 mm of rainfall (i.e., 12.8 % of the annual mean); 65 % of the days had measurable precipitation. However, rainfall was initially low and the decreasing values for lake and groundwater levels suggest greater withdrawals versus additions to soil moisture levels. Maximum cumulative basal area was attained around mid-July when heavy rainfall occurred almost daily. The following strong fluctuations in stem circumference coincided with a series of alternating wet and dry periods (Fig. 2.4).

Mean and minimum air humidity, maximum temperature, and precipitation were the only meteorological factors showing at least six significant correlation coefficients with the trees' daily BA changes and, hence, entered the PCA (Fig. 2.5). The first principal component explained 67.6 % and the second most of the remaining variation in the data (25.9 %). PCA clearly separated the three time periods analyzed (Fig. 2.5). During the early period (June 9 to July 15), the daily BA changes correlated positively with mean and minimum air humidity as well as precipitation but negatively with maximum air temperature. But, none of the correlations with precipitation was significant ($P > 0.199$). This meteorological variable, however, became most important in controlling the daily BA fluctuations during the second period lasting from July 16 to August 1. The slight separation of the trees from the two monitoring sites indicates that stem swelling and shrinkage in the upland site was closer associated with precipitation than in the riparian site (Fig. 2.5). During the third period (August 2 to 17), mean and minimum air humidity as well as maximum temperature exerted the strongest control on stem circumference.

In spite of the diverging trends observed for this period in the curves of the cumulative mean daily BA changes (Fig. 2.3C), PCA did not separate the riparian from the upland trees, indicating similar growth – weather relationships at the two monitoring sites (Fig. 2.5).

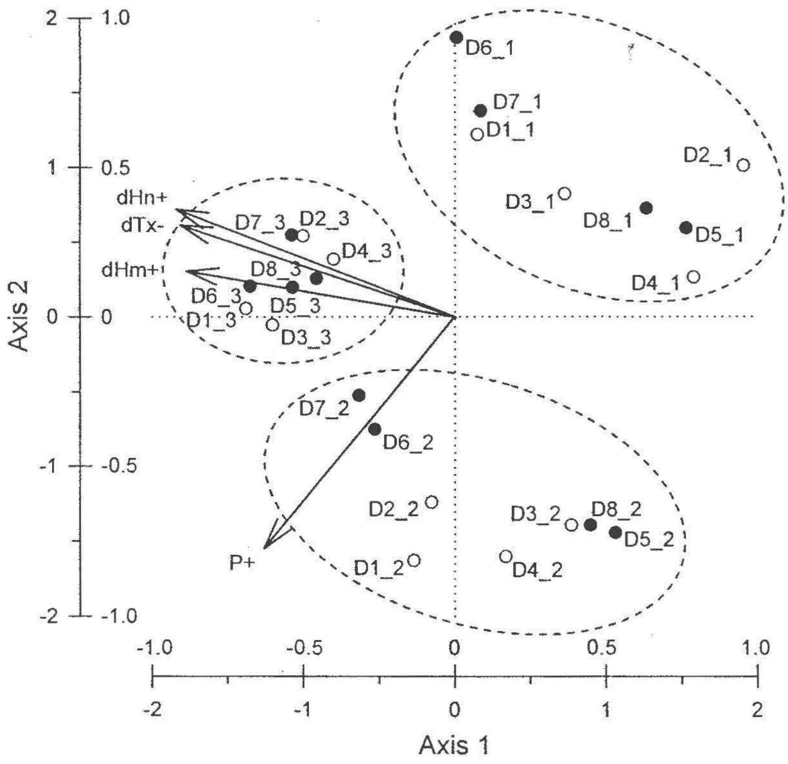

Figure 2.5 Principal component analysis of the Pearson correlation coefficients between the meteorological variables and the daily BA changes of the upland trees (D1 to D4: empty circles) and the riparian trees (D5 to D8: filled circles). The ordination diagram shows the position of the descriptors (axes scales inward) and the trees (axes scales outward) along the first two axes. The descriptors are precipitation (P) as well as the daily changes (= first-order differences) in mean air humidity (dHm), minimum air humidity (dHn), and maximum air temperature (dTx). The plus/minus signs designate positive/negative influence of the corresponding variable. The number after each tree code refers to the three periods distinguished: June 9 to July 15 (1), July 16 to August 1 (2), and August 2 to 17 (3).

2.5.3 Annual growth

The standard chronologies of the eight dendrometer trees showed similar variations (Fig. 2.6) and cross-correlated all significantly for the period 1905 to 1998 ($P < 0.01$; Table 2.2). The index series of the upland trees were generally closer related among each other (mean $r = 0.646$) than were those of the riparian site (mean $r = 0.587$). The individual nearest to the lake, D8, showed the lowest mean correlation coefficient with the other trees. Ring width of 1996, the year of monitoring, was relatively small for all trees but D7 and D8 (Fig. 2.6). Growth response to flooding, based on the eight years with the highest spring water levels in the 20th century, was significantly different between the two sites ($F = 33.217$, $P = 0.001$; Table 2.3). The riparian white-cedar generally showed a less extreme growth reduction respectively a more distinct growth release in flooding years relative to the upland trees, suggesting a positive flooding effect on their annual growth. However, this analysis was based on a low number of trees per site and should be taken with caution.

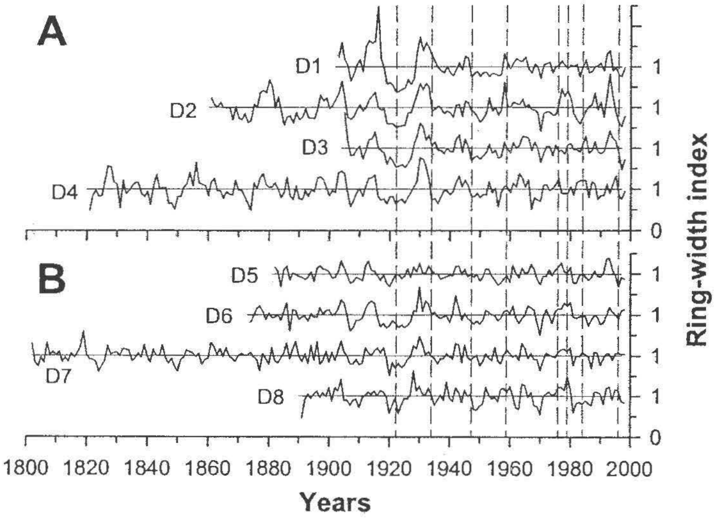

Figure 2.6 Standard ring-width chronologies for each of the eight dendrometer trees ordered by elevation and grouped by the upland (A) and riparian (B) site. The vertical dashed lines indicate years with extreme spring water levels of Lake Duparquet in the 20th century: 1922, 1934, 1947, 1959, 1976, 1979, 1984, and 1996.

Table 2.2 Cross-correlation matrix of the eight tree standard chronologies for the period 1905 to 1998 (n = 94 years)

	Upland site				Riparian site			
	D1	D2	D3	D4	D5	D6	D7	D8
D2	0.653	—						
D3	0.666	0.732	—					
D4	0.526	0.572	0.727	—				
D5	0.417	0.599	0.546	0.416	—			
D6	0.544	0.665	0.665	0.610	0.650	—		
D7	0.545	0.553	0.586	0.521	0.551	0.644	—	
D8	0.308	0.558	0.382	0.285	0.486	0.527	0.665	—
Mean	0.523	0.619	0.615	0.522	0.524	0.615	0.581	0.459

Note: All correlations were significant ($P < 0.01$).

Table 2.3 Annual growth response of the monitored white-cedar to major flooding of Lake Duparquet

Flooding year	Index difference[a] (mean ±SD)		Between-site difference[b]
	Upland site (n = 4)	Riparian site (n = 4)	
1922	-0.138 ±0.042	0.028 ±0.157	0.166
1934	-0.385 ±0.192	-0.161 ±0.063	0.224
1947	-0.311 ±0.107	-0.006 ±0.067	0.305
1959	-0.238 ±0.235	0.030 ±0.095	0.268
1976	0.067 ±0.177	0.110 ±0.047	0.044
1979	0.074 ±0.138	0.047 ±0.192	-0.027
1984	0.160 ±0.106	0.020 ±0.057	-0.140
1996	-0.308 ±0.123	-0.093 ±0.124	0.215
All	-0.135 ±0.020	-0.003 ±0.041	0.132

Note: The result of the GLM Repeated Measures procedure indicates significantly different growth response to flooding between the two sites ($F = 33.217$, $P = 0.001$).

[a] = ring-width index of the flooding year minus the index of the preceding year

[b] = mean of the riparian site minus mean of the upland site

2.6 DISCUSSION

2.6.1 Initiation of radial increment and flooding

Changes in stem circumference registered by band dendrometers reflect not only the increment of the xylem but also that of phloem and periderm as well as diurnal and periodic swelling and shrinkage of the extensible tissues driven by changing water potential (Kozlowski and Winget 1964; Kozlowski 1971; Hinckley and Bruckerhoff 1975; Keeland and Sharitz 1993; Herzog et al. 1995). It is thus difficult to determine exactly the date of the onset of the xylem formation. A first swelling of the stem in early spring should not be confused with the beginning of cambial growth because it is instead caused by the rehydration of the living tissue (Fraser 1956; Kozlowski and Peterson 1962; Kozlowski and Winget 1964). The time-lag between the recovery of cell turgor and the cambium activation of eastern white-cedar was found to vary from few days (Bannan 1955) to several weeks (Tardif et al. 2001). The initial swelling was probably not registered by our dendrometers because monitoring only started at the end of May. A study of the radial growth of eastern white-cedar and several other boreal tree species on an island in Lake Duparquet recorded the initial stem swelling in 1997 near April 20, followed by a prolonged period of stagnating stem circumferences until the beginning of secondary growth in early June (Tardif et al. 2001). Since ice-breakup of Lake Duparquet in 1996 was almost two weeks later than in 1997 (see Fig. 2.1) rehydration of the trees might also have happened later, probably in the first half of May 1996.

The beginning of a general upward trend of the mean cumulative daily BA increment curves on June 9 suggests that cell division started around that day. Such a long-term upward trend has been recognized to reflect wood increment (Belyea et al. 1951; Fraser 1956). In spite of the later ice breakup of Lake Duparquet, growth in 1996 seems to have started at about the same time as in 1997 (Tardif et al. 2001). Both years were characterized by a period of high air temperatures in early June that might have activated the cambium. Several studies provide evidence for such a triggering effect of high spring temperatures for the initiation of radial growth (Daubenmire 1950; Turner 1956; Ahlgren 1957; Fraser 1958), whereas others point instead to the predominance of day length (e.g., Daubenmire 1949).

The early part of the mean cumulative daily BA increment curves of the two study sites were quite similar, suggesting that cambial growth began at about the same time. This simultaneous initiation of wood production points to a common environmental trigger such as the above mentioned air temperature or day length. Growth of swamp tree species in the southern USA has also been shown to start at the same time independently from the flooding regime (Conner et al. 1981; Conner and Day 1992). On the level of the individual trees, however, D8 as the tree that was flooded for the longest time (until June 10) emerged because the sustained upward trend in cumulative basal increment only started on June 11, i.e., two days after the other seven trees (see Fig. 2.3A and B). This could indicate a slight delay of growth initiation due to prolonged flooding.

2.6.2 Intra-annual radial increment and flooding

Three particular phases of the mean cumulative BA increment were distinguished between early June and mid-August 1996. The early period from June 9 to July 15 was characterized at both sites by a constant and almost linear upward trend with some distinct short-term decreases. This increase in BA reflected earlywood formation, which normally constitutes the main part of a conifer tree ring (Schweingruber 1988). In 1998, the earlywood-latewood transition also occurred about mid-July as evidenced by histological samples taken from the same trees (unpublished data). Flooding did probably not influence the growth rate of the riparian trees during the early period because the relative circumferential expansion was very similar at both sites. This observation might be explained in two ways. First, dendroclimatic and other studies provide evidence that the earlywood part of a tree ring is formed principally with stored carbohydrates that were produced during the previous growing season, whereas the actual photosynthetic production is of minor importance (Wareing 1951; Fritts 1976; Tardif 1996). Secondly, the water retreated from the stem bases of the riparian trees not later than June 10 (at D8). Even if the soil was saturated for some days more, flooding occurred probably too early in the growing season to adversely affect the growth of eastern white-cedar, which is very tolerant to high soil moisture (Collier and Boyer 1989; Johnston 1990). The non-significant correlations with precipitation during this early growth period indicate that stem expansion was not limited by water availability in neither of the two sites, probably because of high soil moisture after the spring snow-melting. This contradicts the findings of Tardif et al. (2001) who observed a significant positive effect of rainfall on stem expansion of white-cedar and other species on an island in Lake Duparquet during the early growing season of 1997. The lower sensitivity to rainfall in our monitoring sites might be due to lower slopes and thicker organic layers, accumulated during the much longer period since the last forest fire, which both increase storage capacity of the water from spring snow-melting.

After mid-July, precipitation became a significant factor in controlling the stem circumference changes in both study sites, suggesting reduced soil moisture. This water depletion effect was found to be slightly stronger for the upland trees because of the closer positive association of rainfall with their circumferential variations and the more pronounced reductions of their mean cumulative daily BA increments during dry periods. A closer examination of the individual increment curves reveals that the trees closest to the lake, D7 and D8, showed the least pronounced contractions during dry periods indicating a lower drought stress. They might have benefited from higher soil moisture due to the prolonged flooding earlier in the year and the higher clay content, i.e., water storage capacity. In addition, the deepest roots of these trees could have had access to the raised groundwater level during the rainy period of mid-July.

During the entire monitoring, but particularly during the third period covering the first half of August, mean and minimum air humidity were strongly positively and maximum air temperature negatively related to the circumferential changes at both monitoring sites. These associations point to the importance of short-term fluctuations in stem circumference due to changes in the internal water balance. Diurnal swelling and shrinkage of the tree stems have been documented in many studies from the earliest dendrometer records to recent works (Friedrich 1897; Kozlowski and Winget 1964; Braekke and Kozlowski 1975; Kramer and Kozlowski 1979; Herzog et al. 1995). Shrinkage during the daytime of the elastic water conduction system and, hence, stem circumference is caused by the increasing water deficit, which is created by the time-lag between transpirational loss and water absorption through the roots (Kramer and Kozlowski 1979; Hinckley and Lassoie 1981; Herzog et al. 1995; Zweifel et al. 2000). Prevailing water absorption during night, in turn, results in rehydration and, hence, a slight swelling of the stem. Changes of the internal water balance of some longer duration have similar effects on stem circumference as the diurnal variations. Dry periods of several days cause a water stress resulting in stem shrinkage, particularly when drought coincided with high temperatures, whereas the contrary is observed after rainfall (e.g., Kozlowski and Winget 1964). The positive correlations of the daily BA changes with mean and minimum air humidity as well as the negative correlation with maximum air temperature indicate thus a high vapor pressure deficit during dry and hot periods. This resulted in transpirational water loss that surpassed water absorption from the soil and, hence, in a contraction of the tree stems. The changing vapor content in the air could also have caused hygroscopic expansion and contraction of the bark although this effect has been shown for seedlings only and may just be of minor importance (Lövdahl and Odin 1992).

The end of the seasonal cambial activity respectively of the growing season is difficult to determine by dendrometer monitoring because of the small diameter of the latewood cells (e.g., Deslauriers et al. 2003). The slow but sustainable BA increment of the two trees closest to the lake between mid-July and mid-August, however, might reflect latewood formation. Histological samples taken from the monitored trees two years later showed that tree-ring formation in 1998 was completed around the same time, i.e., mid-August (unpublished data). The contemporary contraction of the other six stems does not mean that cambial activity of these trees had stopped but rather that the shrinkage due to internal water stress exceeded the expansion due to cell formation and elongation. It was therefore not possible to test our hypothesis that growth of riparian white-cedar benefited from a lower drought stress later in the season because of higher soil moisture. We just can indirectly deduce that there might be such a beneficial effect of flooding on growth of the riparian trees because in the years with highest spring water levels, annual growth of the riparian trees responded relatively positive on flooding compared to the upland trees. In the absence of any between-site difference of both initiation and rate of radial growth in the early growing season, this growth difference must be related to the late growing season, i.e., to latewood formation. It would thus be interesting to analyze the effect of flooding on the early- to latewood ratio of the tree rings.

2.6.3 Inferences to annual increment

From the results of our study we infer that the extreme spring flood of 1996 had no important adverse effect on the radial growth of riparian eastern white-cedar at Lake Duparquet. In other words, the excessive water did not exert a physiological stress on the trees. However, this does not mean that white-cedar is insensitive to water availability. Dendroclimatic analysis of the same species from xeric sites revealed that high precipitation in the early growing season has a positive effect on annual growth, whereas dry periods are negatively related to radial increment (Archambault and Bergeron 1992; Kelly et al. 1994). Thus, white-cedar is stressed by a lack of water, whereas excessive water at the beginning of the growing season seems not to affect adversely its cambial growth.

This inference seems to contradict evidence for reduced radial increment due to flooding stress provided for many species (e.g., Broadfoot and Williston 1973; Conner et al. 1981; Duever and McCollom 1987; Conner and Day 1992; Kozlowski et al. 1991). But, most of these studies were done south of the boreal forest where flooding generally occurs later in the year and the growing season starts earlier compared to the northern regions. In the boreal area, the main part of the floods precedes the growth period. Several studies have shown that radial growth of temporarily flooded trees does not decrease, but sometimes even increase if the flooding is of short duration or pre-dates the growing season (Broadfoot and Williston 1973; Johnson and Bell 1976; Teskey and Hinckley 1977; Mitsch and Rust 1984; Kozlowski et al. 1991). Nevertheless, dendroclimatic studies of black ash (*Fraxinus nigra* Marsh.) in floodplains (Tardif and Bergeron 1993) and tamarack (*Larix laricina* (Du Roi) K. Koch) in alluvial fens (Girardin et al. 2001) at Lake Duparquet revealed a negative impact of high spring water levels on tree growth. These two species, however, grow on lower elevations than the white-cedar trees analyzed for this study and are thus flooded for a longer period. This might explain why they had a flooding signal in their ring-width pattern.

2.7 CONCLUSION

Monitoring of eastern white-cedar by band dendrometers provided useful information about the period of cambial activity in 1996 and its control by meteorological and hydrological factors. The beginning of cell division occurred near June 9. Stem circumference expanded steadily during the consecutive weeks until mid-July when the formation of the earlywood was supposedly completed. Retracing the latewood formation and determination of growth cessation, however, essentially failed because of the highly fluctuating daily basal area changes and a general downward trend in most of the banded trees reflecting stem dehydration. Histological analyses of wood samples taken in short time intervals during the growing season could provide such information.

The principal aim of this study was to evaluate how flooding in the late spring of 1996 influenced cambial activity of eastern white-cedar. Recording of the intra-annual changes in stem circumference of riparian trees did not reveal any adverse effect of flooding neither on the timing of growth initiation nor on the extent or duration of earlywood formation, when compared to upland trees. Thus, secondary growth of eastern white-cedar was not apparently affected by flooding, which might be explained by both the early retreat of the water before growth initiation and the use of stored carbohydrates from the preceding year for the formation of the earlywood. Therefore, it might be difficult to reconstruct past floods using radial increment analysis of this species. However, further studies are needed to elucidate flooding effects on the cambial activity of riparian tree species, particularly on latewood formation that could benefit from higher soil moisture after flooding.

2.8 ACKNOWLEDGEMENTS

We thank Mike Flannigan for providing us with the manual band dendrometers and Danielle Charron as well as Marie-Hélène Longpré for their assistance during fieldwork. We also thank Tom M. Hinckley for his valuable critiques that allowed improving the manuscript. This research was funded by the Swiss National Science Foundation, the Natural Sciences and Engineering Research Council of Canada, and the Quebec Ministry of Education (FCAR program).

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CHAPITRE III

GROWTH RESPONSE OF EASTERN WHITE-CEDAR (*THUJA OCCIDENTALIS*) TO THE DAMMING OF LAKE ABITIBI, WESTERN QUEBEC, CANADA

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3.1 RÉSUMÉ

Le lac Abitibi, un grand plan d'eau situé dans la région boréale méridionale de l'est du Canada, fut transformé en réservoir suite à la construction consécutive de deux barrages. L'objectif de cette étude fut d'analyser l'impact de ces événements sur les peuplements riverains de cèdre blanc afin de déterminer des paramètres de croissance pouvant servir à la reconstitution de l'augmentation de plans d'eau naturels et pour évaluer si la limite lacustre du cèdre est déterminée par le stress d'inondation ou les perturbations riveraines. Le rehaussement artificiel du niveau d'eau d'environ 1,2 m en 1915 a causé la mort instantanée de tous les arbres qui ont formés l'ancienne lisière de la forêt et les blessures et l'inclination des cèdres survivants qui forment l'actuelle marge forestière. Aucun de ces indicateurs n'a enregistré le changement du régime hydrologique en 1922 suite à la construction du deuxième barrage qui a à peine rehaussé le niveau d'eau. Le stress d'inondation n'a pas affecté l'accroissement radial des cèdres, probablement parce que les crues printanières étaient déjà terminées avant le début de la saison de croissance (1915 à 1921) ou parce qu'elles étaient trop courtes et modérées pour nuire au métabolisme des arbres (après 1921). Nous concluons donc que (i) la limite lacustre du cèdre blanc est plutôt une limite mécanique liée à l'action des vagues qu'une limite physiologique et (ii), les paramètres de croissance reliés aux perturbations, tels le bois de compression et les cicatrices glacielles, sont de meilleurs indicateurs pour reconstituer une augmentation à long terme du niveau d'eau de lacs naturels dont les berges sont fortement exposées aux vagues que l'analyse de la largeur des cernes annuels du cèdre blanc.

3.2 ABSTRACT

Growth response of riparian eastern white-cedar (*Thuja occidentalis* L.) to the double damming of a large pre-existent lake in the south-eastern boreal area of Canada was analysed to determine useful growth parameters to reconstruct long-term water level increases of natural lakes and to evaluate whether flooding stress or physical disturbances determine the lake-side limit of this species. The first damming in 1915 caused an artificial rise in water level of about 1.2 m and resulted in death of the trees that formed the ancient shoreline forest and wounding and tilting of the surviving white-cedar that constitute the present forest margin. The second damming in 1922 just caused a small rise in mean water level but altered the hydrological regime of the lake, which, however, had no consequences on mortality and injuring of riparian white-cedar. Radial growth was not affected by flooding stress, probably because inundation occurred either before the start of the growing season (1915 to 1921) or was too short and moderate to adversely affect tree metabolism (after 1921). Thus, we concluded that (i) the shoreline limit of white-cedar rather is a mechanical than a physiological limit and (ii) disturbance related growth responses (e.g., ice scars and compression wood) are better parameters than ring-width of eastern white-cedar for the reconstruction of long-term water level increases of natural lakes whose shores are heavily exposed to waves.

