UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

IMPACTS DE LA FRAGMENTATION SUR LA CAPACITÉ REPRODUCTRICE ET LA DIVERSITÉ GÉNÉTIQUE DE L'ÉRABLE À SUCRE (*ACER SACCHARUM* MARSHALL) AU QUÉBEC

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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OCTOBRE 2014

Face à la roche, le ruisseau l'emporte toujours,

non pas par la force,

mais par la persévérance...

H. Jackson Brown

AVANT-PROPOS

L'objectif général de cette thèse visait à évaluer la capacité reproductrice et la structure génétique des populations d'érable à sucre au Québec; nous nous sommes intéressés à l'impact sur la diversité et structure génétique (1) de la fragmentation naturelle des populations situées à proximité de la limite nordique de l'aire de répartition de l'espèce et (2) de perturbations d'origine anthropique occasionnée par la coupe forestière telle que pratiquée actuellement au Québec. Le document est composé de six sections : La première partie est consacrée à introduire les thématiques de recherche à travers une revue de littérature et à définir les objectifs de travail. Dans la dernière section, nous avons discuté des principaux résultats et ouvert des perspectives sur des avenues de recherche. Les chapitres II à V forment le corps de cette thèse et ont été dédiés à la vérification et la discussion des hypothèses de travail. Ils ont été rédigés en langue anglaise sous la forme d'articles scientifiques. Les chapitres II et III ont été publiés et deux autres chapitres seront soumis prochainement à des revues avec comité de lecture.

Chapitre II: Graignic, N., Tremblay, F. & Bergeron, Y. (2014) Geographical variation in reproductive capacity of sugar maple (*Acer saccharum* Marshall) northern peripheral populations. *Journal of Biogeography*, **41**, 145–157 (Facteur d'impact (IF): 4,863)

Dans ce chapitre, nous avons comparé la capacité reproductrice de populations nordiques fragmentées situées dans l'aire discontinue de répartition de l'érable à sucre au Québec à celle de populations situées dans l'aire continue (non fragmentées).

Chapitre III: Graignic, N., Tremblay, F. & Bergeron, Y. (2013) Development of polymorphic nuclear microsatellite markers in sugar maple (*Acer saccharum* Marsh.) using cross-species transfer and SSR-enriched shotgun pyrosequencing. *Conservation Genetics Resources*, **5**, 845–848 (IF: 0,708)

Nous avons développé vingt marqueurs microsatellites pour l'érable à sucre. Nous avons aussi mis au point les amplifications par multiplex (plusieurs paires d'amorces dans la même réaction).

Chapitre IV: Graignic, N., Tremblay, F. & Bergeron, Y. Genetic diversity and structure at the northern limit of a widespread North-American tree, sugar maple (*Acer saccharum* Marshall). (à soumettre à Molecular Ecology)

Dans ce chapitre, nous avons comparé la diversité et la structure génétique de populations nordiques fragmentées à celles de populations situées dans l'aire continue de répartition de l'espèce.

Chapitre V: Graignic, N., Tremblay, F. & Bergeron, Y. Genetic consequences of selection cutting on sugar maple (*Acer saccharum* Marshall). (soumis à Evolutionary Applications le 3 juillet 2014)

Nous avons étudié l'effet de la fragmentation anthropique sur la diversité et la structure génétique des populations situées dans l'aire continue de répartition. Nous avons comparé la structure génétique de peuplements traités avec la coupe de jardinage dans les années 1990 à celle de vieilles forêts.

La contribution des auteurs est la même pour tous les articles. Noémie Graignic, Francine Tremblay et Yves Bergeron ont défini la problématique de recherche et l'approche expérimentale. Noémie Graignic a fait l'échantillonnage et la collecte des données sur le terrain, les analyses au laboratoire, les analyses statistiques et a rédigé le manuscrit. Francine Tremblay a contribué aux analyses statistiques, révisé et corrigé les manuscrits. Yves Bergeron a apporté des commentaires sur les manuscrits.

REMERCIEMENTS

Je tiens en premier lieu à remercier ma directrice, Francine Tremblay, et mon co-directeur, Yves Bergeron, pour m'avoir accueillie au sein de leur laboratoire et de m'avoir donné la chance de travailler sur un sujet passionnant avec un « terrain de jeu » magnifique (tout le Québec). Je remercie Francine pour sa confiance, son soutien et toute l'aide qu'elle m'a apportés, surtout, pendant les corrections et pour répondre aux questions et exigences des réviseurs. Je remercie Yves pour sa porte toujours ouverte, sa présence perpétuelle virtuelle (toujours le mettre en copie conforme quand c'est important) et ses interventions ponctuelles, isolées, mais ô combien indispensables et pertinentes !