3.3 INTRODUCTION

Flooding is generally recognised as the most important environmental factor limiting the occurrence of arborescent species on floodplains and arranging them along an elevation gradient reflecting their tolerance to flooding stress (Beschel & Webber, 1962; Bell & Moral, 1977; Robertson, Weaver & Cavanaugh, 1978; Metzler & Damman, 1985). Flooding affects trees mainly through adverse changes of soil properties resulting in a physiological stress (Teskey & Hinckley, 1977; Lugo & Brown, 1984; Kozlowski, Kramer & Pallardy, 1991). Abrupt growth reduction and death of the stressed trees are the predominant response to both naturally (Broadfoot & Williston, 1973; Kozlowski, Kramer & Pallardy, 1991; Tardif & Bergeron, 1993; Astrade & Bégin, 1997), and artificially (Harris, 1975; Harms *et al.* 1980; Duever & McCollom, 1987) prolonged flooding. However, short-term growth improvement (Conner, Gosselink & Parrondo, 1981; Stahle, Van Arsdale & Cleaveland, 1992), and no growth response at all (Johnson & Bell, 1976; Mitsch & Rust, 1984) were also observed. The severity of inundation stress depends on both the flooding characteristics and the tolerance level of the trees. The stress increases with inundation length and depth, and it is more pronounced when flooding occurs during the growing season than in the dormant period (Brink, 1954; Harris, 1975; Teskey & Hinckley, 1977; Harms *et al.*, 1980).

Flooding is often accompanied by physical disturbances caused by waves, ice push, erosion, and sedimentation, which also affect shoreline trees. The main consequences of these riparian disturbances are wounding, tilting, and uprooting of the affected trees. Growth responses to such events were successfully used to analyse riparian disturbance dynamics in river environments (Hupp, 1988; Desrosiers & Bégin, 1992; Langlais & Bégin, 1993) as well as on lakeshores (Bégin & Payette, 1991; Lepage & Bégin, 1996; Tardif & Bergeron, 1997*b*; Bégin, 2000*a*; 2000*b*: 2001). Most of these studies took place in the northern cold regions where both the storage of the winter precipitation as snow and the presence of an ice cover enhance considerably the intensity and frequency of the disturbances during spring high water levels and ice drift.

In this study, we examined growth responses of riparian eastern white-cedar (*Thuja occidentalis* L.) to the damming of Lake Abitibi, a large storage reservoir situated in the south-eastern boreal region of Canada, in 1915. Our goal was to detect growth responses useful for the reconstruction of natural water level increases of unregulated lakes, where this long-lived species is common within the riparian ecotone. We hypothesized that the abrupt rise in water level (about 1.2 m) was followed by: (i) a high mortality of the shoreline white-cedar, (ii) an abrupt decrease in growth of the surviving trees, and (iii) an elevated frequency of disturbance-related growth responses like wounding and compression wood.

Lake Abitibi, in fact, was dammed twice. The second dam caused no additional water level rise but altered considerably the hydrological regime of the lake in 1922. This situation is quite rare because the construction of a dam is mostly followed by either the creation of a completely new reservoir, or by an important rise in water level of a pre-existing lake, which obscures the effects of the change in seasonal water level fluctuations. Thus, the second aspect of our study consisted in the analysis of the consequences of the abrupt change in the hydrological regime of Lake Abitibi on the shoreline white-cedar.

The third objective of this study was to evaluate if flooding stress or disturbance impacts control the lower limit of the riparian eastern white-cedar fringe around Lake Abitibi. We proceeded from two competing hypotheses:

Mechanical limit due to severe disturbance regime — Although flooding might affect riparian white-cedar, this species could survive a higher level of flood-induced stress. But the severe mechanical disturbances like waves, ice-push, and erosion, which attain high intensities at the shores of large water bodies like Lake Abitibi, prevent white-cedar from colonising sites closer to the lake.

Physiological limit due to excessive flooding stress — Physiological stress caused by prolonged flooding prevents white-cedar from occurring closer to the lake. Although the riparian disturbances cause some damages and kill some trees, they are not limiting the occurrence of this species towards the lake.

3.4 STUDY AREA

Lake Abitibi (48°40' N, 79°30' W; 264.7 m a. s. l.) is located approximately 600 km northwest of Montreal and 250 km south of James Bay, straddling the border between the two Canadian provinces of Quebec and Ontario (Fig. 3.1). The Abitibi River drains the lake at its western extremity towards James Bay. Glacial till and rocky outcrops prevail on the higher elevations of the fairly flat area (Bergeron *et al.*, 1983), whereas landscape depressions are mostly covered by clayey deposits originating from the proglacial Lakes Barlow and Ojibway (Veillette, 1994). Mean annual temperature and precipitation for the period of 1971 to 2000 were 0.7 °C and 890 mm at La Sarre (about 10 km northeast of the lake), and 0.9 °C and 776 mm at Iroquois Falls (about 40 km west of the lake), respectively (Environment Canada: http://climate.weatheroffice.ec.gc.ca/climate_normals/).

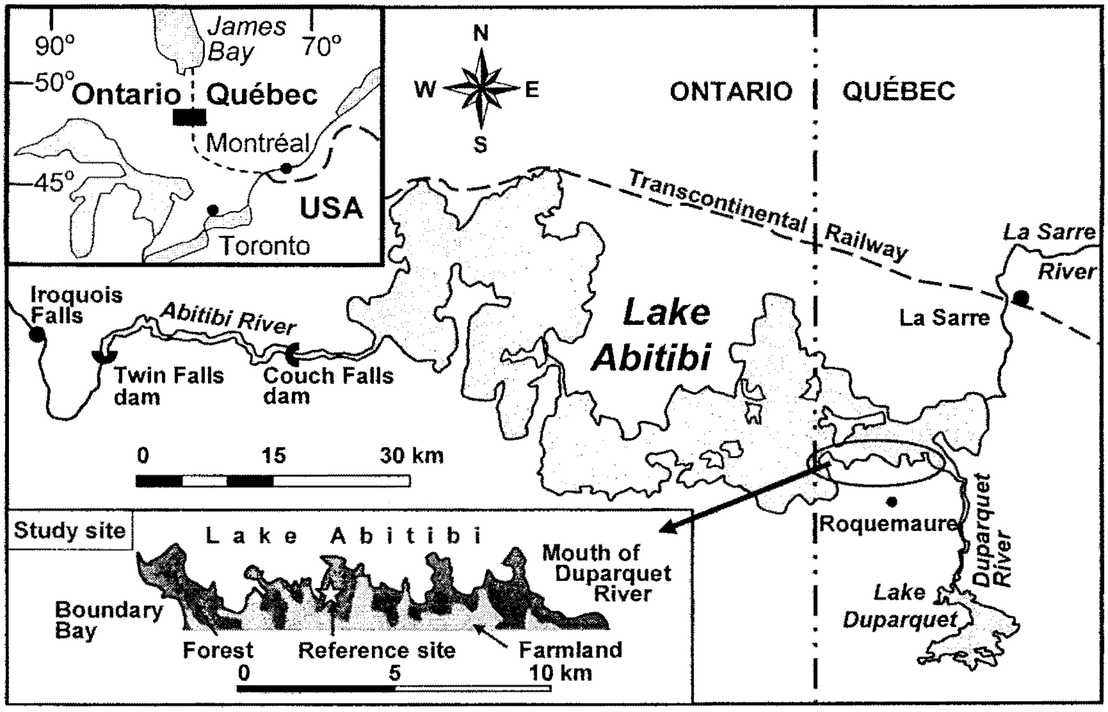

Figure 3.1: Map of the Lake Abitibi study area in the southern boreal region of Ontario and Quebec with enlarged detail showing study and reference sites.

The typical vegetation in this southern boreal area is a mixed forest with balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* (Moench) Voss) dominating on mesic sites (Bergeron & Bouchard, 1983). Tamarack (*Larix laricina* (Du Roi) K. Koch), black spruce (*Picea mariana* (Mill.) B.S.P.), black ash (*Fraxinus nigra* Marsh.), and balsam poplar (*Populus balsamifera* L.) occupy the hydric sites (Bergeron *et al.*, 1983; Tardif & Bergeron, 1992; Denneler, Bergeron & Bégin, 1999). Eastern white-cedar, generally associated with late successional stages (Bergeron, 2000), occurs on a wide range of organic and mineral soils (Bergeron *et al.*, 1983; Denneler, Bergeron & Bégin, 1999). This species is highly susceptible to fire because of its thin and inflammable bark (Johnston, 1990). In areas with severe forest fires, white-cedar is thus most common on relatively protected sites such as lakeshores, islands, and cliffs (Heinselman, 1973; Ericsson & Schimpf, 1986; Larson & Kelly, 1991). There, it can attain ages up to about 900 years (Wells, Thompson & Fons, 1983; Archambault & Bergeron, 1992*a*; 1992*b*; Kelly, Cook & Larson, 1994).

3.4.1 Damming of Lake Abitibi

The following historical reconstructions had to be compiled from secondary information sources because neither the dates of damming of Lake Abitibi nor the corresponding water level changes were recorded. The construction of the transcontinental railway in the early 20th century opened the territory of Abitibi to colonisation around 1912 (Perron, 1989; Asselin & Gourd, 1995). The rapidly developing logging activity led to the establishment of a paper mill by *Abitibi Power and Paper Company Ltd.*[1] (herein referred to as *Abitibi P&P*) at Iroquois Falls, Ontario, in the year of 1914 (Pollock, 1995; see Fig. 3.1). Until the establishment of a road network, almost all pulp and paper wood that was cut within the catchment area

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[1] Today *Abitibi-Consolidated Inc.*

of Lake Abitibi was floated down the tributaries, across the lake, and down the Abitibi River to the plant (Asselin & Gourd, 1995).

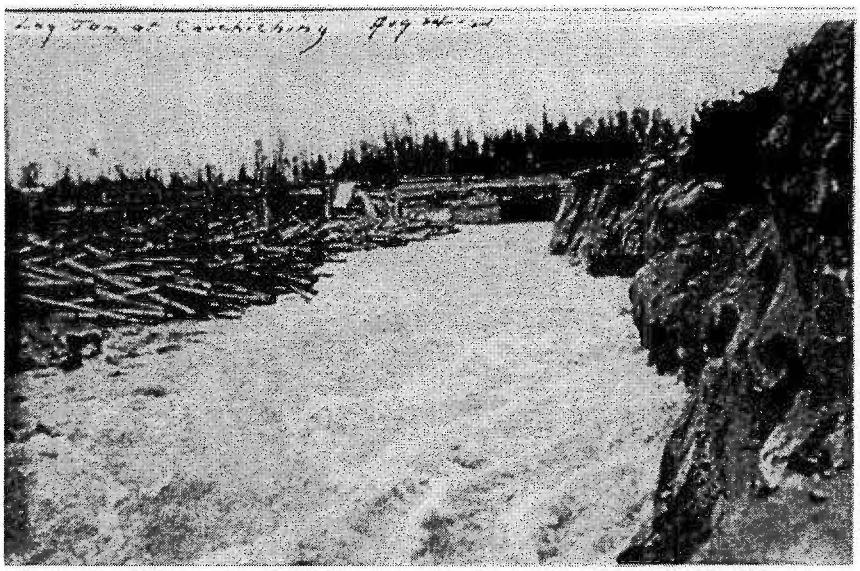

Plate 3.1: The Couch Falls dam on Abitibi River on August 24, 1921. A part of the slots are open to rush down the logs. (Photographer: H. L. Sanborn, at that time engineer for *Abitibi P&P*)

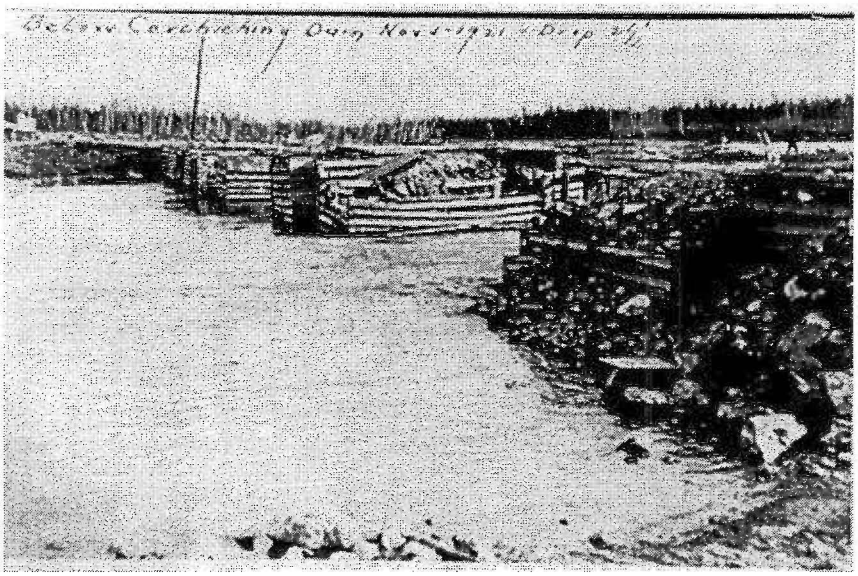

Plate 3.2: The Couch Falls dam on Abitibi River on November 5, 1921. The waters banked-up by the Twin Falls dam have reached but not yet flooded the Couch Falls dam, which is in fairly bad shape just before being submersed. The hand-written note on the upper part indicates that the water dropped about 75 cm (2.5 feet) at this time of the year. (Photographer: H. L. Sanborn)

The shallows of the Abitibi River at Couchiching Falls or, briefly, Couch Falls (about 15 km downstream of Lake Abitibi; Fig. 3.1) were the major obstacles for the floating timber. To facilitate its passage, *Abitibi P&P* built a small dam just upstream of these rapids in 1914 (Lee, 1974; Perron, 1989). This dam consisted of square rock cribs with slots between them to place squared timber or large board down (Plates 3.1 and 3.2). The slots were closed in autumn to hold back the water during winter, and they were reopened the following spring to rush the logs down the rapids after the ice-melt (Michael Palangio[2], *pers. comm.*). According to Christopherson (1915) and Trudelle (1937), the water table of Lake Abitibi rose between 1.5 m and 2.1 m during 1915, which caused important inundation around the lake (see also Hudson's Bay Company, 1915: p. 92-103; Couture, 1983). Since the report of Christopherson (1915) dated from early summer, we suppose that the rise of 1.5 m refers to the spring water level. The hand-written note on Plate 3.2 indicates a drop at the Couch Falls dam of 75 cm (2.5 feet), which might represent the minimum value because this photo was taken in November, i.e., at low water level. It seems thus that the artificial rise in spring water level was more important than that in autumn (Fig. 3.2b).

In 1921, *Abitibi P&P* completed the construction of a second dam as part of a hydroelectric power station at Twin Falls (approximately 35 km downstream of Lake Abitibi; Fig. 3.1) that still is in operation today. The banked-up waters reached the Couch Falls dam in the beginning of November 1921 (see Plate 3.2), and *"in 1922 the Abitibi Power and Paper Company changes the level of the water on Lake Abitibi due to the construction of the Twin Falls Dam"* (Pollock, 1995:104). However, this statement has to be taken with caution because the remnants of the former Couch Falls dam were clearly visible on both sides of the Abitibi River as well on air photos taken on Sep. 14, 1928 (National Air Photo Library, Ottawa, Canada), as on the occasion of an inspection of the site on May 21, 1998. At the time of this inspection, the water table was about 1.5 m below the upper edge of the remnants and, as estimated by comparing plates 3.1 and 3.2 with the actual situation, roughly 0.5 m

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[2] M. Palangio is operator at the power station of *Abitibi-Consolidated Inc.* at Twin Falls.

below the maximum water level under the regime of the Couch Falls dam that prevailed from 1915 to 1921. Hence, it seems that the Twin Falls dam hardly caused any additional rise in water level of Lake Abitibi (Fig. 3.2b).

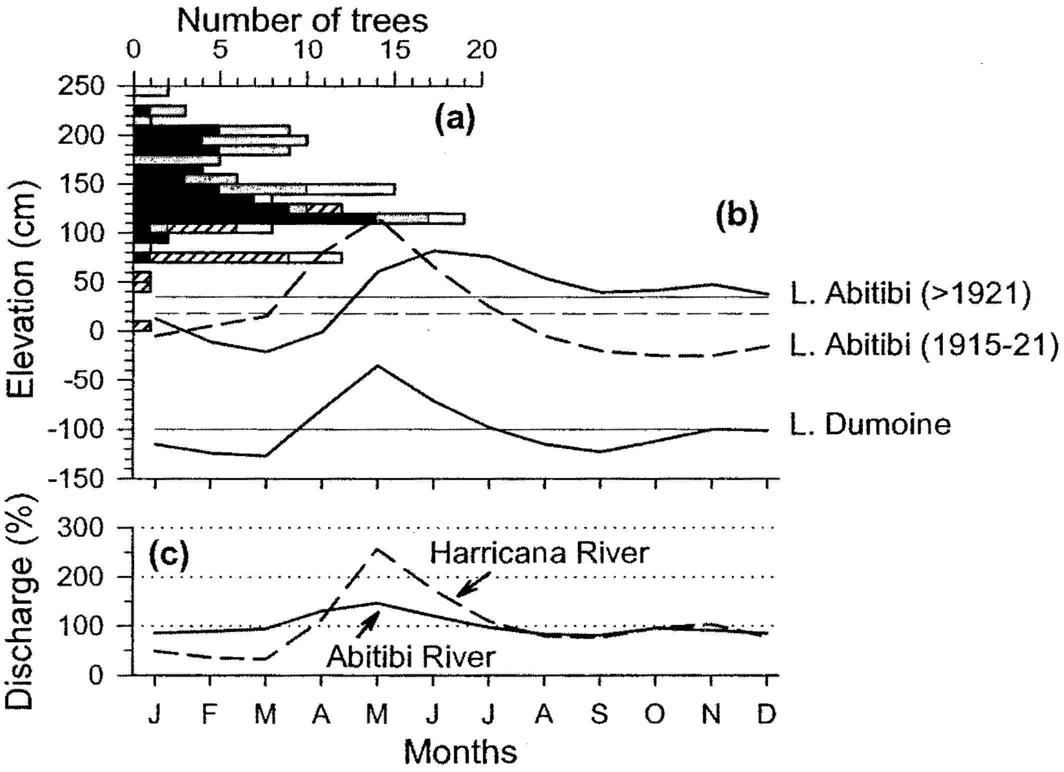

Figure 3.2: Riparian white-cedar in relation with elevation and hydrological regimes of Lake Abitibi (Source of the hydrological data: Water Survey Division of Canada). (a) Frequency distribution of white-cedar along the elevation gradient (lowest tree = 0 cm). The bars indicate dead trees on rock (filled bars; *n* = 61), living trees on rock (grey bars; *n* = 37), dead trees on clay (hatched bars; *n* = 17), and living trees on clay (empty bars; *n* = 14). Only trees that entered in the analyses are shown. (b) Mean monthly water level fluctuations around the annual average (horizontal lines) of Lake Abitibi for the period prior to 1915 (natural regime approximated by Lake Dumoine gauge measurements of 1968 to 1996), 1915 to 1921 (estimation), and since 1922 (L. Abitibi gauge measurements of 1949 to 1997). For explanations see test. (c) Mean monthly discharges of the regulated Abitibi River and the natural Harricana River in percent of the average annual discharge from 1922 to 1993.

3.4.2 Seasonal water level fluctuations

In the absence of any gauge measurements of Lake Abitibi before 1946, we used those of Lake Dumoine, a natural lake located 250 km southeast of the study area (46°50' N, 77°55' W), to approximate the seasonal Lake Abitibi water level fluctuations prior to any damming. The spring to autumn water levels of Lake Duparquet, located only 15 km south of Lake Abitibi (Fig. 3.1), measured for the years 1989 – 1991 (Tardif & Bergeron, 1997*b*) and 1996 – 1998 (unpublished data), showed very similar seasonal patterns, which indicates that Lake Dumoine adequately represents the natural hydrological regime of Lake Abitibi. The Lake Dumoine maximum water level occurred generally in May between two minima in March and September, respectively (Fig. 3.2b).

The mode of operation of the Couch Falls dam (i.e., closing of the slots in autumn and reopening of them in spring) let us assume that, for the seven years from 1915 to 1921, winter and spring water levels of Lake Abitibi were relatively high and decreased rapidly to low levels throughout late summer and autumn (Fig. 3.2b). Maximum water level was supposedly reached in May as under the natural regime. Hence, the construction of the Couch Falls dam changed the hydrological regime of Lake Abitibi only slightly.

The seasonal Lake Abitibi water level regime changed considerably in 1922 due to the hydroelectric power station at Twin Falls. The gauge measurements from 1949 to 1997 indicate that power generation lowered the water table during winter and spring, whereas consecutive refilling of the reservoir resulted in relatively high levels throughout summer and autumn (Fig. 3.2b). Because of its low water level at the end of winter, Lake Abitibi reached the peak level only in June, about one month later than under natural circumstances. These changes in the seasonal patterns of Lake Abitibi water table are confirmed by the comparison of the mean monthly discharges from 1922 to 1993 of the regulated Abitibi River with those of the naturally fluctuating Harricana River at Amos, located about 90 km east of the study area (Fig. 3.2c). The discharge of the Abitibi River was relatively high during winter when hydroelectricity was produced, and relatively low in spring and early summer when the reservoir of Lake Abitibi was refilled.

Summarizing briefly, the prime effect of the Couch Falls dam was the artificial rise in the Lake Abitibi mean water level of about 1.2 m in 1915, whereas the seasonal fluctuations remained almost the same. Its replacement by the Twin Falls dam in 1922 caused only a small additional rise in the mean water table of Lake Abitibi but changed profoundly its hydrological regime particularly by reducing and retarding the spring peak levels.

3.5 MATERIAL AND METHODS

3.5.1 Study site

One large study site at the border of Lake Abitibi was selected instead of several small ones because preliminary observations showed that only few dead respectively old living shoreline trees were preserved and still *in situ* (i.e., not displaced), which could give information about the artificial water level changes in 1915 and 1922. The presence of untouched riparian forests easy of access let us choose that part of the south shore situated between Boundary Bay and the mouth of Duparquet River in the province of Quebec (Fig. 3.1). Although the forest close to the lake was mainly preserved, some stumps of cut trees found during fieldwork suggest that isolated cutting has occurred (see also Perron, 1989; Asselin & Gourd, 1995). The western part of the study site burned for the last time in the 1760s and the central and eastern parts around 1820 (Lefort, Gauthier & Bergeron, 2003).

To distinguish the effects of the changes in water level from other environmental factors influencing tree growth, the largest white-cedar stand close to

Lake Abitibi, but at least 5 m above the high water level, was selected as reference site (Fig 3.1).

3.5.2 Data collection

Along the chosen lake perimeter of about 35 km, we took a cross-section above the root collar of all dead white-cedar trees and snags that were still *in situ*, well preserved (i.e., with at least 50 tree rings to allow crossdating), and situated beneath 2.5 m relative to the water table. Within the same area, we also sampled all living white-cedar with a minimum diameter at breast height (dbh) of 10 cm and whose innermost tree ring dated back to at least 1885, i.e., 30 years before the first damming, to allow comparison of the growth patterns before and after damming. The selected trees were either cored twice or, if coring indicated a non-rotten centre of the stem, two discs were sawn, one at the dbh level to analyse radial growth and formation of compression wood, and the second at the stem base for the ice-scar analysis. Altogether, 89 dead and 51 living riparian white-cedar were sampled. In addition, two cores from 18 white-cedar older than 1885 were taken at the reference site.

The soil and elevation above the water level were determined to take into account the influence of different site conditions on growth of eastern white-cedar. Since surface substrata within the study site were restricted to glaciolacustrine clay and basaltic rock (Anonymous, 1995), only two soil types were distinguished that were supposed to influence the development of the trees root system in different ways. *Clay* — Deposit of at least 25 cm of clay that is partially accompanied by rocks and boulders. The poor soil aeration restricted the root system mainly to the organic layer at the top. *Rock outcrop* — Weathered rock without or with only a thin (< 25 cm) layer of clayey sediment. Most of the trees were deeply rooted within cracks. The substratum was assigned to each of the sampled white-cedar either after a visual check or after having taken a soil core of maximally 50 cm depth close to the stem. Elevation above the lake was measured for each tree, the values being compensated for changing water levels during the data collection period using daily measurements of the Lake Abitibi gauge. Thereupon, each value was converted into the elevation difference with respect to the lowest of all sampled trees (= 0 cm).

3.5.3 Crossdating and chronology development

The wood samples were prepared using standard procedures of dendrochronology (Stokes & Smiley, 1968; Fritts, 1976). The samples from living trees were visually crossdated by a simplified skeleton-plot method (Yamaguchi, 1990). The ring widths of all samples, i.e., cores as well as two radii per disc, were then measured to the closest 0.001 mm with a Velmex UniSlide micrometer. All raw measurement curves were statistically crossdated with two master chronologies of eastern white-cedar from the shores of the nearby Lake Duparquet (Archambault & Bergeron, 1992*a*: AD 1185-1987; Tardif & Bergeron, 1997*a*: AD 1417-1987) using the program COFECHA (Grissino-Mayer, 2001). Conformity of the statistically dated ring-width series from the dead trees was visually checked using pointer values (Schweingruber *et al.*, 1990). A total of 78 dead and 51 living riparian trees were successfully crossdated and entered into the analyses. Eleven of the dead white-cedar were not only used to calculate mortality but also in the other analysing steps because they covered at least the period from 1885 to 1945 (= 1915 ± 30 years), which was the minimum time interval fixed to avoid biased results due to changing sample composition.

Ice scars and compression wood sequences were dated for a subset of 41 trees, for which complete discs could be sawed. Ice scars are partially or completely overgrown wounds on the lake side of the stems, and caused by the abrasive impact of drifting ice, whereas compression wood is composed of tracheids rich in lignin typically formed on the downhill side of tilted coniferous trees (Kaennel & Schweingruber, 1995). After sample preparation, we discovered partial cambium dieback on several cross-sections, which was not detected during sampling either because it was taken for an ice scar or because the bark was still in place and thus not showing the typical strip-bark morphology (Larson, Matthes-Sears & Kelly, 1993; Larson, Doubt & Matthes-Sears, 1994). We included cambial dieback in our analysis to evaluate if it was related to damming of Lake Abitibi.

To evaluate the effects of the water level changes of Lake Abitibi on radial growth of white-cedar, ring-width chronologies were developed for the reference site and five subsets of the riparian sample, which were formed by combining each soil type with 50-cm segments of the elevation gradient. Two chronologies could be developed for trees growing on clay (CL2: 50 – 100 cm of elevation, CL3: 100 – 150 cm) and three for trees rooted in rock (RC3: 100 – 150 cm, RC4: 150 – 200 cm, RC5: 200 – 250 cm). To preserve long-term upward growth trends not related to tree ageing, the ring-width series were standardised by fitting a negative exponential curve or, if it failed, a linear regression line of negative slope or a horizontal line through the mean. The latter method, which does not eliminate any trend, was used for 54.8 % (RC4) to 88.2 % (RC5) of the measurement curves. The standard chronologies were then calculated using a biweight robust mean to remove effects of outliers and to enhance the common signal contained in the data. All chronologies were developed using the program ARSTAN (Cook & Holmes, 1986; Holmes, Adams & Fritts, 1986).

Since the rise in water level of Lake Abitibi could have influenced growth of white-cedar at both riparian and reference site by changing the microclimate, an additional chronology was developed in the same way as described above using 31 ring-width series covering the years 1885 to 1945 from xeric sites at nearby Lake Duparquet that were used for dendroclimatic analysis by Archambault & Bergeron (1992*a*). The corresponding measurement series were downloaded from the International Tree-Ring Data Bank (http://www.ngdc.noaa.gov/paleo/ftp-treering.html).

3.5.4 Data analysis

Frequency distributions of tree mortality, ice scars, compression wood, and partial cambium dieback were calculated to detect differences due to the water level changes of Lake Abitibi in 1915 and 1922, respectively. These growth responses are presented for the entire riparian site because the creation of three subsets for the eastern, central, and western part of the study site as artificial replications revealed very similar frequency distributions.

Pearson's product-moment correlation coefficients were calculated between the reference chronology and each riparian chronology using 25-year segments lagged by 5 years. In addition, mean annual sensitivity (MAS) curves were formed for all six chronologies. The difference between each pair of ring-width indices was divided by the mean of the paired indices and the resulting annual sensitivity indices were subsequently averaged year-by-year over all ring-width index series composing a chronology. Sensitivity is a measure of the high-frequency variation of tree-ring series reflecting causal environmental factors (Kaennel & Schweingruber, 1995). According to Yanosky (1982), increased tilting and wounding of riparian trees caused by a higher exposure to disturbances such as wave activity, ice push, and erosion following a rise in water level should result in increased variability of ring width and, hence, sensitivity.

The chronologies from the reference and the riparian sites were compared using, as for MAS, an approach based on the individual ring-width index series because mean ring-widths can obscure growth responses by mixing trees with reduced and released increment. For each year from 1848 to 1995, the index of the reference standard chronology was subtracted from that of each individual riparian series and adjusted for differences in the means and standard deviations (SD) of both series. These normalised departures were obtained by running the program OUTBREAK (Holmes & Swetnam, 1996) with the default options. The threshold for a significantly positive or negative departure was set at $\alpha = 0.1$ (two-tailed), i.e., at

+1.645 SD and –1.645 SD, respectively. The relative frequency of significantly deviating index series was compiled for each riparian chronology.

3.6 RESULTS

The riparian white-cedar trees growing on clay were restricted to elevations below about 1.5 m, whereas those on rock were most common between 1 m and 2 m (Fig. 3.2a). The median of elevation of the trees on clay increased from 80 cm for the dead individuals to 115 cm for the living ones. The corresponding values for the trees on rock are 140 cm (dead) and 185 cm (alive), respectively.

Seasonal fluctuations of the Lake Abitibi water level resulted in temporary flooding of the riparian eastern white-cedar (Fig. 3.2a). Prior to any damming, only the trees closest to the lake (≤ 50 cm of elevation), two dead individuals, might have been flooded shortly during spring high water levels. After damming of Lake Abitibi, the same trees were flooded during large parts of winter and spring (Couch Falls dam [CFD]) respectively spring to autumn (Twin Falls dam [TFD]). Since all trees within the second elevation segment (50 – 100 cm) used in ring-width analysis were located above 75 cm, the flooding length for these trees decreased considerably from April and May (CFD) to a short period in June (TFD). The trees within the third elevation interval (100 – 150 cm) were only rarely flooded at extraordinarily high water levels, and for short periods of time. Although the trees within the uppermost two elevation classes (150 – 250 cm) were not directly affected by the high water levels, the rising groundwater table may have reached their root systems (Fig. 3.2a).

3.6.1 Tree mortality, wounding, and tilting

The frequency distribution of the dead riparian white-cedar seems to indicate a period of high mortality between about 1890 and 1914 (Fig. 3.3). However, this is misleading because death of these trees could not be dated exactly. In fact, almost all individuals that were killed several decades ago lacked the bark as well as an unknown number of tree rings composing the sapwood. The outermost tree ring preserved on the samples of these trees did thus only indicate the minimum year of their death. The dramatic reduction in mortality rates after 1914 leads us to believe that most of the dead trees that showed the outermost ring between ca. 1890 and 1914 were in fact killed by the rise in lake level in 1915. After this event, mortality of white-cedar was somewhat higher in the 1930s but remained generally on a low level. No peak in tree mortality at all was associated with the second damming in 1922 (Fig. 3.3).

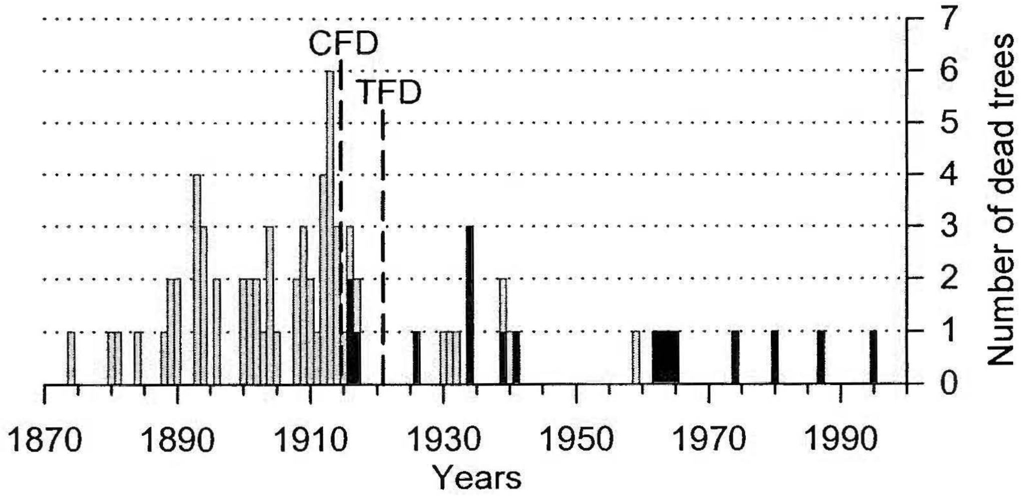

Figure 3.3: Mortality of eastern white-cedar bordering Lake Abitibi (*n* = 76). Filled bars indicate exact dates, whereas shaded bars represent minimum year of death. The vertical dashed lines indicate the dates of the hydrological changes caused by the dam at Couch Falls (CFD) in 1915 and that at Twin Falls (TFD) in 1922.

The frequency distributions of ice scars, partial cambium dieback, and compression wood showed two distinctly different periods (Fig. 3.4). Very few of these disturbance related growth responses dated prior to 1915. A small peak of scars and compression wood appeared in the early 19th century and some reaction wood was also observed between 1855 and 1885. Wounding and tilting became much more common after the transformation of Lake Abitibi into a reservoir in 1915. The following eighty years were characterised by occasional stem wounding (Fig. 3.4a) and a decreasing number of trees with cambium dieback (Fig. 3.4b).

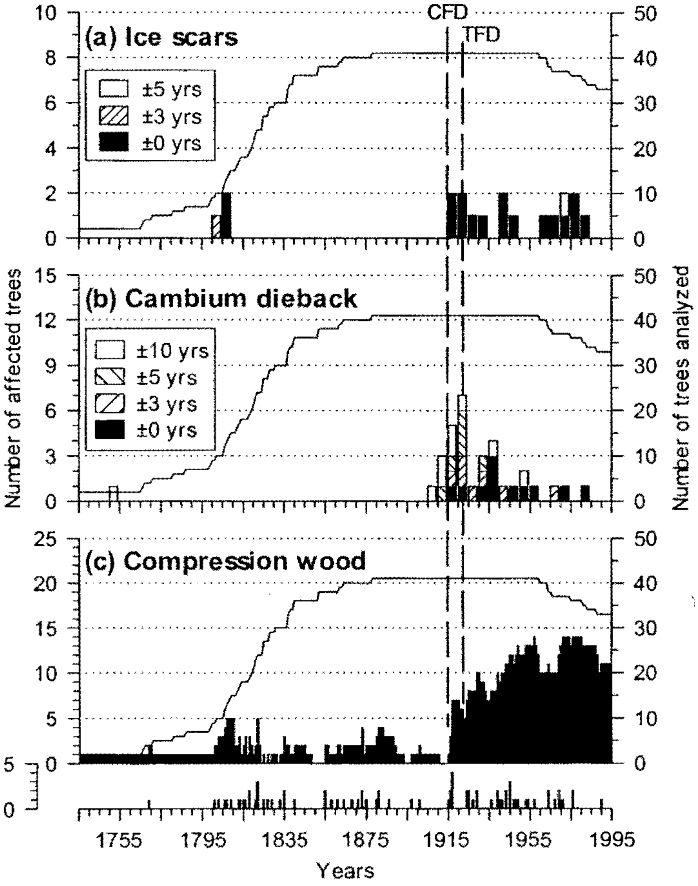

Figure 3.4: White-cedar frequency distributions of (a) ice scars in 5-yr classes, (b) partial cambium dieback (year of the last complete tree ring) in 5-yr classes, and (c) sequences (above) respectively initial years (below) of compression wood for a subset of trees covering at least the period from 1885 to 1945 (*n* = 41). Dating accuracy is given for ice scars and cambial dieback. (CFD = Couch Falls dam; TFD = Twin Falls dam)

The frequency of tilting events (= initial years of compression wood sequences) increased only slightly after damming and showed small peaks around 1917 and in the 1940s (Fig. 3.4c). However, the number of tilting events after 1915 was probably underestimated because of the longer-lasting compression wood sequences, during which repeated tilting of the same tree was impossible to detect. Mean length of the reaction wood sequences increased significantly (independent-samples *t*-test with unequal variances: $t = -5.243$, $df = 44.730$, $P < 0.001$) from 5.0±5.0 years between 1800 and 1914 ($n = 37$ sequences) to 21.4±19.1 years between 1915 and 1995 ($n = 40$ sequences). This may reflect the difference in tree age. In the 19th century when the stems were still thin and flexible, they rapidly returned to a stable upright position after the loss of balance caused by minor but frequent impacts such as a heavy snow load. Some decades later, the stems had increased in size and must thus have been tilted by major events such as an ice push, and they remained unbalanced and formed compression wood for longer periods.

3.6.2 Radial growth

The trees from the reference site, and those growing on clay close to the lake (CL2), registered a higher mean ring width compared to the trees composing the other chronologies (Table 3.1) and also relative to white cedar growing on xeric and mesic sites at nearby Lake Duparquet (Archambault & Bergeron, 1992*a*; Tardif & Bergeron, 1997*a*). Due to the detrending option chosen (see chap. *Material and Methods*), all standard chronologies show a very high first-order autocorrelation. The descriptive statistics indicate that the two clay (CL2 and CL3) and the highest rock (RC5) chronologies have more common variation among the trees (variance in the first principal component and intertree correlation) than the other chronologies (Table 3.1). The mean correlation between the cores and between the trees composing the two lower rock chronologies (RC3 and RC4), in contrast, are relatively low.

Table 3.1: Descriptive statistics of the six standard ring-width chronologies of eastern white-cedar from Lake Abitibi

	Reference site	Riparian site				
		CL2	CL3	RC3	RC4	RC5
Chronology length	1834-1995	1808-1995	1806-1995	1750-1995	1637-1995	1796-1995
Number of trees / radii	18/32	6/12	11/21	12/24	23/42	9/17
Absent rings [a] (%)	0.02	0.05	0.00	0.09	0.04	0.00
Mean ring width (mm)	0.76	0.76	0.54	0.55	0.47	0.66
Mean sensitivity	0.13	0.14	0.13	0.14	0.18	0.13
Standard deviation	0.19	0.36	0.39	0.30	0.36	0.34
First-order autocorrelation	0.61	0.86	0.89	0.82	0.80	0.88
	Common interval analysis (1885 – 1945)					
Number of trees / radii	18/32	6/12	11/21	12/24	22/41	9/17
Signal-to-noise ratio	10.60	4.37	13.98	4.27	5.55	8.54
Variance in first PCA vector (%)	43.41	58.79	62.55	40.62	36.14	55.47
Expressed population signal	0.914	0.814	0.933	0.810	0.847	0.895
Intercore correlation	0.38	0.46	0.57	0.28	0.21	0.51
Intertree correlation	0.37	0.42	0.56	0.26	0.20	0.49
Intratree correlation	0.61	0.85	0.80	0.76	0.72	0.92

[a] = tree rings absent on the sampled discs or cores.

All five riparian standard chronologies correlated highly significant ($P < 0.0001$) with the Lake Abitibi reference chronology for the period of 1848 to 1995, the correlation coefficients differing only slightly (CL2: $r = 0.669$, CL3: $r = 0.643$, RC3: $r = 0.580$, RC4: $r = 0.700$, and RC5: $r = 0.638$). The chronologies showed most similar patterns during the predamming period until 1914: relatively high index values around 1860 were followed by reduced increment in the 1870s and a distinct growth reduction prior to 1907 (Fig. 3.5b-g). Few riparian index series showed significant normalized departures from the reference standard chronology in the years prior to 1915 (Fig. 3.6). Only three years emerged with a majority of the index series deviating positively (1848 and 1849) or negatively (1866; except CL2) from the corresponding index value of the reference chronology.

During the operational period of the Couch Falls dam (1915 – 1921), all riparian chronologies showed a growth reduction in 1916 and again in 1919 (Fig. 3.5c-g). The similar patterns over all elevation intervals, for clay as well as for rock, and the observation of analogous decreases in ring width at the reference site (Fig. 3.5b) indicate that these abrupt growth reductions were not caused by adverse effects of flooding. Also, the growth reduction in the late 1910s was not particularly important if compared to others during the predamming period, e.g., in the late 1840s or around 1907. The normalised departures even show that the individual index series composing each of the riparian chronologies deviated positively rather than negatively from the reference chronology, particularly in 1919 (Fig. 3.6). In addition, the white-cedar chronology from Lake Duparquet correlated very well with that from the Lake Abitibi reference site for the period from 1848 to 1987 ($r = 0.527$, $P < 0.001$) and showed similar growth drawbacks in 1916 and particularly in 1919 (Fig. 3.5a).

After the second damming in 1921, ring-width indices of all six chronologies increased considerably and remained mostly at high values compared to those before any damming (Fig. 3.5). The rise in growth at the reference site lasted until about 1930, whereas that of riparian white-cedar continued until the 1940s and was more extreme. The increase in growth of the riparian chronologies ended abruptly in 1947. Relative to the predamming period, index series with significant departures

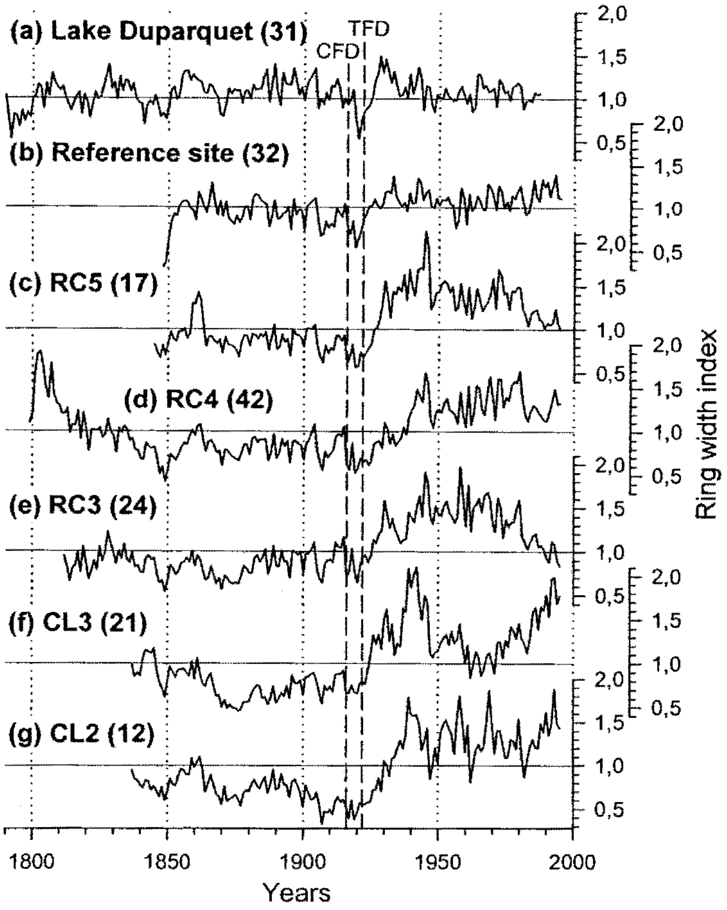

Figure 3.5: Standard chronologies of eastern white-cedar from (a) xeric sites at Lake Duparquet, (b) Lake Abitibi reference site, and (c-g) Lake Abitibi riparian site. The graphs only show those parts of the curves that are composed of at least 10 index series and the maximum numbers of series are indicated between brackets. (CFD = Couch Falls dam; TFD = Twin Falls dam)

were distinctly more common after the second damming of Lake Abitibi in 1921 (Fig. 3.6). However, significant departures of a majority of the index series were only observed for 1933 (CL2 and RC4), 1957 (CL2), 1990 (RC5), and 1993 (RC3 and RC5). Positive deviations were most frequent around 1940 (only CL2, CL3 and RC5) and in the late 1950s, whereas peaks of negative departures were observed around 1930 and after 1985. During these most recent years, negative departures were particularly common for the three rock chronologies that all experienced a downward trend of the ring-width indices in contrast to the reference and clay chronologies where growth increased (Fig. 3.5 and 3.6).

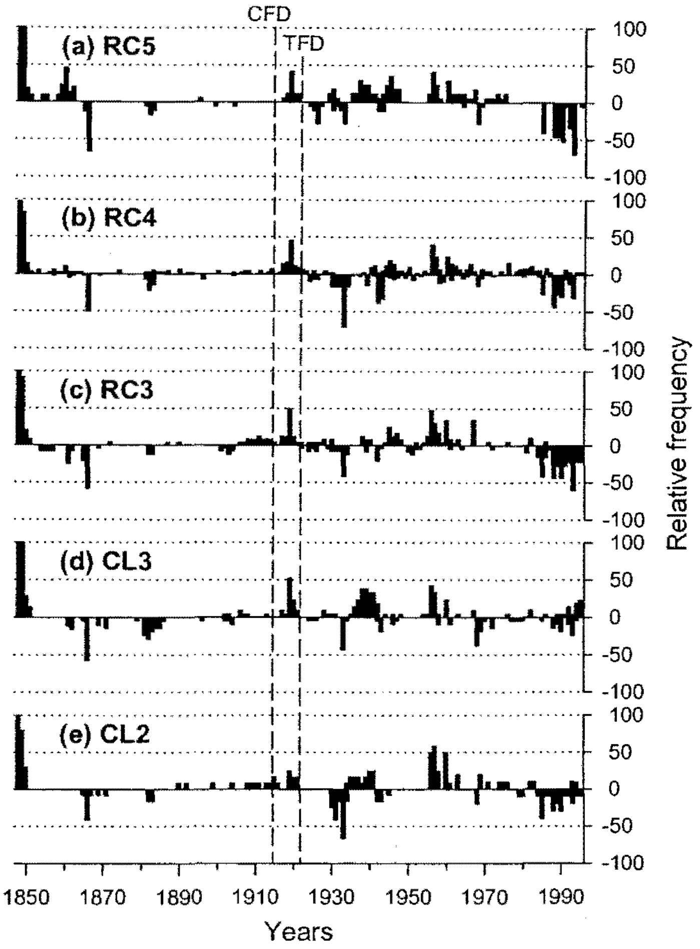

Figure 3.6: Relative frequencies of index series composing the five riparian chronologies with significant normalised departure from the reference standard chronology. Positive values are for series with positive departures and vice versa. (CFD = Couch Falls dam; TFD = Twin Falls dam)

The Pearson's correlations between the reference standard chronology and each of the five riparian chronologies, calculated for the 25-year segments, were mostly significant and showed similar variations (Fig. 3.7). The generally high coefficients in the late 19th and early 20th century were followed by a decrease to low values in the 1940s, reflecting the diverging growth trend of the riparian chronologies relative to the reference chronology in the 1930s and 1940s. Similarly, the correlation coefficients of the rock chronologies dropped to nonsignificant values during the two most recent decades because of the falling ring-width indices in contrast to the upward trend observed for the reference and clay chronologies (Fig. 3.5 and 3.7).