Je remercie aussi les membres du jury qui ont accepté d'évaluer ma thèse et pour leurs questions, corrections et suggestions: Annie DesRochers de l'Université du Québec en Abitibi-Témiscamingue (UQAT), présidente du jury; ainsi que les membres externes: Nathalie Isabel du Service Canadien des Forêts (SCF) et Antoine Kremer de l'Institut de Recherche en Agronomie (INRA) de Pierroton, France.

Je tiens à remercier le CRSNG (Conseil de recherches en sciences naturelles et en génie du Canada) d'avoir octroyé à Francine une subvention pour ce projet. Le CEF (Centre d'étude de la forêt) m'a permis de présenter lors de nombreuses conférences au Québec, de financer une conférence aux États-Unis (Botany 2012) et de me fournir une aide indispensable grâce aux professionnels des services aux membres, je remercie cette organisation. Je tiens particulièrement à remercier Mélanie Desrochers et Daniel Lesieur pour l'obtention de diverses bases de données, Marc J. Mazerolle sans qui mes articles n'auraient pas atteint ce niveau en statistique (voir pas le niveau du tout ! tu as été indispensable !) et enfin William F. J. Parsons pour les corrections en anglais de mon article dans *Journal of Biogeography*, ma note

technique, le chapitre V et peut-être pour les articles suivants; ils sont tous professionnels au CEF et ils sont grandement appréciés pour leur travail et leur disponibilité.

Je remercie Marie-Hélène Longpré et Danielle Charron pour leur travail de logistique impeccable et leur dévouement, mon doctorat n'aurait pas été pareil sans vous. Je remercie mes aides de terrain, pour leur travail et pour m'avoir endurée un par un (jusqu'à 17 jours sans vraie pause) : Elizabeth Turcotte, Sylvain Larouche, Chelsea Archambault, Emilie Tarroux, Manuella Strukelj-Humphery, Hedi Kebli, Dave Gervais et pour finir la meilleure et la première : Geneviève Trudeau. Je remercie très sincèrement Arvin Beekharry d'être venu avec moi pour mes premiers sites et de m'avoir initiée à la forêt québécoise et à l'érable à sucre, sans toi j'aurais été perdue. Je remercie Norman Villeneuve et Claude Poulin du MRN (Ministère des Ressources naturelles) du Québec qui m'ont permis de trouver d'autres sites potentiels sur les cartes (la forêt non perturbée d'érable à sucre n'est pas si facile à trouver). Merci à eux et à Renaud Dostie de m'avoir permis d'aller avec Claude et Renaud sur mon site du Lac Pénobscot (2-D-A) qui est peut-être maintenant une EFE, ce fut très agréable. Michèle Bettez et Jean-Pierre Faust du Centre de semences forestières de Berthier du MRN du Québec ont fait les tests de germination, je les remercie.

Je remercie pour leur travail : Stéphanie Ferreira, Stéphanie Duthoy et toute l'équipe de GenoScreen en France (www.genoscreen.fr), ainsi que Valérie Catudal et Alexandre Belisle de Génome Québec (gqinnovationcenter.com).

Je tiens à remercier, tout particulièrement, Marie-Eve Sigouin de m'avoir très chaleureusement accueillie au Québec et à l'UQAT, tu fus la première Québécoise rencontrée, merci à toi pour tout ça ! Merci à Emilie Tarroux et Julien Moulinier de m'avoir grandement aidée au début de mes statistiques. Je remercie Hedi Kebli et Xavier Cavard pour la suite de l'aide en statistique. Je remercie aussi Véronique Paul

pour les données, les explications et le cours accéléré en ARCMAP, Ingrid Cea-Roa et Osvaldo Valeria pour leur aide ponctuelle sur ARCGIS et Igor Drobyshev pour BIOSIM. Je remercie Hedi Kebli, Mark Fox, Yi-Qin Zhou et leur directeur Pascal Drouin de l'URDAAT (Unité de recherche et de développement en agroalimentaire) de m'avoir permis d'utiliser leur matériel pour faire des gels d'agarose et pour les échanges d'autres matériels de biologie moléculaire. Je remercie Marie-Pier Ethier et l'URSTM (Unité de recherche et de service en technologie minérale) pour l'eau déminéralisée quand nous ne pouvions plus en faire nous-mêmes, et Mathieu Villeneuve et Janie Guimond Rousson de l'URSTM pour nous avoir prêté leur bonbonne d'azote liquide. Je remercie Françoise Bégin et Yves Poirier puis Nadine Neveu et Marc Boucher de l'UQAT, pour leur travail dans les commandes de produits. Je remercie Ann Gervais d'avoir simplifié la vie des étudiants étrangers à l'UQAT. J'en profite pour remercier tout le personnel de l'UQAT que j'ai fait travailler et que je n'ai pas cité. Je remercie Brian Harvey d'avoir discuté avec moi des types de coupes et Suzanne Brais pour son aide sur les types de sols (ce n'est pas dans cette thèse, mais qui sait ? cet article verra peut-être le jour un jour). Je remercie Venceslas Goudiaby d'avoir répondu à mes diverses questions sur le doctorat à l'Université du Québec. Je remercie Marie-Pier Ethier pour m'avoir super bien logé pendant les quelques jours où je suis revenue à Rouyn pour présenter ma soutenance de thèse.