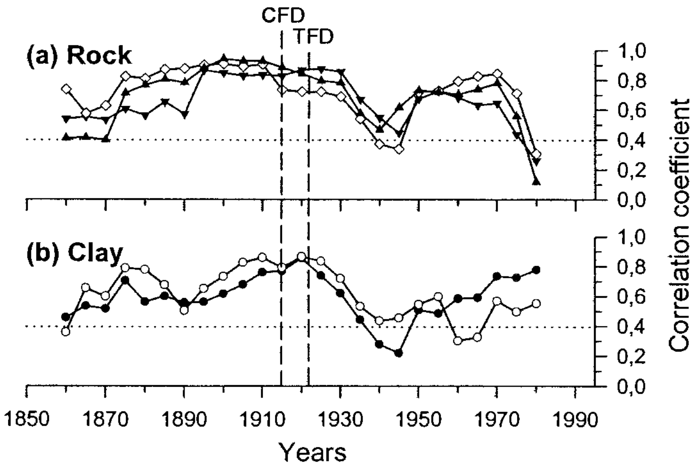

Figure 3.7: Pearson's correlations between the reference standard chronology and each of the five riparian chronologies. The correlation coefficients were calculated using 25-year segments lagged by 5 years. The curves are grouped by the substrata rock (RC3 = filled downward triangles, RC4 = empty diamonds, RC5 = filled upward triangles) and clay (CL2 = filled circles, CL3 = empty circles). The dotted lines indicate the critical value at $P = 0.05$. (CFD = Couch Falls dam; TFD = Twin Falls dam)

Mean sensitivity of the six standard chronologies, ranging from 0.13 to 0.18 (Table 3.1), is relatively low but similar to the values of other white-cedar chronologies in the area (Archambault & Bergeron, 1992*a*; Tardif & Bergeron, 1997*a*). Mean annual sensitivity (MAS) based on the individual index series of the reference chronology did not show any long-term trend but rather three isolated peaks around 1898, 1920, and 1960, respectively, and relatively low values in the mid-1850s, the 1920s, and the early 1950s (Fig. 3.8a). Compared to the reference site, the interannual variations in ring width of the trees composing the riparian chronologies showed similar patterns with slightly higher mean MAS values (Fig. 3.8b, c). The year-to-year fluctuations of the three rock chronologies were particularly high for the 1915-1945 segment and those of the clay chronologies during the period 1860-1900 (CL3) and 1915-1965 (CL2), respectively. The trees composing CL2 also showed a unique peak in sensitivity in the 1930s (Fig. 3.8c).

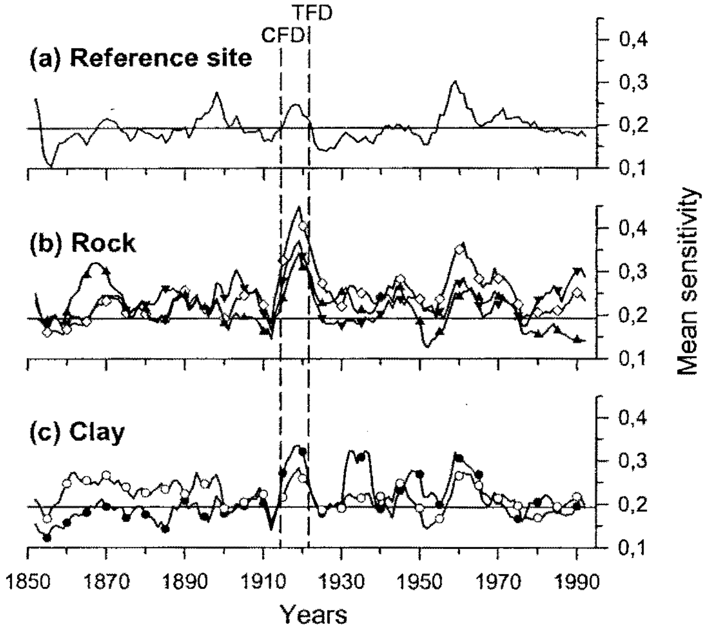

Figure 3.8: Mean annual sensitivity curves based on the individual ring-width index series composing the six standard chronologies from Lake Abitibi. The curves for the riparian site (b and c) are grouped by the substrata rock (RC3 = filled downward triangles, RC4 = empty diamonds, RC5 = filled upward triangles) and clay (CL2 = filled circles, CL3 = empty circles). The curves were smoothed using a running mean of 7 years. The horizontal line in all three graphs represents the mean value of the reference site (0.193) to ease comparison. (CFD = Couch Falls dam; TFD = Twin Falls dam)

3.7 DISCUSSION

3.7.1 Tree response to damming

According to historical data sources, the Lake Abitibi water level prior to 1915 was about 1.2 m lower than today. Thus, the older white-cedar that form the present-day forest limit were at that time in the forest interior and out of reach of the riparian disturbances caused by waves, ice push, and erosion. Damming of the lake in 1915 resulted in the quick death of all trees that constituted the former riparian zone, whereas the surviving white-cedar at higher elevations started to be injured and tilted. This is well documented by the considerable and abrupt increase in the frequencies of ice scars, cambium dieback, and compression wood. Although relatively well protected from the waves, the large embayments were severely affected by erosion because of the poorly resistant clay of which they are composed. The many unstable slopes show that this process is still going on. Evidence for this geomorphological activity is revealed by the lowest dead cedar astonishingly still *in situ* when found as an upright snag in the shallow water of a bay about 20 m beyond the present shoreline. Its outermost preserved tree ring dated to 1902. Supposing that this tree grew at the former shore, and that heavy erosion began after damming in 1915, we estimate the mean shoreline regression rate within this bay at about 25 cm/year (20 m in 80 years).

Since all but one partial cambium dieback events dated from 1915 or later, it was assumed that they were closely related to the artificially high water levels. This is further supported by the fact that all diebacks occurred on the lake-facing side of the tree stems. Eastern white-cedar was found to be radially sectored with respect to its hydraulic pathways in the xylem (Larson, Doubt & Matthes-Sears, 1994). Thus, the loss of roots on one side of a tree causes the subsequent death of cambium and shoots on the same side, as observed for old white-cedar growing on the cliffs of the Niagara escarpment in Ontario, Canada (Larson, Matthes-Sears & Kelly, 1993). The same process might have been at the origin of partial cambium mortality observed at the shores of Lake Abitibi where erosion of the lakeside roots took place quite often.

If compared to the reference site, radial growth of the riparian white-cedar did not show any response to the damming of Lake Abitibi in 1915. This absence of a between-site difference in radial increment might be due to changes in *local climate* after damming of Lake Abitibi that affected both sites. Such an effect was observed for black spruce growing on a small island in Robert-Bourassa Reservoir after flooding of this giant artificial water body in subarctic Quebec (Tremblay & Bégin, 2000). However, we exclude an analogous change of the local climate around Lake Abitibi because the comparison of the present extent of Lake Abitibi with that shown on a map dating from 1906 (Obalski, 1907), i.e., prior to any damming, revealed almost no increase of its area. In addition, ring widths of white-cedar on xeric and mesic sites at Lake Duparquet showed a similar period of reduced increment in the late 1910s (Archambault & Bergeron, 1992*a*; Tardif & Bergeron, 1997*a*). Thus, the low increment of the trees bordering Lake Abitibi after 1915 reflected regional climate patterns rather than any flooding stress due to the artificial rise in water level.

Although the trees closest to the lake (50 – 100 cm of elevation) were inundated from April to early June under the water level regime of the Couch Falls dam, they did not show any growth response to flooding. The few dendrometric data available for eastern white-cedar in the southern boreal area indicate that tree-ring formation only starts in late May (unpublished data) to early June (Tardif, Flannigan & Bergeron, 2001). It seems, therefore, that the trees were still in the dormant period when flooding occurred, which has been shown to less affect trees than if it would occur during the growing season (Broadfoot & Williston, 1973; Teskey & Hinckley, 1977; Kozlowski, Kramer & Pallardy, 1991).

3.7.2 Tree response to the altered hydrological regime

The principal consequence of the replacement of the Couch Falls dam by the Twin Falls dam in 1922 was not an additional rise in water level of Lake Abitibi, but rather an abrupt alteration of its hydrological regime characterised by delayed and lowered maximum lake levels in spring and relatively high water tables during summer and autumn. Riparian eastern white-cedar, however, did not show any growth response to these changes. The lower peak water levels might explain the absence of any signal in mortality and disturbance related growth response. Compared to the reference chronology, the riparian chronologies registered a delayed growth release in the 1920s, temporarily lowered correlation coefficients, and a higher number of trees with significant growth departures. However, these differences were common to all riparian chronologies and did not change along the elevation gradient as one would expect if they were related to flooding. Thus, the differences between the reference and the riparian sites were rather due to the relative change in position of the trees from the closed forest interior before 1915 to the lakeshore forest limit after destruction of the former riparian forest following damming in 1915. The absence of any response in radial growth to flooding in spite of the delayed high water levels might be explained by the relatively short-lasting inundations that did not affect radial growth as was observed in other studies (Broadfoot & Williston, 1973; Teskey & Hinckley, 1977; Mitsch & Rust, 1984; Kozlowski, Kramer & Pallardy, 1991).

3.7.3 Reconstruction of natural water level increases

Since radial growth of riparian eastern white-cedar did not clearly reflect the rapid rise in water level of 1.2 m of Lake Abitibi after damming in 1915, it appears difficult to reconstruct a climate-driven long-term water level increase of unregulated lakes using simply ring-width measurements of this common but quite complacent species. The relatively low magnitude and speed of a natural water level rise compared to damming of a reservoir such as Lake Abitibi not only obscures the long-term trend by a lot of noise (i.e., seasonal water level fluctuations), but also allows the affected trees to adapt their root system to the slowly changing environmental conditions. Nevertheless, such a flooding-stress related approach might be useful if the riparian white-cedar are well protected from ice push and wave impact as in the case of small lakes or at some specific sites of larger water bodies (e.g., behind a beach ridge or within the forest of a large floodplain) where they can grow on low elevation.

The approach consisting in the use of growth response to riparian disturbances could result in more success because death, wounding, and tilting represent distinct events that are relatively easy to date. Frequency and maximum height of ice scars, e.g., have been used successfully to reconstruct long-term changes of high lake levels over the last centuries in the northern (Bégin & Payette, 1988; 1991; Payette & Delwaide, 1991; Bégin, 2000*a*; 2000*b*; 2001) as well as in the southern (Tardif & Bergeron, 1997*b*) boreal area of Quebec.

3.7.4 Factors controlling the lower limit of the white-cedar fringe

Analysis of the growth responses of riparian eastern white-cedar to the first damming in 1915 revealed a strong disturbance signal. The intensified disturbance regime caused tilting, wounding, and uprooting to many trees. However, the analysis of radial growth did not provide clear evidence for a flooding stress induced by the high water table in spring (Couch Falls dam) respectively early summer (Twin Falls dam). It seems that eastern white-cedar could survive higher levels of flooding stress or, in other words, colonise sites closer to the lake. Nonetheless, the combined effects of wave activity, ice push, and erosion, which all reach high intensities given the large size of Lake Abitibi, keep the lacustrine limit of this species at higher elevations where flooding does not affect its radial growth. Therefore, we suggest that the shoreline limit of *Thuja occidentalis* towards Lake Abitibi represents a mechanical rather than a physiological limit.

In general terms, we suggest that the more severe the disturbance regime, the more the mechanical forces become significant controlling factors of the lower limit of occurrence of the shoreline tree species. Consequently, their role is more prominent in the case of the large boreal lakes with their important spring floods and the concurrent ice-break compared to smaller lakes and those further south where the spring flood is of minor importance. Thus, we should somewhat modify the concept that flooding tolerance represents the prime factor in the ordination of tree species along a flood-stress gradient (Beschel & Webber, 1962; Bell & Moral, 1977; Robertson, Weaver & Cavanaugh, 1978; Metzler & Damman, 1985) because this implies that the lower limit of those species reaching the shoreline is a physiological limit. This might apply to large river floodplains in southern areas where the high water periods fall generally into the growing season, and ice push as well as wave impact are almost absent. Such conditions enhance the importance of the flooding stress effects relative to those created by mechanical disturbances. The results of our study, however, suggest that the riparian disturbance regime can play an important role in delimiting the occurrence of tree species at boreal lakes as it was shown for eastern white-cedar.

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CHAPITRE IV

THE EFFECTS OF FLOODING AND FIRE ON RIPARIAN TREE POPULATION DYNAMICS IN SOUTHWESTERN BOREAL QUEBEC, CANADA

Bernhard DENNELER et Yves BERGERON

Article à soumettre

4.1 RÉSUMÉ

Nous avons évalué l'importance relative des deux principales perturbations naturelles, feux de forêt et inondations, sur la dynamique des populations du cèdre blanc (*Thuja occidentalis* L.) et du frêne noir (*Fraxinus nigra* Marsh.) dans huit sites lacustres dans la région boréale méridionale du Québec, Canada. Les sites étudiés sont caractérisés par une topographie en forme de terrasse et un degré variable d'exposition à l'activité des vagues et des glaces. Nous sommes partis de l'hypothèse que les peuplements riverains de cèdre blanc i) sont en déséquilibre démographique causé par les niveaux d'eau montants depuis la fin du ‘Petit Âge Glaciaire‘ (ca. 1850) et ii) ne sont pas affectés par les feux de forêt au contraire des peuplements des hautes terres. À l'intérieur des transects larges de 10 m et s'étendant du bord du lac jusqu'à 300 cm au-dessus du niveau d'eau, tous les individus de cèdre et de frêne (≥ 1 cm de diamètre à hauteur de la poitrine (dhp)) furent datés en appliquant des méthodes dendrochronologiques, et leur élévation au-dessus du niveau d'eau fut mesurée. La régénération (individus < 1 cm dhp) fut échantillonnée le long des mêmes transects mais larges de 2 m seulement. L'âge des individus fut déterminé en comptant le nombre de cernes de croissance et/ou d'internodes et l'élévation au-dessus du niveau d'eau fut mesurée à chaque mètre. La distribution du frêne noir est restreinte à la zone riveraine (< 200 cm d'élévation) alors que les arbres du cèdre blanc sont absents au-dessous de 100 cm. La structure d'âge du cèdre le long du gradient d'élévation montre que les arbres qui s'étaient établis avant le dernier feu de forêt furent presque complètement restreints aux basses terres (< 175 cm) où la survie de cette espèce susceptible au feu bénéficia probablement de la proximité du lac. La distribution composée cumulative d'âge du cèdre blanc suit une fonction négative exponentielle typique pour des peuplements inéquiens avec un apport continu de graines. Cependant, la structure d'âge des peuplements exposés aux perturbations riveraines révèle un manque de recrutement après feu alors que celle des peuplements plus protégés indique une reproduction relativement continue. La distribution d'âge du frêne noir montre que cette espèce, plus tolérante aux inondations et aux poussées glacielles que le cèdre, commença à envahir les terrasses riveraines autour de 1850, c'est-à-dire à la fin du ‘Petit Âge Glaciaire'. Il semble donc que les parties exposées de la frange de cèdre autour du lac soient en train de se désintégrer, particulièrement à cause du faible taux de survie des semis et que le cèdre y sera graduellement remplacé par le frêne noir. L'élévation changeante de la limite inférieure du cèdre blanc selon l'âge des arbres témoigne des fluctuations à long terme du niveau d'eau, dont trois périodes purent être distinguées: (1) les niveaux relativement élevés d'avant ~ 1500 furent suivis par (2) une regression des eaux d'environ 20 cm pendant le ‘Petit Âge Glaciaire' (~ 1500 – 1850), une période relativement froide et sèche, qui fut suivie par (3) une augmentation graduelle du niveau d'eau de 20 à 40 cm jusqu'à la fin du XXe siècle. Ces changements à long terme du niveau d'eau correspondent aux résultats d'autres études effectuées au Québec boréal et subarctique.

4.2 ABSTRACT

We evaluated the relative importance of two major boreal forest disturbances, fire and flooding, on the population dynamics of eastern white-cedar (*Thuja occidentalis* L.) and black ash (*Fraxinus nigra* Marsh.) in eight old-growth riparian stands of southwestern boreal Quebec, Canada. The study sites are characterized by terrace-like topography and different degrees of exposure to wave and ice activities. We hypothesized that the riparian white-cedar populations are: i) in a non-equilibrium state due to increasing water levels since the end of the 'Little Ice Age' (ca. 1850) and, ii) not affected by forest fires, in contrast to upland populations. Within 10-m wide transects, perpendicular to the lake and from the shoreline up to 300 cm above the water level, all white-cedar and black ash trees (≥ 1 cm in diameter at breast height (dbh)) were aged using dendrochronological methods and their elevation above the water level was measured. Recruitment (individuals < 1 cm dbh) was sampled along 2-m wide transects. Individuals were aged by counting the number of tree rings and/or internodes and their elevation was measured in 1-m increments. Black ash was found to be restricted to the riparian zone (< 200 cm of elevation), whereas white-cedar trees did not occur below 100 cm. Age structure of white-cedar along the elevation gradient shows that the trees pre-dating the last forest fire were almost completely restricted to low elevations (< 175 cm) probably because survival of this fire-susceptible species benefited from the barrier function of the lake. The cumulative composite age distribution of white-cedar followed a negative exponential function typical of uneven-aged stands with sustained seedling input. At the stand level, however, the age structures revealed a lack of post-fire recruitment in stands exposed to riparian disturbances, whereas relatively continuous recruitment occurred at protected sites. The frequency distributions of black ash showed that this species, more tolerant to flooding and ice push than white-cedar, started to invade the shore terraces around 1850, i.e., at the end of the 'Little Ice Age'. The white-cedar fringe around the lake appears to disintegrate at parts of the lake perimeter most exposed to the riparian disturbances because of poor seedling suvivorship, and is gradually replaced by black ash. The long-term water-level fluctuations were reflected in the changing elevation of the lower limit of white-cedar. Three periods could be distinguished: (1) high water levels before ~ 1500 were followed by (2) a shoreline regression of about 20 cm during the cold but dry 'Little Ice Age' (~ 1500 – 1850), after which (3) the water level rose progressively for 20 – 40 cm until the late 20th century. These long-term water-level changes concur with the results of other studies from the same area as well as from subarctic Quebec.

4.3 INTRODUCTION

Forest dynamics has been recognized to be strongly influenced by natural disturbances such as fire, insect outbreaks, and floods (White 1979; Pickett 1980; Pickett and White 1985; White 1987). In the boreal forest, fires are the principal natural disturbances (Johnson 1992; Payette 1992; Bergeron et al. 1998). Frequent and intense crown fires result generally in a forest mosaic of even-aged post-fire stands, whereas uneven-aged stands develop under a less severe fire regime (Johnson 1992; Frelich and Reich 1995; Bergeron et al. 2001). Fire-sensitive species are often related to landscape features acting as firebreaks (e.g., wetlands, lakes, rivers, and cliffs) that allow them to grow in areas with severe forest fires (Heinselman 1973; Bergeron 1991). At the northern limit of their range, red pine (*Pinus resinosa* Ait.) and white pine (P. *strobus* L.) are restricted to such fire-protected habitats (Bergeron and Gagnon 1987; Bergeron and Brisson 1990; Flannigan and Bergeron 1998; Engelmark et al. 2000). Eastern white-cedar (*Thuja occidentalis* L.) has been shown to occur in greater abundance and to attain higher ages at shores and on islands (Heinselman 1973; Ericsson and Schimpf 1986; Archambault and Bergeron 1992a, 1992b) as well as on cliff faces (Kelly et al. 1994).

Although lake margins are relatively well protected from fire, they are exposed to periodic flooding, which is the main disturbance affecting bottomland forest dynamics (White 1979). Tolerance to flooding varies considerably according to species and tree size (Broadfoot and Williston 1973; Teskey and Hinckley 1977; Lugo and Brown 1984; Kozlowski et al. 1991). Flood related physical damaging, caused by erosion, sedimentation, water current, waves, and ice drift, is an important factor for tree mortality (Sigafoos 1964; Yanosky 1982; Hupp 1988; Barnes 1985; Kozlowski et al. 1991). Flooding can also have a beneficial effect on seed germination, seedling survival, and growth of seedlings and trees when soil humidity is increased during an otherwise dry summer (Hosner 1957; DuBarry 1963; Broadfoot and Williston 1973; Kozlowski 1984; Streng et al. 1989; Kozlowski et al. 1991; Cordes et al. 1997). However, survivorship of trees, and particularly seedlings, is adversely affected by long-lasting immersion (Hosner 1958; Kozlowski 1984; Peterson and Bazzaz 1984).

Changing climate acts directly upon vegetation and forest dynamics, but, indirect effects via climate-induced changes of natural disturbance regimes might be even more important (Martin 1993; Fleming 1996; Bergeron et al. 1998; Flannigan et al. 1998). Since the end of the Little Ice Age, a relatively cool period lasting from about 1450 to 1850 (Lamb 1982), the global average surface temperature has considerably increased, amounting to 0.6±0.2°C over the 20th century (Houghton et al. 2001). In eastern North America, both temperature and precipitation have increased since the end of Little Ice Age (Bradley et al. 1987; Gullett and Skinner 1992; Jones and Briffa 1992; Karl et al. 1993; Houghton et al. 2001). The induced changes in natural disturbances regimes have affected forest dynamics in different ways. In riparian forests, stand degradation due to excess soil moisture and erosion, reduced tree growth, and limited regeneration were the principal effects of a water level rise of climatic (Alestalo 1971; Bégin and Payette 1988; Payette and Delwaide 1991) or isostatic (Clark 1986; Bégin et al. 1989) origin. Shore disturbances such as erosion and, particularly important in the northern regions, ice push were more effective during periods of high spring water levels, injuring and killing shoreline trees and shrubs and promoting vegetative regeneration (Hupp 1988; Bégin et al. 1991; Bégin and Payette 1991; Desrosiers and Bégin 1992; Langlais and Bégin 1993; Lepage and Bégin 1996; Bégin 2000). In contrast, downward expansion of shoreline shrub and tree populations were observed in studies about the inverse process, i.e., the lowering of the water level caused by recent periods of low precipitation (Bégin and Filion 1995) or by isostatic rebound of the shore (Ericson 1980; Cramer 1985; Bégin et al. 1993; Grégoire and Bégin 1993; von Mörs and Bégin 1993).

In the southwestern boreal area of Quebec, proxy records confirmed the long-term climate trend towards higher temperatures and precipitation observed for the entire eastern North America for approximately the last 150 years. The reconstruction of fire history provided evidence for a distinct decrease in fire frequency since the mid 19th century that has been accentuated during the 20th century (Bergeron 1991; Bergeron and Archambault 1993; Flannigan et al. 1998; Bergeron et al. 2001). Dendroclimatic analysis of drought-sensitive eastern white-cedars on rock outcrops at Lake Duparquet, Quebec, indicated moisture deficits during the Little Ice Age followed by an upward trend of summer precipitation (Archambault and Bergeron 1992a). The analysis of frequency and maximum height of ice scars on white-cedar stems bordering the same lake revealed increasing ice-push activity related to rising spring high water levels, estimated at about 1 m since ~ 1850 (Tardif and Bergeron 1997b). The more severe flooding regime of Lake Duparquet also caused a change of the recruitment pattern of riparian black ash (*Fraxinus nigra* Marsh.) from sexual towards vegetative regeneration (Tardif et al. 1994; Tardif and Bergeron 1999).

The white-cedar fringe around Lake Duparquet, by its exposure to both fire and flooding, allows studying the indirect effects of climate changes. Previous observations made by Denneler et al. (1999) suggest that this fringe might not be in equilibrium with present conditions because mean stem size of white-cedar within the riparian zone was considerably higher than in upland sites. The same study also provided evidence for recent invasion of black ash on the lower parts of the shoreline terraces, which was also observed by Tardif and Bergeron (1999). In this study, we examined forest population dynamics at the land-water interface of Lake Duparquet i) to understand stand dynamics in relation to fire and flooding, ii) to evaluate how recent climatic changes have affected dynamics, and iii), to predict the future dynamics in the context of continuing climate change. We hypothesized that i) the large white-cedar pre-dated the last forest fire reported for the area because of their relatively protected position close to the lake, and ii) the rising water level since the mid-19th century caused a lack of sexual reproduction and/or low seedling survivorship of this species. Black ash, however, started to invade the lower parts of the shore terraces because it is more tolerant to flooding and better adapted to severe disturbances than white-cedar.

4.4 METHODS

4.4.1 Study area

Lake Duparquet (48°28'N; 79°17'W) is situated about 600 km northwest of Montreal and embedded within the slightly undulating landscape of western Quebec, Canada (Fig. 4.1). Colonization of this region and forest exploitation started in the early 20th century (Vincent 1995). However, large scale clearcutting within the catchment area of Lake Duparquet took place as late as the 1970s (Bergeron and Harvey 1997). Clayey deposits originating from the pro-glacial Lakes Barlow and Ojibway cover large parts of the area (Veillette 1994), whereas glacial tills are found mainly on the slopes of the rocky hills (Bergeron et al. 1983). From 1971 to 2000, mean annual temperature and precipitation at La Sarre (about 40 km to the north) were 0.7°C and 890 mm, respectively (Environment Canada: http://climate.weatheroffice.ec.gc.ca/climate_normals/). The region is situated at the southern border of the boreal forest within the domain of the balsam fir – white birch mixedwood forest (Grandtner 1966; Richard 1987). Mature stands on mesic sites are characterized by balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.), which are accompanied by white spruce (*Picea glauca* (Moench) Voss) and eastern white-cedar (Bergeron and Bouchard 1983). Tamarack (*Larix laricina* (DuRoi) K. Koch), black spruce (*Picea mariana* (Mill.) B.S.P.), white-cedar, black ash, and sporadically balsam poplar (*Populus balsamifera* L.), dominate the hydric sites around Lake Duparquet (Bergeron et al. 1983; Tardif and Bergeron 1992; Denneler et al. 1999; Girardin et al. 2001). Eastern white-cedar grows on organic as well as mineral soils and occupies a wide range of soil moisture regimes (Bergeron et al. 1983; Collier and Boyer 1989). Associated with late successional stages (Bergeron 2000), white-cedar reproduces best on rotten wood (Scott and Murphy 1987; Simard et al. 1998). The shade intolerant black ash typically occupies rich but poorly drained sites in bogs or along rivers and lakeshores where it is exposed to seasonal flooding (Bergeron and Bouchard 1983; Wright and Rauscher 1990; Tardif and Bergeron 1992).

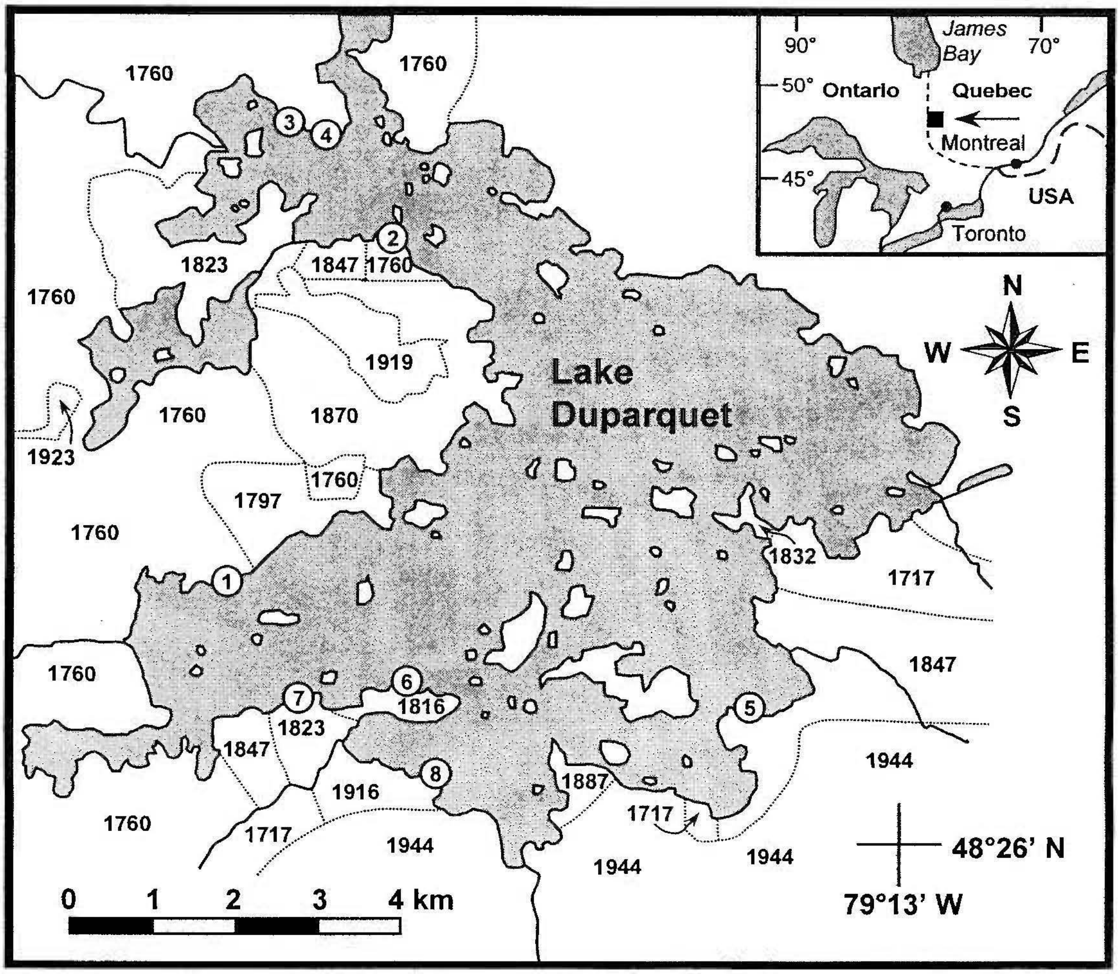

Figure 4.1 Map of Lake Duparquet area showing the forest fire history, i.e., the years of the last fire (taken from Bergeron 1998), and the location of the eight study stands (numbered circles).

Lake Duparquet covers about 40 km^2 and drains north through Duparquet River, Lake Abitibi, and Abitibi River towards James Bay (Fig. 4.1). The rapid controlling its water level, called Rapide Danseur, seems not have been altered by man in historical time. Until the mid-1930s, canoes, the only way for long distance travelling, and floating timber detoured the rapid using a short portage (Perron 1989; Asselin and Gourd 1995). Although the Duparquet River has been transformed into a part of Lake Abitibi (~ 15 km north) after the construction of a dam in 1915 (see chapter III), only the lower part of the Rapide Danseur was submerged by the backed-up waters. The construction of three bridges just upstream from the rapid in the years ~1935, 1937 and 1964, respectively, did not change its shape and capacity as revealed by old photographs (*pers. comm.* Alain Boutin). We infer therefore that Lake Duparquet kept its natural hydrological regime. Unfortunately, only few water level measurements of this lake were taken (Fig. 4.2). Nevertheless, the six years partially covered (1989 - 1991 and 1996 - 1998) indicate considerable variations with respect to spring flood levels and annual amplitudes.

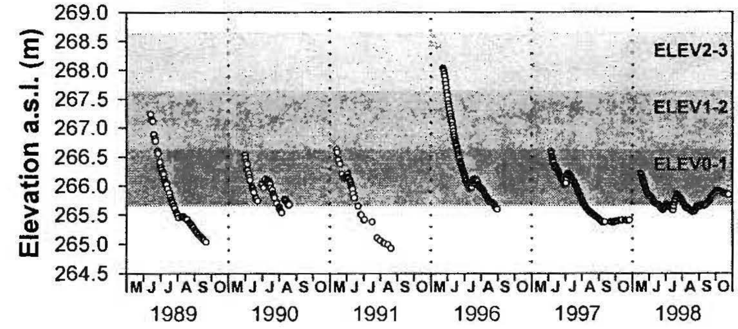

Figure 4.2 Seasonal water level fluctuations of Lake Duparquet between May and October of 1989 to 1991 (data from Tardif and Bergeron, 1997b) and 1996 to 1998. The first four years represent manual measurements, whereas 1997 and 1998 are daily means from a hydrograph installed on the bottom of Lake Duparquet. The shaded rectangles indicate the position of the three elevation intervals of 1 m (ELEV0-1, ELEV1-2, and ELEV2-3) relative to the water level in August 1998.

4.4.2 Stand selection

Stand selection was restricted to shoreline sections constituted of terrace-like topography because a former study revealed particularly large specimens of eastern white-cedar on this type of riparian zone (Denneler et al. 1999). In addition, the asymmetric crown form with branches much further down the stem on the lake side compared to the opposite side indicates that these large white-cedars constituted the lower tree limit since their youth, which would allow us to retrace changes of the tree limit due to long-term water level fluctuations.

We chose eight points at the border of Lake Duparquet where the shore terrace was as large as possible, and where large individuals of white-cedar were present, avoiding areas with visible human impact (Fig. 4.1). The eight study stands differed with respect to their exposure to wave activity and forest stand initiation. The fetch towards the opposite lakeshore in direction of the predominant northwestern winds (Archambault 1989) was used to quantify exposure. Stands 1, 3, and 4 were considered as relatively well protected because oriented to the south, whereas stand 5 is the most exposed with its long fetch (Table 4.1). Four stands are supposed to have burned for the last time in 1760, one of the most devastating fires that ever happened in the area (Dansereau and Bergeron 1993; Lefort 1998), three others burned in the first half of the 19th century, and one burned in 1916 (Table 4.1; Fig. 4.1). However, these dates were taken from fire history studies covering large areas with restricted spatial resolution (Bergeron 1991; Dansereau and Bergeron 1993) and may thus not correspond to the last fires that affected the riparian zones, which are somewhat more protected from fire.

Table 4.1 Descriptive statistics for the eight study stands on Lake Duparquet

Statistic	Stand number[a]								Lake[b]
	1	3	4	8	7	2	6	5	
Length (m)	15	16	25	17	13	17	26	30	19.9 (±6.2)
Fetch to NW (km)	0.0	0.0	0.0	1.1	1.9	2.4	2.4	4.9	1.6 (±1.7)
Last forest fire[c]	1760	1760	1760	1916	1823	1760	1816	1847	—
Plot size (m^2)									
ELEV2-3	24.5	45.3	74.4	34.0	15.4	51.1	21.9	—[d]	38.1 (±20.5)
ELEV1-2	95.0	92.5	137.3	68.2	66.8	71.0	180.9	161.3	109.1 (±44.8)
ELEV0-1	35.2	26.5	43.4	72.1	55.9	51.1	59.6	139.3	60.4 (±34.9)
Substratum									
ELEV2-3	Till	Till	Till	Till	Rocky till	Till	Till	—[d]	—
ELEV1-2	Clayey till	Clayey till	Clayey till	Till	Till	Clayey till	Clay	Clayey till	—
ELEV0-1	Clayey till	Clayey till	Clayey till	Till	Till	Clayey till	Rock	Clayey till	—
Mean percentage cover (± 1 SD) of the seedbeds in the upper riparian zone (ELEV1-2)									
2-m^2 plots (n)	10	10	14	7	7	7	18	16	89
Wood	13.0 (±11.6)	8.0 (±6.3)	10.7 (±10.0)	24.3 (±12.7)	12.9 (±13.8)	25.7 (±15.1)	6.1 (±6.1)	2.5 (±5.8)	10.7 (±11.7)
Moss	11.0 (±11.0)	22.0 (±19.3)	11.4 (±14.1)	24.3 (±25.1)	15.7 (±12.7)	4.3 (±5.3)	4.4 (±5.1)	63.1 (±30.9)	21.2 (±27.1)
Litter	69.0 (±19.1)	62.0 (±20.4)	75.0 (±13.4)	38.6 (±24.8)	35.7 (±19.0)	65.7 (±14.0)	78.9 (±24.7)	28.1 (±22.6)	58.5 (±27.9)
Mineral soil	0.0 (±0.0)	4.0 (±7.0)	1.4 (±3.6)	2.9 (±4.9)	0.0 (±0.0)	1.4 (±3.8)	0.0 (±0.0)	2.5 (±6.8)	1.5 (±4.4)
Rocks	7.0 (±9.5)	4.0 (±7.0)	1.4 (±3.6)	10.0 (±10.0)	35.7 (±19.0)	2.9 (±4.9)	10.6 (±25.5)	3.8 (±5.0)	8.1 (±16.0)

Note: All transects started from the same reference water level of Lake Duparquet (265.65 m).

[a] The stands are presented, from left to right, in the order of increasing exposure to riparian disturbances (fetch to NW).

[b] Composite information from the eight study stands (mean ± 1 SD).

[c] The fire years were taken from Bergeron (1991) and Dansereau and Bergeron (1993).

[d] Stand 5 is located on a small peninsula with a maximum elevation of only about 1.5 m above lake level.

From each shoreline point, a 10-m wide transect was drawn perpendicular to the lake up to 3 m above the water level (in August 1998), resulting in lengths varying between 13 m and 30 m (Table 4.1). For the analysis of population dynamics, we subdivided the transects into three plots with an elevation interval of 1 m each. The lowest plot between 0 and 1 m (ELEV0–1), flooded during large parts of the spring and summer (Fig. 4.2), covered the rocky shore and the subsequent riparian shrub belt with some trees in it. The highest plot from 2 - 3 m (ELEV2–3), in contrast, was completely within the forest above the mean high water level, which is situated approximately at 2 m above the lake as indicated by a small erosion talus and the upper limit of deposited driftwood. The lower part of this upland plot, however, can be flooded for short periods during extraordinarily high spring floods like that of 1996 (Fig. 4.2). The third plot (ELEV1-2) corresponded to an intermediate position with respect to flooding and represented the transition zone between the shrub belt and the forest. Thus, elevation reflected not only a flooding gradient but also a gradient of incident light between the unshaded shrub belt at the immediate shore to the closed canopy of the upland forest.

4.4.3 Data collection

Within all plots, we measured the diameter at breast height (dbh) of each tree with a minimum dbh of 1 cm. Both living and *in situ* dead trees of all species encountered were considered, but, black spruce was later omitted because only one individual was found. If the trunk of a dead tree was not any more present, such as for trembling aspens cut by beaver (*Castor canadensis*), we took the diameter at the upper limit of the stump. Each living eastern white-cedar and black ash was cored as close as possible to the base of the stem. Since many white-cedar trunks were rotten or even hollow inside, a core was taken higher up on the stem to reach the pith or to get at least as close as possible. Height above ground as well as the stem diameter at the coring level were measured to allow later estimation of the germination age. For the same perspective, we took two samples at different heights on the trunk of

16 randomly chosen white-cedars with intact centers to calculate a sampling height correction factor for age. Sampling procedure for the dead individuals was analogous with the difference that we cut cross sections instead of taking cores. Elevation above the lake level of each white-cedar and black ash tree was measured using a WILD-T2 theodolite (WILD, Heerbrugg, Switzerland), equalizing at the same occasion changes of the water level that occurred during fieldwork. The trees of all other species were just assigned to the corresponding 1-m elevation interval in which they were found.

We took a 50-cm long sediment core with a tube sampler at the center of each plot to determine the type of substratum. This evaluation revealed glacial till, a morainic sediment composed of all granulometric fractions from clay up to boulders, as the predominant substratum (Table 4.1). Glacial till was found to be the most common sediment constituting the shore terraces around Lake Duparquet (Denneler et al. 1999). The till was generally richer in clay in the lower plots compared to the highest ones. This might be the consequence of sedimentation with consecutive incorporation into the soil of fine mineral sediments during repeated flooding, or just reflect topographic differences in sedimentation conditions during the deposition of the till when the glaciers still covered the area. On all sites, podzols were found to be the soil type above the high water level limit.

For tree recruitment analyses, all living individuals smaller than 1 cm in dbh were sampled within a 2-m wide strip perpendicular to the lake in the middle of each transect. These strips were subdivided into 1 x 2 m^2 rectangles, and elevation (rounded to the nearest 5 cm) above the water level of Lake Duparquet was measured at their center points, i.e., in 1-m steps along the transect. Thus, all individuals within the same plot were assigned to the same elevation. After identification of both the species and the regeneration mode (sexual or vegetative), each individual was aged directly in the field by counting the number of scars left by the terminal buds (Simard et al. 1998), and, if they weren't clearly visible, the number of tree rings just above the root collar. Some samples with particularly narrow tree rings were brought to the laboratory where the number of rings was counted under a stereomicroscope. If the two dating methods resulted in different values, we retained the higher age.

We originally hypothesized that the rising water level since the mid-19th century caused a lack of sexual reproduction and/or low seedling survivorship of eastern white-cedar. However, this could also be due to the absence of useful seedbed that allows the seeds to germinate and the seedlings to grow. We noted therefore the seedbed substratum for each seedling found within the upper riparian zone (ELEV1-2) by distinguishing five types: dead wood (logs ≥ 5 cm diameter and laying on the ground), living moss, litter (fine dead organic material principally composed of needles, leaves, mosses, and small wood debris), mineral soil, and rocks (gravel and boulders). In addition, we estimated visually the percentage cover of each seedbed (Table 4.1). Since only individuals of vegetative origin were found on mineral soil, this potential seedbed, as well as the rock type, were omitted from the statistical analysis of the seedbed preferences, and the percentage covers were recalculated without them.

4.4.4 Ring-width measurement and crossdating

The cores and cross sections of the white-cedar and black ash trees were prepared using standard dendrochronological procedures (Stokes and Smiley 1968; Fritts 1976). Ring-width of all samples had to be measured for exact dating because eastern white-cedar produced quite uniform ring-widths (complacency) with few pointer years (*sensu* Schweingruber et al. 1990) and incomplete as well as missing rings were expected to occur in both species, but also to allow crossdating of the samples from the dead trees. Therefore, we used a VELMEX UniSlide micrometer with a resolution of 0.001 mm. The ring-width series were then statistically crossdated for each plot separately using the program COFECHA (Holmes et al. 1986), and the conformity of dating was visually verified using pointer values (*sensu* Schweingruber et al. 1990).

4.4.5 Germination age estimation

Age correction of eastern white-cedar trees was necessary for those samples without pith (pith correction) and where the sampling height did not correspond to the base of the stem (sampling height correction). We estimated the number of missing tree rings visually when the innermost ring of the sample was very close to the pith (< 1 cm). In all other cases pith correction was based on the estimation of the distance from the innermost tree ring on the sample to the pith. We applied three different methods to estimate the length of the missing radius. If a cross section with concentric tree rings had a hollow center, we just took half of the diameter of the hole. For incomplete cross sections and the cores we used the arc of the innermost tree ring on the sample to calculate the distance to the pith using the formula of Duncan (1989). In this approach, the relation between length (L_A) and height (H_A) of the arc is used to calculate the missing radius (R):

$$R = L_A^2/8H_A + H_A/2 \qquad [1]$$

If the inner tree rings did not show any arc, we calculated the missing radius (R) as difference between the half of the stem diameter at coring height (D) and the length of the core (L_C), the latter being the sum of the widths of all tree rings and the bark:

$$R = D/2 - L_C \qquad [2]$$

The estimated length of the missing radius obtained by one of the three above mentioned methods was then divided by the mean width of the 20 innermost tree rings present on the sample to get the number of missing rings to the pith.

The 16 trees with intact center and sampled at two different heights along the stem were used to calibrate the sampling height correction. The regression of the mean width of the 20 innermost tree rings of the lower sample on the age difference of the two samples standardized for 10-cm height difference resulted in a highly significant relationship: $R^2 = 0.66$, $P = 0.0001$, $n = 16$, $\log_e y = 2.304 - 2.775x$, where x = mean width of the inner 20 tree rings, and y = number of years per 10 cm height difference on the stem. Thus, to calculate the number of missing rings due to the sampling height of a tree, the mean width of the 20 innermost tree rings entered as independent variable in the equation, and the resulting y-value was then multiplied with the sampling height in decimeter. Finally, we got the approximate germination age of the trees by adding the number of estimated missing years determined by the pith and the sampling height correction methods (median = 32 years) to the number of tree rings present on the samples.

Correction for sampling height and lacking pith needed to be applied to 16 black ash trees only. The number of missing years due to sampling height was estimated as "best guess" (mostly plus 1 year if sampling was not done directly at the stem base), and that due to a rotten center was estimated either visually or by the above mentioned method of Duncan (1989).

Since the age of most (92 %) of the eastern white-cedar trees had to be estimated, we generally present the tree age distributions in 20-yr classes. To compensate for the unequal size of the plots and to allow comparisons between the stands, we multiplied the frequencies of each size and age class by an appropriate area conversion factor to transform the data to number of stems per 0.01 ha.

4.4.6 Statistical analyses

Population dynamics analyses of tree species are based on both static and cumulative size and age distributions that are mainly described by two models, the negative exponential and the power function, respectively (Hett and Loucks 1976; Parker and Peet 1984; Bergeron and Gagnon 1987; Ågren and Zackrisson 1990; Tyrell and Crow 1994; Tardif and Bergeron 1999). The negative exponential model assumes constant recruitment and constant mortality rate over time. Static distributions of such a type approach the form of an inverse "J" that is typical for uneven-aged but stable forest stands with sustained seedling input (Leak 1965). The power function, however, is a more adequate model if the chance of survival increased through time. For both models, the y-intercept and the slope of a linear regression of the $\log_e$-transformed data are a measure for initial recruitment and mortality, respectively, of the population.

In this study, riparian population dynamics were characterized by the size structure of all tree species present in the stands and the age structure of eastern white-cedar and black ash. Frequency distributions were calculated for each plot separately as well as for all stands together, i.e., on the scale of Lake Duparquet. To cover the whole life span, we used the complete data set composed of trees (dbh ≥ 1 cm) and recruitment (dbh < 1 cm) for these analyses.