Je remercie mes amis d'Abitibi : Emilie Tarroux, Manuella Strukelj-Humphery, Marie-Pier Ethier, Julie Arseneault, Myriam Paquette, Samira Ouarmim, Marie-Eve Sigouin, Yi-Qin Zhou, Benoît Tendeng, Sylvie Gewehr, Xavier Cavard, Huaitong Xu, Mark Fox, Besma Bouslimi, Julien Moulinier, Caroline Trudeau, Véronique Paul, Joël Soucy, Jessica Smith... Je remercie aussi toutes les personnes avec qui j'ai discuté et qui m'ont encouragée : Hassan Bouzahzah, Thomas Genty, Aissa Zalagou Moussa Hamani, Virginie Derycke, Sandrine Picq... Je remercie Sandrine Picq,

Mathieu Latutrie, Nahla Sellami et Simon Savinel pour leur vent de fraîcheur au labo. Je remercie mes amis de France qui sont venus me voir ici : Christelle et Johnny Hardelin et les autres pour leur soutien. Et enfin, le meilleur pour la fin, merci à Hedi Kebli de m'avoir soutenue, encouragée et surtout supportée !

Merci à ma famille de m'avoir permis de faire des études supérieures.

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RÉSUMÉ

Cette thèse visait à mieux comprendre la dynamique de répartition de l'érable à sucre (*Acer saccharum* Marshall) à sa limite nordique au Québec en évaluant la capacité reproductrice et la structure génétique des populations. L'érable à sucre atteint sa limite de répartition continue nordique dans le nord-est du Canada à la transition entre la forêt feuillue tempérée et la forêt boréale mixte. Nous avons étudié : (1) le potentiel de régénération et la diversité génétique des populations naturelles fragmentées situées à la limite nordique discontinue de répartition de l'érable à sucre et (2) la structure génétique des peuplements affectés par une perturbation de type anthropique, la coupe de jardinage.

Le territoire d'étude était localisé entre 45 ° 51 '–48° 59' N et 70 ° 21'–79 ° 27 'O et a été divisé en deux zones, continue et discontinue, sur la base de l'abondance des peuplements d'érable à sucre dans chacune des zones. La zone continue se situait dans le domaine bioclimatique de l'érablière à bouleau jaune et la zone discontinue se trouve dans les domaines bioclimatiques de la sapinière à bouleau jaune et de la sapinière à bouleau blanc. Vingt-quatre sites répartis le long de trois transects latitudinaux (situés dans l'ouest, le centre et l'est du Québec) ont été utilisés. Nous avons examiné la capacité reproductrice, et la diversité et structure génétique de ces populations. En ce qui a trait à la capacité reproductrice, nous avons analysé la structure d'âge des peuplements, la production et la germination des graines d'érable à sucre, de même que la densité et la structure d'âge des plantules. Les analyses génétiques ont été réalisées avec des marqueurs microsatellites développés spécifiquement pour cette espèce. Elles ont été réalisées sur 2 cohortes : jeunes arbres et arbres matures. L'impact de la coupe de jardinage sur la structure génétique des peuplements d'érable à sucre a été analysé dans trois paires de peuplements situés dans la zone de répartition continue du transect central. Chaque paire était composée d'une forêt ancienne et d'un peuplement coupé en 1990–1991. Nous avons comparé la diversité génétique de ces peuplements pour trois cohortes : plantules, jeunes arbres et arbres matures.

Les résultats ont montré que (1) la régénération de l'érable à sucre est bonne dans tous les sites étudiés et (2) que cette espèce possède une grande diversité génétique et une faible différenciation entre les populations, sur l'ensemble du Québec. Les peuplements d'érable à sucre avaient une structure d'âge inéquienne dans les zones continue et discontinue. Toutefois, nous avons observé moins de samares pleines et de plantules dans la zone discontinue par rapport à la zone continue sur le transect ouest. La limite nordique de l'érable à sucre est influencée en partie par le climat (années semencières et densité de plantules). La différence entre les zones se