In the age structure analysis, we applied both the negative exponential as well as the power function models to evaluate which of them better described the observed cumulative frequency distributions of eastern white-cedar and black ash at the scale of the lake. The linear regressions were calculated separately for each of the three elevation intervals using SPSS (SPSS Inc. 1997). However, we dropped the lowest interval (ELEV0-1) for white-cedar and the upland interval (ELEV2-3) for black ash, because both species were too rare within the corresponding plots. Considering that the white-cedar populations bordering Lake Duparquet (ELEV1-2) seemed overaged, indicating high regeneration mortality but increasing survival chance with age, we hypothesized that the power function model would better describe the variation in the data. Since only living trees were used for the age structure analysis, we excluded the dead trees from the calculation of cumulative frequency distributions, mortality rate, and initial recruitment. Nevertheless, they are shown in the size and age structure profiles, and used for interpretation.

Lake-scale relationships between age and elevation of the tree recruitment (dbh < 1 cm) were assessed by the calculation of linear regressions. Single-classification *G*-test for goodness of fit with Williams' correction to better approximate the Chi-square distribution (Sokal and Rohlf 1995) was applied for the analysis of seedling-seedbed associations. The seedlings were first grouped into two age classes, first-year and older individuals, respectively, to detect eventual changes in seedbed preferences during age class transition. In the case of categories without any observation, we replaced the zero by 0.1 before calculating the *G*-values. The (fixed) expected frequencies were based on mean percentage cover of each seedbed (wood, moss, and litter). Standardized residuals were obtained by subtracting the expected number of seedlings on a seedbed according to its cover from the observed number of seedlings on that seedbed and subsequent division by the expected frequency. Thus, high positive residual values indicate positive seedling-seedbed associations, and vice versa. The recruitment analyses were restricted to the seedlings of balsam fir, white spruce, white-cedar, and black ash as well as aspen root suckers (only regression of age on elevation), which were numerous enough to meet test conditions.

4.5 RESULTS

4.5.1 Stand species composition and diameter distribution

The stand size structure diagrams show a predominance of broadleaf species, particularly black ash, within the plots of the lowest elevation interval (Fig. 4.3). But both recruitment and trees were rare and had small diameters. Stands 3 and 4 even completely lacked individuals of any tree species (Fig. 4.3B, C). Conifers were present in stand 5 only with some seedlings of white-cedar and white spruce, whereas black ash stems of less than 1 cm dbh were not found there in spite of the presence of several trees of this species (Fig. 4.3H). The plots of intermediate elevation (ELEV1-2) were mostly dominated by conifers, particularly eastern white-cedar, but, broadleaf species were also present (Fig. 4.3). They even dominated in stands 5 and 6 where black ash and balsam poplar were common (Fig. 4.3G, H). The largest trees within each plot, however, were white-cedars and some stumps of trembling aspen cut by beaver. In stand 4 and, to a somewhat lesser degree, in stand 3, the static size distribution of white-cedar was similar to the inversed "J" that

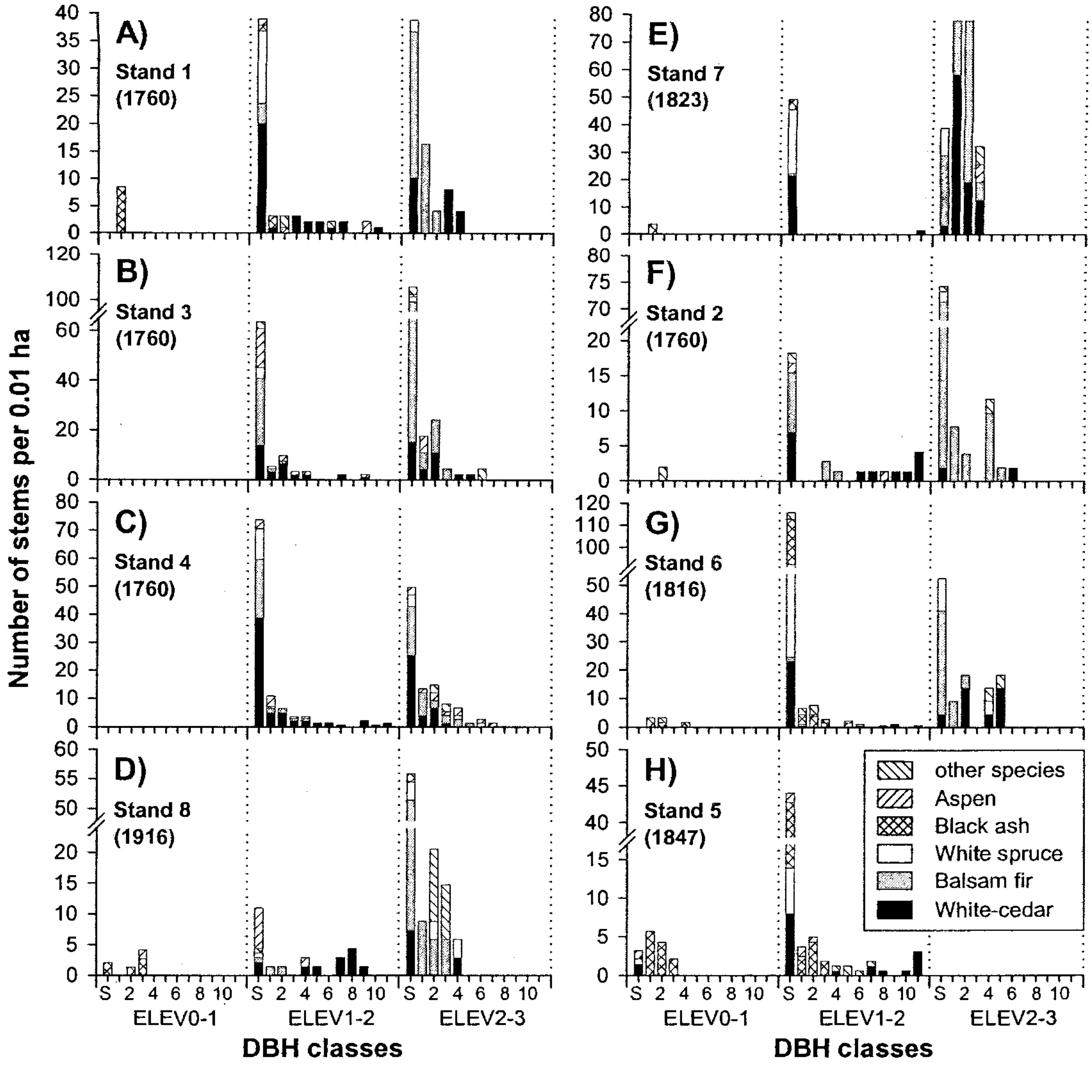

Figure 4.3 Stand size structures of all species differentiated by the three elevation intervals ELEV0-1, ELEV1-2, and ELEV2-3. The dbh classes used are (S) for seedlings and sprouts with stems < 1 cm dbh, 1 to 10 for trees by 5-cm dbh classes from 1 cm up to 51 cm, and a last class for stems ≥ 51 cm dbh. The number of stems within the first size class of all plots was divided by 10. The category other species contains the relatively rare species white birch, balsam poplar, and some willows (*Salix discolor*, S. *heterophylla*, S. *lucida*, and S. *rigida*). The stands are presented in order, from A to H, of increasing exposure. The year of the last forest fire is given in brackets.

is typical of uneven-aged populations (Fig. 4.3B, C). In all other stands, it was rather characterized by a more or less distinct gap between the small and large size classes. Although no tree of white spruce was found below of 2 m elevation, seedlings of this species were found in six of eight stands at ELEV1-2, and in stand 6 (Fig. 4.3G), they were even very numerous. Both recruitment and tree layer within the upland forest (ELEV2-3) were dominated by balsam fir and eastern white-cedar, but, the latter species did not reach as large diameters as within the riparian zone (Fig. 4.3). Only stand 8, the youngest one (last fire in 1916), represented rather a mixed forest of balsam fir and white birch (Fig. 4.3D).

4.5.2 Composite age distribution along the elevation gradient

With the exception of only three first-year seedlings, eastern white-cedar was not found closer to Lake Duparquet than 1 m above the water table in August 1998 (Fig. 4.4). The composite age distribution between 1 m and 3 m showed a distinct trend towards lower ages with increasing elevation: Almost all trees older than 300 years were found between about 120 and 160 cm, whereas just a few individuals above 200 cm exceeded 150 years in age. Only a few stems below 200 cm were aged from 200 to 280 years, whereas many trees between 220 and 255 cm had about the same age, i.e., ca. 80 years. The lower limit of occurrence of white-cedar changed slightly with time (Fig. 4.4). From about 500 – 250 years, it advanced about 20 cm towards the lake, after which it regressed until nowadays. During the last 150 years, the tree-line was driven back for at least 20 cm, eventually even for 40 cm if a few young trees are omitted. However, a considerable number of seedlings of less than 5 years in age occurred down to 1 m above the lake, the lowest of them being found at 65 cm (Fig. 4.4).

Black ash was restricted to the interval between 50 and 200 cm above the lake and, hence, occupied lower elevations on the lakeshore terraces compared to white-cedar (Fig. 4.4). The highest ages up to approximately 150 years were attained between about 70 and 150 cm, whereas only few trees were found above this elevation. Recruitment was very poor below 115 cm but abundant above. Dead black ash trees were slightly more frequent close to the lake.

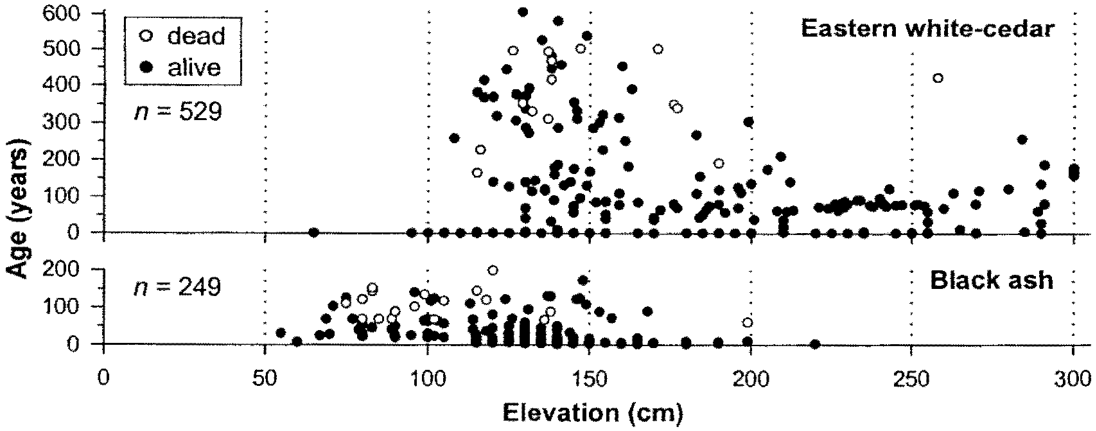

Figure 4.4 Composite age distribution of living and dead stems of eastern white-cedar and black ash along the elevation gradient between 0 cm (= water level in August 1998) and 300 cm above the water level of Lake Duparquet. The age of the dead individuals is their germination age. Elevation of the trees (≥ 1 cm dbh) was measured individually and that of the recruitment (< 1 cm dbh) at 1-m steps along the transects.

4.5.3 Lake-scale age and size distribution

The age structure profiles of eastern white-cedar for the two upper elevation intervals reflected the above mentioned patterns by showing distinct differences with respect to mortality and maximum age (Fig. 4.5A). At ELEV1-2, this species attained ages of more than 600 years and (almost) continuous recruitment started at the end of the 16th century. The late 17th century emerged slightly by its higher number of stems, whereas the period around 1970 (i.e., the second 20-yr age class) and particularly the second half of the 18th century were characterized by relatively low numbers of trees. The 1780s also saw the beginning of continuous recruitment of white-cedar within ELEV2-3 (Fig. 4.5A). However, the oldest, dead, tree at this elevation dated back to about 1575. The age structures for the two elevation intervals were well described by both the negative exponential model and the power function model (Table 4.2). The constant mortality model, however, attained higher R^2-values of 91% for ELEV1-2 and 97 % for ELEV2-3 compared to 79 % and 80%, respectively, for the decreasing mortality model. Mortality rate and initial recruitment of the constant mortality model were both significantly higher for ELEV2-3 than for ELEV1-2 (Table 4.2). The abrupt change in the slope of the cumulative age distribution of ELEV1-2 at the beginning indicates a very high mortality rate from the first to the second 20-yr age class, followed by rather low mortality that increases again as the trees get older (Fig. 4.5A). This juvenile mortality was much less pronounced within the upper elevation interval which might explain the better results of the constant mortality model compared to that of ELEV1-2.

Table 4.2 Results of the linear regression analysis applied to the cumulative age distributions of black ash and eastern white-cedar

Statistic	Black ash		Eastern white-cedar	
	ELEV0-1	ELEV1-2	ELEV1-2	ELEV2-3
Negative exponential model (constant mortality)				
n	8	9	31	13
R^2 adj.	0.941	0.944	0.907	0.967
Intercept	1.890^a	3.922^b	3.414^a	4.685^b
Slope	-0.025^a	-0.038^a	-0.009^a	-0.024^b
Power function model (decreasing mortality)				
n	8	9	31	13
R^2 adj.	0.863	0.917	0.788	0.802
Intercept	5.217	10.039	9.103	9.988
Slope	-1.287	-2.254	-1.543	-1.832

Notes: All linear regressions were significant at $P < 0.0006$. Values of intercept and slope of the negative exponential model sharing the same superscript letter do not differ significantly between the two elevation intervals of the same species ($P < 0.05$); *n* = number of age classes in the cumulative distribution.

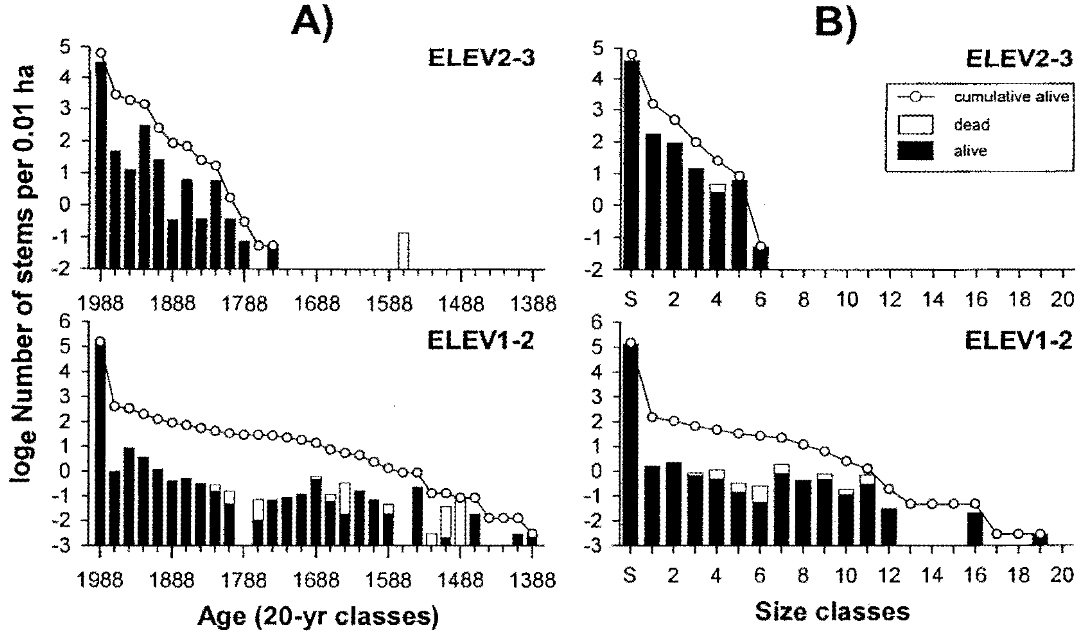

Figure 4.5 Lake Duparquet age and size structures of eastern white-cedar.

(A) Static age distributions in 20-yr classes of the area converted and $\log_e$-transformed numbers of living and dead stems for the upper (ELEV2-3) and intermediate (ELEV1-2) elevation interval, respectively. The lines denote the cumulative frequency distributions of the living stems only. The years represent the medians of the 20-yr classes.

(B) Static diameter distributions of the area converted and $\log_e$-transformed number of living and dead stems for the upper (ELEV2-3) and intermediate (ELEV1-2) elevation interval, respectively. The lines denote the cumulative frequency distributions of the living stems only. The size classes used are (S) for seedlings and sprouts with stems < 1 cm dbh, and 1 – 20 for trees by 5-cm dbh classes from 1 cm up to 101 cm.

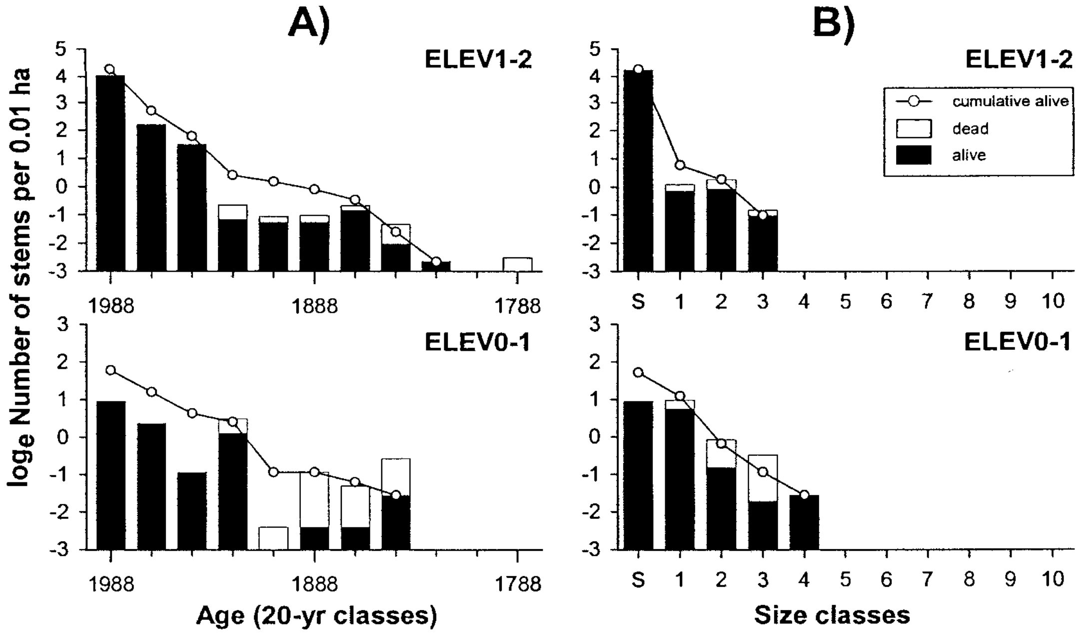

Figure 4.6 Lake Duparquet age and size structures of black ash.

(A) Static age distributions in 20-yr classes of the area converted and $\log_e$-transformed numbers of living and dead stems for the intermediate (ELEV1-2) and lower (ELEV0-1) elevation interval, respectively. The lines denote the cumulative frequency distributions of the living stems only. The years represent the medians of the 20-yr classes.

(B) Static diameter distributions of the area converted and $\log_e$-transformed number of living and dead stems for the intermediate (ELEV1-2) and lower (ELEV0-1) elevation interval, respectively. The lines denote the cumulative frequency distributions of the living stems only. The size classes used are (S) for seedlings and sprouts with stems < 1 cm dbh, and 1 – 10 for trees by 5-cm dbh classes from 1 cm up to 51 cm.

The combined size structure profiles of white-cedar resemble those of stem age (Fig. 4.5B). At ELEV1-2, the diameter distribution is characterized by a sharp drop of the number of stems from the first (dbh < 1 cm) to the second (1 – 6 cm dbh) size class followed by a very slow diminishment until the highest class (maximum dbh: 91 cm). At ELEV2-3, however, the $\log_e$-transformed cumulative frequency distribution decreases relatively rapidly until the abrupt decline from the fifth (21 – 26 cm dbh) to the sixth (26 – 31 cm dbh) tree size class (maximum dbh: 26.5 cm).

Relative to eastern white-cedar, maximum age and mortality of black ash differed much less between the two elevation intervals (Fig. 4.6A). Continuous recruitment within ELEV1-2 began at about 1825 when the oldest living tree got established. Only one dead tree was found to be older (~ 200 years). The static frequency distribution corresponded quite well to that of an uneven-aged population with constant mortality, although the 20-yr age classes between 1878 and 1938 were slightly underrepresented. Compared to ELEV1-2, maximum age of black ash within ELEV0-1 (~140 years) was only slightly lower. However, since several of the oldest trees sampled were dead, continuous recruitment started as late as the 1920s. The lack of recruitment at ELEV0-1 is less visible in the age structure profile than in Figure 4.4 because several trees just entered the first age class (Fig. 4.6A). Both population dynamics models, negative exponential function and power function, were highly significant for both elevation intervals (Table 4.2). The constant mortality model, however, explained slightly larger parts of the variation in the two data sets. The distinctly lower numbers within most of the age classes of ELEV0-1 and the similar frequency distributions of the two elevation intervals resulted in a significantly higher initial recruitment for the upper riparian zone but non-significantly differing mortality rates. The diameter distribution of black ash reflects the predominance of stems with less than 1 cm dbh at ELEV1-2 and their relatively low number at ELEV0-1 (Fig. 4.6B). In spite of the higher ages the stems attained at ELEV1-2, maximum size was about 5 cm lower than at ELEV0-1.

4.5.4 Stand age distribution

Eastern white-cedar at low elevations grew considerably older than within the upland forest in almost all stands (Fig. 4.7). Maximum age of the living trees varied between ~ 600 years (stand 5) and ~ 300 years (stand 1) for ELEV1-2, but only between 250 years (stand 2) and 60 years (stand 8) for ELEV2-3, respectively. The oldest, dead tree within ELEV2-3 of stand 8 established at about the same time as the oldest tree of ELEV1-2 (~ 1575) but much earlier than the living individuals within the same plot (Fig. 4.7D). Its youngest preserved tree ring dated from 1882. Since not only the bark but also the sapwood was lacking, we supposed that this tree, as all others within this elevation interval, had been killed by the fire of 1916. In contrast, only one tree in the ELEV1-2 plot of stand 1 pre-dated the oldest individual within the higher plot, and it was completely tilted to the ground but still living when sampled (Fig. 4.7A). Eccentric tree rings and the presence of compression wood starting in 1761 lets us suggest that tilting was related to the fire event just one year before. We suggest therefore that the fire front advanced close to the lakeshore at this place and killed all white-cedars (and all trees of the other species) but this one, which was subsequently tilted perhaps by a falling tree or by stronger winds after the canopy opening. Several of the trees established during the 19th century had effectively germinated on the rotten part of this tilted tree.

The static age distributions of eastern white-cedar on the plot scale showed considerable deviations from constant mortality and recruitment population dynamics as observed on the lake level. The first 20-yr age class dominated in 14 of the 15 plots, whereas no tree at all fell into the next two age classes (21 – 60 years) in all but two ELEV1-2 plots (Fig. 4.7). The stand with the most recent fire year, number 8, was the only one with considerably fewer individuals of eastern white-cedar within the lowest 20-yr age class of the intermediate elevation interval compared to the ELEV2-3 plot (Fig. 4.7D). The age distributions of the ELEV1-2 plots were characterized by episodic recruitment phases occurring at different times, but, distinct peaks were rather rare (Fig. 4.7). Stand 4, for example, showed three peaks

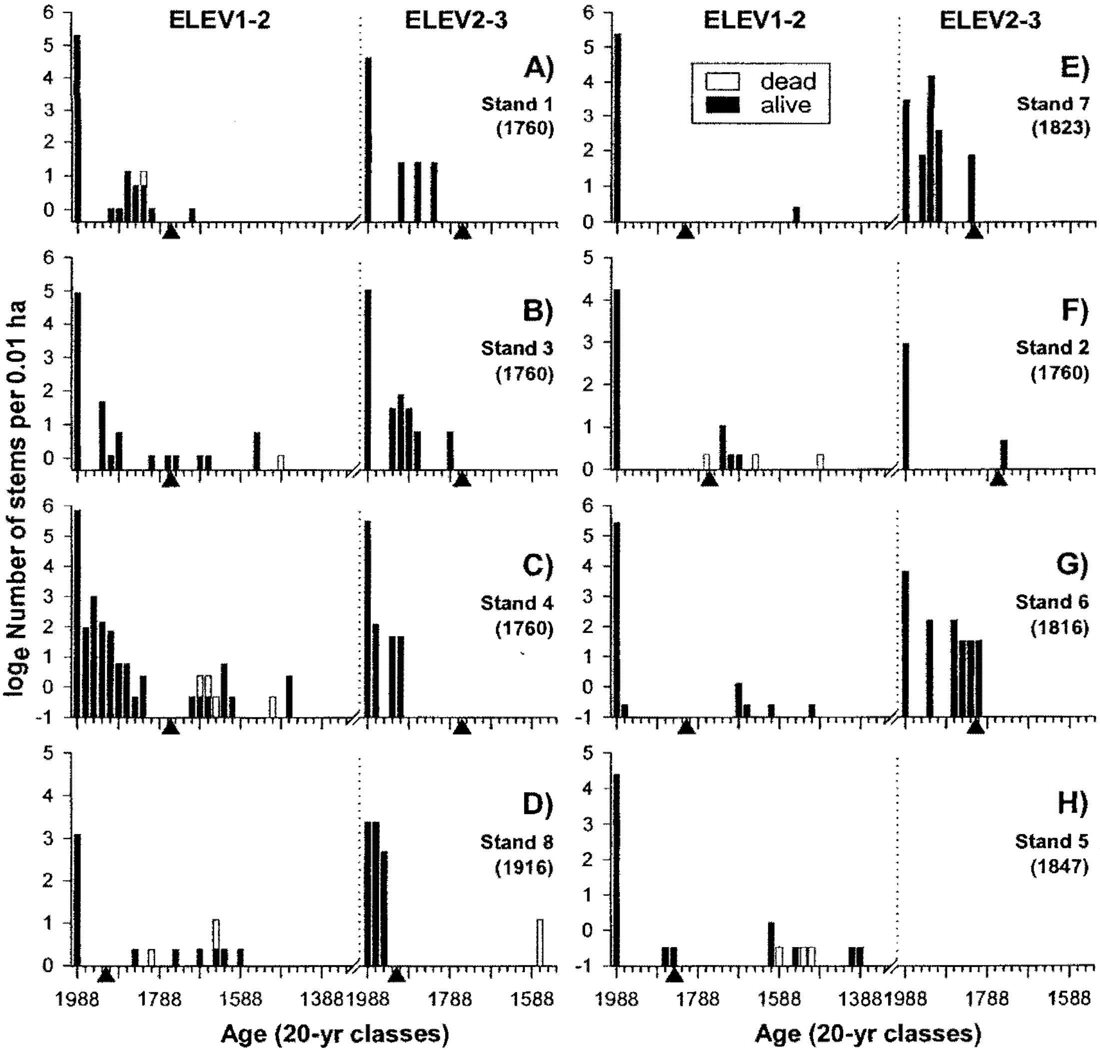

Figure 4.7 Log$_e$-transformed static stand age distributions in 20-yr classes of living and dead eastern white-cedar stems within the intermediate (ELEV1-2) and upper (ELEV2-3) elevation intervals. The stands are presented in order, from A to H, of increasing exposure. The fire year of each stand is given in brackets and as black triangles on the abscissa.

of recruitment: a first cohort might have established around 1500, the second during the 17th century, and continuous recruitment started at about 1820. The three stands well protected from riparian disturbances (stands 1, 3, and 4) were the only ones with considerable post-fire recruitment within the riparian zone (Fig. 4.7A-C). The other stands more exposed to the riparian disturbances, however, showed almost no post-fire white-cedars although in each of these stands, recent recruitment of this species was present (Fig. 4.7E-H). In addition, a period of more than hundred years preceding the fire year without any white-cedar was observed in stands 5 to 7 (Fig. 4.7E, G, H). The lack of post-fire recruitment within the riparian zone of three of the exposed stands (number 6, 7, and 8) contrasts with the relatively abundant regeneration within the upland forest of the same stands (Fig. 4.7D, E, G). Only stand 2 emerges with no post-fire recruitment within both elevation intervals (Fig. 4.7F). In general, post-fire recruitment of the upland eastern white-cedar started immediately or less than 50 years after the fire (Fig. 4.7).

The stand age distributions of black ash, differentiated by the two elevation intervals considered, are shown in Figure 4.8. Three stands were omitted because this species was either completely absent (stand 2) or only 1 stem was found within the whole sampling area (stands 3 and 4). Very few living stems of black ash were encountered in stands 1, 7, and 8, respectively, and they were almost all restricted to the first two 20-yr age classes (Fig. 4.8A-C). Black ash was most common and attained the highest ages at the most exposed stands 5 and 6 (Fig. 4.8D, E). However, no living tree was established before the last fire years of 1847 and 1816 respectively. The relatively sparse forest at stand 5 had more black ash stems of less than 60 years than did the denser population at stand 6. Differences in the stand age structures according to elevation were relatively small with the exception of the first age class that is empty in all plots of ELEV0-1 except in stand 8 but predominates at ELEV1-2 in all stands except number 7.

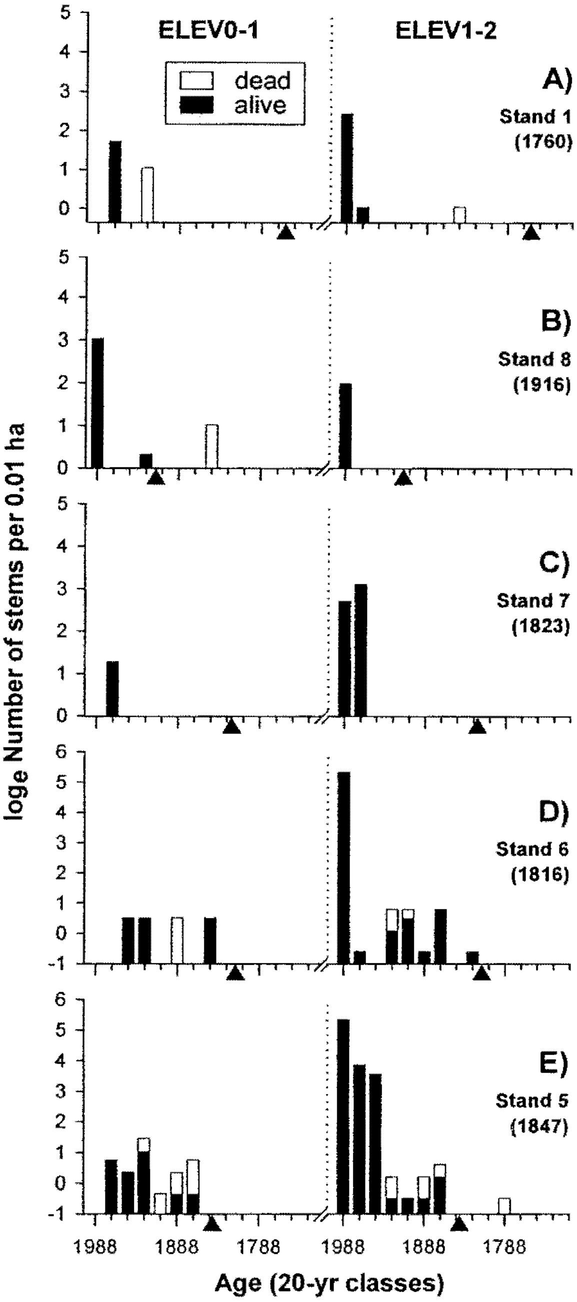

Figure 4.8 Log$_e$-transformed static stand age distributions in 20-yr classes of living and dead black ash stems within the lower (ELEV0-1) and upper (ELEV1-2) riparian zone. The stands are presented in order, from A to E, of increasing exposure. Stands 2 to 4 are not shown because of very low number of stems. The fire year of each stand is given in brackets and as black triangles on the abscissa.

4.5.5 Effects of elevation and seedbed on recruitment

The linear regressions of the recruitment age on elevation above the water level of Lake Duparquet revealed mostly significant relationships (Table 4.3). Seedling age of all conifers (balsam fir, white spruce, and eastern white-cedar) increased with rising elevation as indicated by the positive slopes. The variation in the data explained by the regression amounted to 23.0 % for balsam fir, to 36.2 % for white spruce, but only to 5.3 % for white-cedar seedlings. The regression of black ash seedlings, however, was significantly negative with a relatively steep slope and explained 13.9 % of the variation, whereas the age of the root suckers of trembling aspen did not significantly change along the elevation gradient (Table 4.3).

Table 4.3 Results of the linear regressions of age on elevation above the water level of Lake Duparquet of the recruitment (dbh < 1 cm) data for the different species and origin

Statistic	Species[a]/Origin[b]				
	ABA/sex	PGL/sex	TOC/sex	FNI/sex	POT/veg
n	358	382	382	171	55
Intercept	-9.749***	-5.939***	-1.408*	44.060***	4.810*
Slope	0.082***	0.056***	0.019***	-0.218***	n.s.
R^2 adj.	0.230	0.362	0.053	0.139	n.s.

Note: Elevation above water level was measured at 1-m steps only; *n* = number of individuals; n. s. = not significant; * $P \leq 0.05$; *** $P \leq 0.001$

[a] Species: ABA = Balsam fir PGL = White spruce FNI = Black ash
POT = Aspen TOC = Eastern white-cedar

[b] Origin: sex = sexual veg = vegetative

At the scale of Lake Duparquet, the area covered by the seedbed litter averaged 64 % within the upper riparian zone followed by moss with 25 % and wood with 12 % (Fig. 4.9). The *G*-tests revealed statistically significant ($P \leq 0.05$) seedbed preferences for all species and age classes, i.e., the number of seedlings observed within the upper riparian zone did not correspond to the expected frequencies based on the mean percentage cover of the three seedbeds. The standardized residuals illustrate the deviations from the expected frequencies (Fig. 4.9). The residuals for wood were all negative and took mostly the value –1, indicating low frequencies or absence of seedlings on this seedbed. Both black ash and white spruce were also negatively associated with moss but positively with litter. In contrast, balsam fir and first-year seedlings of white-cedar were overrepresented on moss, whereas their residuals for litter were very small. The negative age class differences of the residuals for white spruce and white-cedar on wood and moss indicate difficult survival of the first-year seedlings on these seedbeds in contrary to litter. The opposite tendency can be observed for balsam fir seedlings, for which survivorship was best on moss. No age class differences of the residuals exist for black ash seedlings since they were found on litter only (Fig. 4.9).

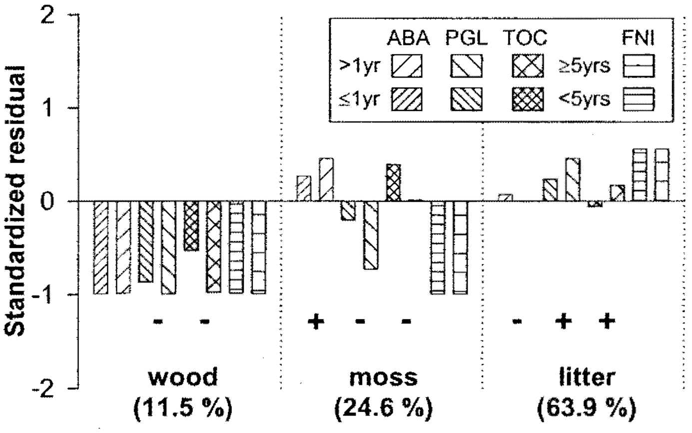

Figure 4.9 Standardized residuals from single-classification *G*-tests with Williams' correction with the age-differentiated seedling frequencies of balsam fir (ABA), white spruce (PGL), eastern white-cedar (TOC), and black ash (FNI) from the upper riparian zone (ELEV1-2). High positive residual values mark positive seedling-seedbed associations, and vice versa. The signs indicate negative (-) or positive (+) residual differences between the two age classes of a same species. Notice the different age class division of black ash that had to be made to keep seedling numbers high enough to meet test conditions. Percentages in brackets are the mean cover of the three seedbeds after omission of mineral soil and rocks.

4.6 DISCUSSION

4.6.1 Species composition

Composition and importance of the tree species changed considerably in the three meter range in elevation between the shore of Lake Duparquet and the upland forests. The lowest sites were occupied by some willows and balsam poplars, but, they were clearly dominated by black ash, a very flood tolerant species forming almost pure stands on the floodplains of this lake (Tardif and Bergeron 1992, 1999; Denneler et al. 1999). In most of our shore terrace stands, however, this species occurred only sparsely, forming more or less closed populations only on the two largest terraces of stands 5 and 6 where it was accompanied by balsam poplar and trembling aspen. Black ash was limited to about 2 m above the water level, which corresponds roughly to the mean maximum high water level of Lake Duparquet. The high flooding tolerance in combination with the capacity to reproduce vegetatively by stem sprouting allows this species to persist in this highly disturbed habitat. On the other hand, its high water requirements and shade intolerance (Wright and Rauscher 1990) might explain its absence within the upland forest where interspecific competition is greater.

Beside black ash and balsam poplar, several other tree species like aspen, balsam fir, and white spruce were found within the upper riparian zone between 1 and 2 m above the lake. Trembling aspen was more abundant within the well lit riparian zone than within the upland forest. However, many of these trees have been cut by beaver, stimulating the formation of root suckers. Since beavers can be active quite far from the lakeshore (Bordage and Filion 1988), the age of the suckers did not significantly change with elevation. Although sexual recruitment of a spen was rare, it occurred even within the lowest plot (ELEV0-1) in stand 5. These seedlings were all 2 years old and thus germinated just after the area had been flooded the last time in spring 1997 (see Fig. 4.2). Balsam firs were rarely found and white spruce trees were completely absent within the flooded area, although a few trees of this latter species have been found within the flooding zone at other places along the perimeter of Lake Duparquet (Denneler et al. 1999). However, spruce seedlings were particularly abundant and occurred in almost every riparian stand, indicating successful reproduction at the edge of Lake Duparquet, probably by wind-dispersed seeds from adult trees in the surroundings. Survivorship of the seedlings of both species, however, was low compared with upland sites as shown by the positive regression of age on elevation. Possible reasons for the high mortality of the first-year seedlings close to the lake could be intolerance to flooding or summer drought (Frank 1990; Nienstaedt and Zasada 1990).

The dominant species in the upper part of the shore terraces was eastern white-cedar with many large and old individuals. Recruitment of this species was present in every stand and was positively associated with moss and litter. Despite the low number of individuals older than one year on all seedbeds, seedling survivorship was slightly better on litter. Rainfree periods during summer might dry the mosses and wood and kill the first-year seedlings, which are very sensitive to drought during the first weeks after germination (Nelson 1951; Johnston 1990). Although former studies have shown that decomposing logs are a preferred seedbed for white-cedar (Scott and Murphy 1987; Simard et al. 1998), our results revealed that wood was a particularly poor seedbed not only for white-cedar but also for fir, spruce, and black ash. However, the logs within the riparian zone were mostly composed of only slightly decomposed deposited driftwood that might be moved too often during floods to be colonized permanently. On stable logs, however, white-cedar established successfully as in stand 1, where several trees from the 19th century were rooted in the partially rotten base of a still living but heavily tilted old tree at the lower forest limit.

Balsam fir and, to a lesser degree, eastern white-cedar dominated within the upland forest plots, whereas the two pioneer species trembling aspen and paper birch were rarely found. This species composition reflects an advanced stage of succession because post-fire stand initiation dated from more than 150 years in all but one stand. In this stand, number 8, which burned in 1916, paper birch co-dominated with balsam fir. Bergeron (2000) has shown for the southern boreal mixed wood forest that post-fire cohorts of aspen increasingly disintegrate after the age of about 100 years and secondary recruitment is restricted to canopy gaps. Hence, the low number of trembling aspen and white birch within the highest plots of our study stands might be due to a lack of gap-creating disturbances. White spruce trees were restricted to the upland forest of stands 4, 6, and 9, respectively, whereas seedlings occurred in all stands but were less numerous than in the lowland. As an intermediately shade tolerant species (Nienstaedt and Zasada 1990), white spruce might depend on the creation of gaps to grow into the canopy.

4.6.2 Upland population dynamics subject to fire

Population dynamics of eastern white-cedar above the riparian zone was found to be strongly influenced by forest fire. Both the negative exponential model and power function model were highly significant in describing the composite cumulative frequency distribution of white-cedar. But, the constant mortality model explained a larger part of the variation in the data. The comparison with the fire years revealed that almost no tree survived from before the last fire. The oldest dead tree, dating back to the year 1575 (estimated), shows that at least in stand 8, white-cedar was present before the forest burned. The significantly higher mortality rate compared to that observed in the lowland was thus due to the elimination of the pre-fire population, i.e., the elimination of the old age classes, or, less probable, the absence of white-cedar within the upland forest.

White-cedar was present in the upland forest of all eight stands. Re-establishment after fire was somewhat delayed. In stand 4, the time lag was about 150 years and in stand 2, it is not clear if white-cedar just recently began to regenerate or if the recruitment cannot survive. The time lag for the other five stands analyzed, however, varied only between 0 and 50 years. These delays are relatively short if compared to the ca. 120 years observed in a study about post-fire species dynamics along a chronosequence in the area of Lake Duparquet (Bergeron 2000). The position at the edge of the burned area close to the surviving and seed-producing lowland white-cedars might have accelerated post-fire re-invasion of this species.

Because eastern white-cedar does not grow as tall and as fast as other species (Johnston 1990), the trees within the upland forest were often suppressed by larger and faster growing individuals of balsam fir, white spruce, trembling aspen, and white birch. This subcanopy position is illustrated by the sustained long-term growth release observed for most of the white-cedar trees (data not shown) reflecting their slowly improving position with respect to competition for light.

4.6.3 Lowland population dynamics subject to flooding and fire

The age distribution of eastern white-cedar within the riparian zone provided evidence for a mitigated fire disturbance regime relative to the upland forest. Trees of this fire-sensitive species pre-dating the last fire event were found in every riparian stand. Since fire probability has been shown to depend significantly on soil moisture (Hébert 1995), we suppose that the relatively humid soil within the riparian zone resulted in unfavorable conditions to burn the vegetation. The oldest individuals were found in stand 5, which was particularly well protected from fire by its location on a peninsula on the southeast side of the lake, and thus in the windward side of the dominant northwestern winds. Nevertheless, the maximum estimated age of 608 years does not represent the maximum natural life span of eastern white-cedar. Much older individuals have been found on xeric rock outcrops on the islands in Lake Duparquet (ca. 900 years; Archambault and Bergeron 1992a, 1992b) and on the cliff faces of the Niagara escarpment in southern Ontario (855 years; Kelly et al. 1994). This reduced tree longevity might be caused by a higher exposure to i), devastating crown fires at the mainland shores compared to non-lethal surface fires predominating on the relatively small islands in Lake Duparquet (Bergeron and

Gagnon 1987; Bergeron and Brisson 1990; Bergeron 1991) and, ii), aquatic disturbances like ice push and erosion.

There is some evidence that the forest fires generally did not just stop at the upper limit of the riparian zone. It is highly probable that the relatively low number of white-cedars within the riparian zone that originated from the second half of the 18th century was related to the fire of 1760 when four of the eight study stands burned for the last time. We even suppose that the fire reached the immediate lakeshore in most of the stands. In stand 1, for example, only one white-cedar pre-dated the last forest fire, and its tilting, initiating formation of eccentric tree rings and compression wood from 1761 onwards, was probably related to the fire just one year before that might have killed all other trees. However, the situation was different in stands 4 to 8 which lacked trees that dated from the several decades immediately preceding the fire years. We assume that the lethal crown fires decreased in intensity at these sites and advanced to the lakeshore as low-intensity surface fires that killed the young but not the old white-cedars. Bergeron and Brisson (1990) as well as Hély et al. (2003) have shown that small trees resist less to fire than taller individuals. These fires could have stimulated somewhat the sexual (by seeds from surviving adult trees) and vegetative reproduction of the shade-intolerant black ash in stands 5 and 6 that started very soon after the corresponding fire years of 1847 and 1816, respectively.

The composite cumulative frequency distribution, representing the meta-population of riparian eastern white-cedar, was very well described by the constant mortality model. At the stand level, however, important deviations from this model were observed for most of the plots. The static age distribution in stand 4 could rather be described by a damped sine wave with recruitment phases around 1500, during the 17th century, and after 1800. This pattern could be the result of three forest fires, one in the early 15th century, one in the mid-16th century, and the fire of 1760, respectively. Stands 2, 5, 6, 7, and 8 approximated bimodal age structures with very old and very young stems but almost none of intermediate age. The above mentioned surface fires are not believed to explain completely the lack of post-fire recruitment within these plots. Seed input and germination would have assured regeneration as indicated by the high number of stems in the first 20-year age class. The successful reproduction within the upland forest in all these stands, except number 2, points rather to unfavorable conditions for seedling survivorship within the riparian zone of these stands. These unfavorable conditions were probably independent of the seedbed since survival of recent white-cedar recruitment was found to be equally low on wood, moss, and litter. The most probable reason for the lack of white-cedar recruits is rather a high exposure to riparian disturbances. In fact, these stands represent exposed sites with their long fetches to the opposite shore of the lake towards northwest (see Tab. 4.1), which is the predominant wind direction. On the other hand, the stands with the most abundant white-cedars established after fire, numbers 1, 3, and 4, were the less exposed because they are orientated to the south. Relative basal area of this species on shore terraces of Lake Duparquet has been shown to be highest on sites with northeastern aspect that are also relatively well protected from the northwestern winds (Denneler et al. 1999). We thus infer that the riparian white-cedar populations at the exposed sites along the lake perimeter are, as hypothesized, over-aged and that they will decline under the present environmental conditions because of the low survivorship of the recruits. In contrast, the populations at more protected sites reproduce successfully, at least occasionally, and can, thus, persist despite high seedling mortality.

The composite cumulative frequency distribution of black ash in both the upper and lower riparian zones followed a negative exponential function. However, only the initial recruitment was significantly higher for the upper zone relative to the lower part, whereas the mortality rates did not differ significantly. Hence, the number of black ash stems was generally smaller close to the lake, but it decreased with a similar rate from one age class to the next. Nevertheless, the higher exposure to the riparian disturbances on low elevations resulted not only in a slightly lower maximum age, but also in a period of high mortality that lasted from the late 19th century to about 1920. We assume that many of the smaller black ash trees have been killed by an extreme spring flood of Lake Duparquet in 1922 that was reconstructed using maximum height of ice scars (Tardif and Bergeron 1997b). This would also explain the subsequent increase in the number of trees as stem sprouting was stimulated.

As for eastern white-cedar, black ash population dynamics at the stand level differed considerably from the constant mortality model. High exposure to riparian disturbances on the relatively narrow shore terraces of the stands 1 to 4, 7, and 8 allowed black ash to establish and survive just sporadically, as indicated by the rare and mostly young individuals. The competition for light in the relatively protected stands 1, 3, and 4, where riparian white-cedars were common, could also have restricted the occurrence of black ash. In stands 5 and 6, however, black ash reproduced more continuously and attained greater age, probably because waves and ice push were reduced by the larger riparian zones and competition for light was low. Except in stand 8, recent recruitment up to 20 years in age occurred only above the elevation of about 110 cm, which is expressed by the negative slope of the linear regression of seedling age on elevation. This points to problematic regeneration of black ash close to the lakeshore. In addition, seedlings younger than 5 years were sparse and first-year seedlings absent within the whole riparian zone of all stands. This lack of reproduction on all elevations might be due to several years of poor seed production (Wright and Rauscher 1990).

4.6.4 Long-term water level changes of Lake Duparquet

The preceding discussion has shown that the riparian eastern white-cedar populations along the exposed parts of the perimeter of Lake Duparquet are not in equilibrium with the present water level. Since those white-cedars constituting the lower forest limit towards the lake showed mostly the asymmetric crown form typical for a forest edge – the branches facing the illuminated lake side reached further down the stem than on the shaded opposite side – the changing elevation of the lakeside tree limit with time can be used as an indicator for the long-term water level fluctuations of this lake. Based on the composite age distribution of white-cedar along the elevation gradient (see Fig. 4.4), three periods with respect to the water level of Lake Duparquet were distinguished. Before about 1500, the lake level might have been relatively high because white-cedar did not occur closer to the lake than about 125 vertical centimeters. Between approximately 1500 and 1850, i.e., during the relatively cool and dry period known as Little Ice Age (Lamb 1982), the lacustrine limit of this species advanced to the lake for about 20 vertical centimeters because, as we assume, the lake level had receded. Since then, the tree limit was driven back progressively for at least 20 cm, maybe even 40 cm, if a few young trees further down are neglected. This tree-line regression is supposed to reflect the water level increase of Lake Duparquet since the end of Little Ice Age. Even if the higher value of 40 cm is accepted, this would still be considerably less than the increase of the spring flood levels, which has been estimated by Tardif and Bergeron (1997b) at about 100 cm for the same period using changes of the maximum height of ice scars on white-cedar stems bordering Lake Duparquet. However, this 100-cm increase of the spring floods was principally restricted to very few years with extreme water levels since the 1920s. The floods of most of the other years after 1920, however, were at least half a meter lower and are, thus, within the range of our results.

The observation of numerous white-cedar seedlings at low elevations is not likely to indicate a recent withdrawal of the water level of Lake Duparquet because 93 % of those below 130 cm elevation were less than 1 year old and none of them attained 5 years in age. However, they show that seed germination is possible even under the regime of an elevated water level. Thus, we suggest that the main effects of the water level rise during the 20th century was neither uprooting of the old trees, which were already tall when the water level began to rise, nor inhibition of seed germination, but rather to prevent the establishment of white-cedar below about 150 cm. Since white-cedar successfully recruits in the protected parts of the lake perimeter, we infer that the die-back of the seedlings is mainly caused by physical injury caused by drifting ice and driftwood during the increasingly frequent high spring floods, and less by flooding stress that affects the seedlings in the same way around the whole lake.

Black ash provided further evidence for a water level increase of Lake Duparquet after the Little Ice Age (see Fig. 4.4). The oldest living tree was approximately 175 years old, which is not very old in comparison to floodplain trees that can attain more than 300 years (Tardif and Bergeron 1999). Since about 1850, this species started to invade in greater number the riparian zone of the shore terraces, whereas older individuals were exceptional. In addition, tree age tended to decrease with rising elevation, a trend that would be expected from a species that invaded new territory from the lakeshore towards the upland as the water level rose.

Our results correspond to other dendroecological studies done at Lake Duparquet that pointed to a distinct climate change since the end of the Little Ice Age with increased precipitation, and thereby causing rising lake water levels (Bergeron 1991; Archambault and Bergeron 1992a; Tardif and Bergeron 1992; Bergeron and Archambault 1993; Tardif and Bergeron 1993, 1997a, 1997b). The supposed pattern of long-term water level fluctuations of Lake Duparquet for the last 500 years agrees at least partly with the results of dendroecological and stratigraphical studies from subarctic Quebec (Bégin and Payette 1988; Payette and Delwaide 1991; Payette and Filion 1993). According to these authors, low water levels prevailed until the mid-18th century, followed by a rise that attained its maximum in the 20th century. The rising water levels in subarctic Quebec have been attributed to increased snow precipitation due to the temperature increase (Payette 1980; Bégin and Payette 1988; Payette and Delwaide 1991; Payette and Filion 1993). Thus, it seems that subarctic and southern boreal Quebec might have undergone similar climate changes during at least the last 500 years.

4.6.5 Climate change: what the future might bring

What will be the impact of future global warming on the water level of Lake Duparquet and the eastern white-cedar populations within the riparian zone? The most recent scenarios of the Intergovernmental Panel on Climate Change predict a continuing temperature rise for at least another century that, depending on the climate model, can attain between 1.4 and 5.8 °C, i.e., considerably more than the 0.6 ± 0.2 °C observed for the 20th century (Houghton et al. 2001). On the other hand, simulations of the future fire regime in Quebec under the assumption of a doubled

CO_2 concentration (660 ppm) pointed to a ongoing decrease in fire frequency due to more abundant precipitation (Bergeron and Flannigan 1995; Bergeron 1998; Flannigan et al. 1998, 2001). We assume therefore that the water level of Lake Duparquet will continue to rise, maybe even faster than in the past, which will result in increased frequency and amplitude of extreme spring floods. Hence, survivorship of the riparian eastern-white cedars, be they seedlings or large, old trees, will decrease as they run a higher mortality risk from wave and ice activities. Thus, we suppose that white-cedar will regress, i.e., the actual riparian fringe will gradually disintegrate, and be replaced by black ash, which is more tolerant to both flooding and physical injuries. If the water level stabilizes with time, a new white-cedar fringe might develop on higher elevations. Our results show that these processes have already started at the exposed parts of the lake perimeter, whereas relatively protected sites are not yet affected.

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CONCLUSION GÉNÉRALE

L'environnement riverain se distingue de celui de la terre ferme non seulement par l'influence qu'exercent les perturbations riveraines, telles que les inondations, les vagues, les poussées glacielles, l'érosion et la sédimentation, mais aussi par l'effet moins prononcé des perturbations terrestres, telles que les feux de forêt. L'étude présentée a permis d'augmenter les connaissances sur la distribution, la croissance et la dynamique des peuplements riverains de cèdre blanc entourant le lac Duparquet qui sont soumis à de telles conditions environnementales.

Les variations sur de courtes distances du substrat, de la topographie, ainsi que des processus géomorphologiques ayant retravaillé les sédiments et modelé les rives par l'érosion et la sédimentation pendant des milliers d'années, ont créé un rivage très diversifié et complexe au lac Duparquet. Nos résultats indiquent que la composition et la dominance des espèces arborescentes varient considérablement selon le type de rive. Les plaines de débordement sont généralement le domaine du frêne noir (voir aussi Tardif et Bergeron 1992), alors que les tourbières des plaines alluviales sont plutôt dominées par le mélèze et partiellement par l'épinette noire (voir aussi Girardin et al. 2001a). Le cèdre blanc, moins tolérant aux hauts niveaux d'eau que le frêne et le mélèze, y occupe les zones plus élevées sur les levées et à la transition vers les hautes terres. Par contre, l'érosion des sédiments dénudant les escarpements rocheux et faisant régresser les plages y empêche le développement d'une végétation typiquement riveraine. La végétation est la plus diversifiée sur les terrasses riveraines avec la présence du frêne noir, de saules, du peuplier faux-tremble, du bouleau, du sapin, de l'épinette blanche et surtout du cèdre blanc. Cette dernière espèce est la seule qui est omniprésente dans les cinq types de rives distingués. De plus, le cèdre y atteint les diamètres les plus élevés.

L'analyse de l'accroissement radial du cèdre blanc sous l'effet des inondations a donné des résultats clairs malgré que leur interprétation ne soit pas si simple. Ni la crue printanière extrême du lac Duparquet en 1996, ni le rehaussement artificiel du niveau d'eau du lac Abitibi après la construction d'un barrage en 1914 se sont clairement identifiés par la largeur des cernes de croissance des cèdres riverains. Trois raisons peuvent expliquer cette absence d'un effet négatif tel que prévu: i) les perturbations riveraines sévères empêchent le cèdre d'approcher le lac suffisamment de façon à ce que le stress d'inondation puisse avoir un effet adverse, ii) le cèdre est très tolérant aux inondations, ou iii) les crues printanières se produisent essentiellement pendant la période de dormance pendant laquelle le métabolisme des arbres est réduit. Les résultats de notre étude suggèrent que toutes ces trois raisons peuvent contribuer à la non-sensibilité du cèdre blanc au stress d'inondation, ce qui concorde avec une partie de la littérature pertinente. Quoique les arbres temporairement inondés réduisent généralement leur accroissement radial (Harris 1975, Harms et al. 1980, Duever et McCollom 1987, Tardif et Bergeron 1993, Astrade et Bégin 1997), il fut montré qu'ils puissent aussi être indifférents aux inondations ou même en bénéficier si celles-ci sont d'une durée très restreinte ou se produisent avant le début de la saison de croissance (Broadfoot et Williston 1973, Teskey and Hinckley 1977, Conner et al. 1981, Mitsch et Rust 1984, Kozlowski et al. 1991). Au lac Duparquet, les peuplements de frêne noir occupant les plaines de débordement ont enregistré une accélération à long terme de l'accroissement radial malgré une hausse du niveau des crues printanières (Tardif et Bergeron 1999). Cet effet positif des crues sur la croissance du frêne fut expliqué par la prolongation de la saison de croissance à cause des débâcles printanières de plus en plus hâtives (Tardif et Bergeron 1997, 1999). Cependant, l'étude de Tardif et Bergeron (1999) n'a pas pris en considération qu'au moins une partie de cette augmentation de la croissance aurait pu être causée par la diminution graduelle de la suppression causée par la compétition pour la lumière au fur et à mesure que les arbres ont grandi et se sont taillés une place dans la canopée supérieure.

Se basant sur notre étude, on ne peut pas exclure un effet négatif d'inondations se prolongeant dans la saison de croissance sur l'accroissement radial des cèdres affectés. Il serait donc intéressant d'étudier la croissance de cèdres riverains sur les sites les plus bas qui sont exposés aux crues printanières mais en même temps protégés des perturbations physiques telles les poussées glacielles afin d'isoler l'effet des inondations prolongées. De tels peuplements peuvent être observés derrière quelques frênaies et mélèzaies occupant les zones riveraines les plus étendues. De même, le suivi sur plusieurs années de la croissance du cèdre à l'aide de dendromètres et d'échantillons de bois pourrait permettre une meilleure compréhension de l'influence des inondations sur la formation des cernes de croissance chez cette espèce.

Finalement, le cèdre blanc ne semble pas être aussi sensible à un surplus d'eau qu'à un manque d'eau. La croissance d'individus sur des escarpements rocheux, et donc sous des conditions xériques, est grandement diminuée pendant des périodes de sécheresse (Archambault et Bergeron 1992a, Kelly et al. 1994) et accélérée au fur et à mesure que les précipitations ont augmenté (Archambault et Bergeron 1992a). Cela démontre que le manque d'eau limite plus fortement le métabolisme du cèdre blanc que le surplus d'eau.

L'analyse de la dynamique des populations de cèdre blanc, une espèce très susceptible aux feux (Johnston 1990), montre que les peuplements riverains sont moins affectés par les feux de forêt que ceux des hautes terres où l'élimination presque complète des arbres pré-établis par le dernier feu est responsable d'un taux de mortalité significativement plus élevé que celui des peuplements des basses terres. Ceci s'explique sans doute par la plus grande intensité des feux de couronne qui peuvent détruire la forêt sur des grandes superficies (Bergeron 1991, Johnson 1992, Bergeron et Dansereau 1993). La présence de vieux cèdres dans tous les sites riverains analysés est un indice distinct pour leur position relativement protégée des feux, ce qui serait dû aux sols plus humides près du lac (Hébert 1995). Les cours d'eau, comme aussi les marais et les escarpements rocheux, représentent des barrières importantes pour la progression des feux (Heinselman 1973) et, par cela, ils sont des éléments importants pour la structuration spatiale des forêts au niveau du paysage (Pickett et White 1985). Cependant, notre analyse de la structure d'âge indique que les feux ne se sont souvent pas simplement éteints à la limite supérieure de la zone riveraine. L'absence d'individus pour les quelques décennies précédant le feu, observée dans plusieurs peuplements, nous laisse supposer que les feux correspondants ont plutôt diminué en intensité et avancèrent en forme de feux de surface jusqu'au bord de l'eau, ne tuant que les cèdres de petits diamètres alors que les individus plus grands et vieux ont survécu. Bergeron et Brisson (1990) et Hély et al. (2003) ont mis en évidence que les arbres de petit diamètre et hauteur ont une plus faible résistance aux feux, ce qui diminue leur probabilité de survie. L'absence de vieux cèdres à certains endroits le long du périmètre lacustre suggère que les feux de couronne peuvent aussi se propager jusqu'à la rive immédiate du lac quand les conditions y sont propices (vents forts ou grande sécheresse). Le régime de feu caractéristique de la zone riveraine du côté de la terre ferme reflète donc sa position intermédiaire entre, d'un côté, la terre ferme éloignée des eaux avec une prédominance des feux de couronne létaux et, à l'autre extrême, les îles dans le lac Duparquet où les feux de surface sont normalement de faible intensité (Bergeron 1991).

La structure d'âge composée des peuplements de cèdre blanc occupant les terrasses riveraines montre une influence moins forte qu'attendue des perturbations riveraines sur le taux de mortalité des arbres parce que celui-ci fut très bas pour les classes d'âge intermédiaires. La mortalité juvénile, par contre, y fut distinctement plus élevée que dans la zone supra-riveraine. Plusieurs études ont montré que les semis et gaulis sont particulièrement susceptibles aux inondations à cause de leur petite taille, de sorte qu'ils peuvent être complètement submergés même quand les crues ne sont pas très hautes (Sigafoos 1964, Kozlowski 1984). Cependant, ce stress d'inondation ne semble pas être le facteur principal pour la mortalité juvénile du cèdre parce qu'il aurait affecté les peuplements de la même façon tout au long du périmètre lacustre, ce qui ne fut pas observé. La mortalité des semis et gaulis fut beaucoup plus élevée dans les sites exposés aux perturbations riveraines que dans les sites protégés. Nous concluons donc que l'impact physique des vagues, du bois dérivant et des glaces flottantes est le facteur principal qui limite la survie des jeunes cèdres alors que la survie des individus plus âgés en est beaucoup moins affectée.

La régénération végétative ne semble pas être une stratégie importante pour le cèdre blanc dans l'environnement des terrasses riveraines malgré une exposition relativement élevée aux perturbations. Le recrutement de tous les peuplements analysés fut clairement dominé par des individus d'origine sexuée. Ceci contraste avec le frêne noir dont la régénération se fait surtout végétativement dans les sites les plus exposés aux crues printanières (Tardif et al. 1994, Tardif et Bergeron 1999). Cette différence pourrait s'expliquer par la méthode spécifique de la régénération végétative. Le frêne forme des rejets à la base des troncs morts (Wright et Rauscher 1990) qui sont nombreux à cause des perturbations fréquentes. Le cèdre, par contre, régénère végétativement par des marcottes quand les branches touchent au sol (Johnston 1990). Dans notre étude, même les arbres inclinés ne formaient guère de marcottes, possiblement parce que celles-ci se développent de préférence sur sphaignes (Johnston 1990) qui sont absentes sur les terrasses riveraines.

À proximité du lac, les tiges d'origine végétative du peuplier faux-tremble furent les plus communes. Les nombreuses souches coupées par le castor témoignent du rôle important que ce rongeur semble jouer dans la distribution et la dynamique démographique du peuplier à l'intérieur et même au-dessus de la zone riveraine du lac Duparquet. Alors que l'influence des perturbations biotiques telles les épidémies d'insectes sur la dynamique et la croissance des espèces hôtes fut analysée intensément dans la région boréale (Morin et al. 1993, Bergeron et Charron 1994, Morin 1994, Bergeron et al. 1995, Bergeron et Leduc 1998, Girardin et al. 2001b, 2002), celle du castor n'a reçu que peu d'attention (Bordage et Filion 1988). Les effets directs de l'activité du castor sur ses espèces hôtes, mais aussi les effets indirects sur les espèces non-hôtes par l'élimination de concurrents mériteraient sans doute une analyse approfondie.

Grâce à la longévité extraordinaire des cèdres riverains, cette étude a permis pour la première fois d'évaluer les fluctuations du niveau d'eau du lac Duparquet pour la période dépassant les derniers 200 à 300 ans à laquelle d'autres études ont dû se restreindre. La limite lacustre élevée des cèdres de plus de 500 ans suggère un plan d'eau relativement haut avant environ 1500 qui fut probablement presque aussi élevé que pendant la plupart du XXe siècle. Durant les 300 années suivantes, c'est-à-dire pendant le «Petit Âge Glaciaire» (~1500 – 1850; Lamb 1982), le niveau d'eau était, selon toute vraisemblance, une quarantaine de centimètres plus bas qu'aujourd'hui tel qu'indiqué par la position rapprochée du lac des cèdres les plus bas qui s'étaient établis au cours de cette période. Par la suite, une régression graduelle des arbres s'est poursuivie jusqu'à nos jours, suggérant un rehaussement du plan d'eau du lac Duparquet d'une quarantaine de centimètres depuis environ 1850. Cette suggestion est confirmée par d'autres études basées sur l'analyse de cicatrices glacielles (Tardif et Bergeron 1997) et du recrutement du frêne noir (Tardif et al. 1994, Tardif et Bergeron 1999). Cependant, deux facteurs pourraient limiter ces conclusions quant à la reconstitution des fluctuations à long terme du niveau d'eau du lac Duparquet: i) le nombre d'arbres représentant la limite lacustre du cèdre au cours des siècles était relativement restreint pour la période avant 1500 et, à cause de la grande superficie couverte par le feu de 1760, entre approximativement 1700 et 1800 et ii) une datation exacte des cèdres fut rarement possible à cause du centre très souvent pourri ou même creux de leurs troncs. Un échantillonnage plus exhaustif des cèdres proches de la limite lacustre pourrait permettre de renforcer nos résultats.

Les résultats de cette étude fournissent des évidences à l'effet que les parties exposées de la frange riveraine de cèdre blanc présentent actuellement un déséquilibre démographique à cause d'un régime plus extrême de perturbations riveraines physiques reliées à l'augmentation du niveau d'eau du lac Duparquet. Les prévisions climatiques à long terme laissent présumer que la température atmosphérique (Houghton et al. 2001) et les précipitations (Flannigan et al. 1998, 2001) vont continuer à augmenter sous l'influence de l'effet de serre pendant au moins encore quelques décennies. Par conséquent, il faut s'attendre à ce que la régénération du cèdre blanc dans les sites les plus exposés restera précaire, ce qui peut finalement mener à la disparition quasi-totale de ces peuplements au fur et à mesure que les vieux individus vont mourir. De même, les peuplements de cèdre dans les sites plus protégés pourraient aussi être affectés si le régime de perturbations riveraines continue à s'aggraver. La disparition de ces vieux cèdres riverains bordant le lac Duparquet, par contre, représenterait, comme celle des vieilles forêts suite aux coupes forestières, la perte d'une archive biologique précieuse pour l'étude des écosystèmes naturels et des changements climatiques

(Cook and Sheppard 1988). Si le niveau d'eau se stabilise avec le temps une nouvelle lisière de cèdre blanc pourrait s'établir plus à l'intérieur. Ceci justifierait la protection à long terme d'une bande de la rive assez large pour permettre un tel ajustement avec les nouveaux niveaux d'eau.

Si le recrutement du cèdre blanc sur les terrasses riveraines *subit* les effets du rehaussement du plan d'eau du lac Duparquet, le frêne noir semble plutôt en profiter. L'expansion de cette espèce depuis le milieu du XIXe siècle laisse supposer qu'elle a commencé à coloniser cet habitat parce que les conditions devinrent de plus en plus favorable au fur et à mesure que le niveaux des eaux augmenta. Cependant, cette expansion du frêne se concentre aux zones littorales relativement larges où il y a assez d'espace pour le développement des peuplements. Aux parties du périmètre lacustre avec un littoral étroit, seulement peu d'individus plus ou moins isolés les uns des autres ont réussi à s'établir et à se maintenir, probablement parce que le régime des perturbations physiques est trop sévère même pour une espèce bien adaptée à de telles conditions environnementales. Ces résultats confirment ceux d'analyses synécologiques effectuées dans les frênaies occupant les plaines de débordement du lac Duparquet où une expansion similaire vers les terres plus élevées fut observée depuis la fin du «Petit Âge Glaciaire» (Tardif et Bergeron 1992, 1999).

Avant de terminer, j'aimerais encore ajouter deux voies de recherche à développer à celles déjà proposées dans cette thèse qui me semblent d'une grande importance. D'abord, les connaissances écologiques et paléohydrologiques sur l'environnement riverain acquises pour la région de la forêt boréale méridionale du Québec se basent presque uniquement sur des études effectuées aux bords du lac Duparquet (voir Bergeron et al. 2002 pour une synthèse des travaux dendroécologiques des 15 dernières années). Malgré les conditions favorables pour la recherche écologique de la végétation riveraine (régime hydrologique naturel et végétation riveraine presque intacte), il me semble important d'élargir la base des connaissances acquises à ce lac en effectuant pareilles recherches syn- et autécologiques en marge d'autres lacs naturels dans la même région. Cela permettrait d'augmenter la représentativité spatiale pour ainsi avoir une meilleure idée de la variabilité naturelle des facteurs environnementaux, de la dynamique des populations, de la croissance des espèces et de leur interdépendance.

Le deuxième point concerne un handicap majeur pour toute étude paléoécologique de l'environnement riverain du lac Duparquet et pour *toute étude* paléoclimatique, soit le manque de connaissances du régime hydrologique et du climat local à long terme. Le suivi saisonnier (de mai à octobre) des conditions météorologiques dans les environs du lac n'a commencé qu'en 1990 et celui des fluctuations quotidiennes du niveau d'eau avec un hydrographe automatique qu'en 1997. La poursuite à long terme de ces mesures et leur extension à l'année entière permettraient, i) de mieux caractériser le régime hydrologique en relation avec le climat, ii) de mieux prédire l'influence du changement climatique sur le régime hydrologique et la dynamique de la végétation riveraine et iii) l'utilisation de modèles hydrologiques (p.e., Vassiljev et al. 1995). La création de la *Forêt d'Enseignement et de Recherche du Lac Duparquet* en 1995 a mis en place une structure idéale pour un tel suivi à long terme du climat local et du régime hydrologique du lac Duparquet.

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