retrouvait aussi au niveau génétique. Ainsi, la diversité génétique était inférieure et la différenciation entre les populations était plus importante dans la zone discontinue par rapport à la zone continue sur l'ensemble du Québec et, plus particulièrement, sur le transect ouest (en Abitibi-Témiscamingue). Nous n'avons pas détecté de différences significatives d'un point de vue génétique entre les deux cohortes. Nous avons observé un motif de structure génétique particulier chez l'érable à sucre au Québec : les populations les plus nordiques formaient un groupe distinct et l'on a observé un flux génique plus important des populations du sud vers celles de nord. Les données génétiques et palynologiques indiquent que l'érable à sucre serait arrivé au Québec par deux voies migratoires, l'une en provenance de l'est et plus tardivement une seconde provenant du sud-ouest de la province. L'étude de la coupe de jardinage nous a révélé une différence significative entre les cohortes d'érable à sucre pour tous les types de peuplements : les arbres matures possédaient un taux d'hétérozygotie observée plus élevé comparativement aux jeunes arbres et aux plantules. Ceci pourrait indiquer une sélection naturelle en faveur des hétérozygotes dans le temps. La coupe de jardinage n'a pas eu d'effet important sur la structure génétique des peuplements. Toutefois on a détecté la présence d'un goulot d'étranglement dans tous les peuplements jardinés. Ceci pourrait refléter la perte de certains allèles à la suite du prélèvement d'une partie des arbres matures.

Dans un contexte de réchauffement climatique, il ressort clairement de cette étude que les populations nordiques d'érable à sucre au Québec ont le potentiel d'être à l'origine de l'expansion de cette espèce au nord de sa limite de répartition discontinue. Toutefois, avec leur patron distinct (capacité reproductrice et diversité génétique plus faibles), les populations au nord-ouest du Québec mériteraient une attention particulière. La détection d'un goulot d'étranglement dans les peuplements jardinés demanderait un suivi à plus long terme afin d'éviter une certaine érosion génétique suite à des coupes successives.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1. Effets de la fragmentation dans un contexte de changements climatiques

1.1.1. Les populations nordiques marginales

Durant la dernière période interglaciaire de l'Holocène (à partir de 10 000 ans avant l'actuel (AA)), les essences forestières ont migré vers le nord, suivant le recul de la calotte glaciaire dans l'est du Canada (Liu, 1990; Prentice & Jolly, 2000; Williams *et al.*, 2000). La période Néoglaciaire (depuis environ 4 500 ans AA), qui a suivi, aurait été accompagnée d'un retrait vers le sud de certaines espèces méridionales pour atteindre leur limite de répartition actuelle (Liu, 1990; Richard, 1993). Ce retrait aurait laissé des populations résiduelles, isolées les unes des autres dans un couvert forestier formé d'espèces plus nordiques et dominé par les conifères. Le climat plus froid et sec en été à cette période, coïncide avec une augmentation des feux de forêt (vers 3 000 ans AA) et pourrait aussi avoir contribué à la fragmentation chez certaines espèces moins adaptées au feu de forêt (Carcaillet & Richard, 2000; Ali *et al.*, 2008). Les populations nordiques isolées et fragmentées d'espèces méridionales, pourraient également être issues d'évènements ponctuels de dispersion sur de longues distances (« sauts de puce ») lors de la migration vers le nord (Cain *et al.*, 2000).

Nous sommes dans une période interglaciaire où un réchauffement climatique rapide du fait de l'activité humaine est établi (Hegerl *et al.*, 2007). Selon les prévisions de l'IPCC en 2007 (Intergovernmental Panel on Climatic Change : Groupement Intergouvernemental sur les Changements Climatiques), une augmentation de la température et des précipitations, respectivement de l'ordre de +2,1°C à +5,4°C (moyenne: +3.3°C) et de -17% à +13% (moyenne: +1%), sont à prévoir dans l'est de l'Amérique du Nord durant la saison de croissance en 2080–2099 comparativement à 1980–1999 (Christensen *et al.*, 2007). Dans ce contexte, les arbres forestiers, et plus particulièrement l'érable à sucre, auront-ils la capacité de s'adapter à ce changement?

En Amérique du Nord, les modèles prédisent une migration vers le nord pour plusieurs espèces d'arbre, dont l'érable à sucre (Goldblum & Rigg, 2005; Iverson *et al.*, 2008). Afin d'affiner les modèles, il est important de comprendre l'influence de nombreuses variables comme le climat, les caractéristiques du peuplement, de l'espèce (capacité de reproduction et diversité génétique), le type de sol, la topographie, les autres espèces (compétition des autres végétaux, animaux se nourrissant de graines et les pathogènes) sur la répartition d'une espèce (McMahon *et al.*, 2011) et plus particulièrement sur les populations les plus nordiques (Parmesan *et al.*, 2005).

1.1.2. La coupe forestière

Le terme fragmentation est plus généralement associé à la fragmentation du couvert forestier et à la fragmentation de l'habitat. La fragmentation peut-être d'origine naturelle ou anthropique (Saunders *et al.*, 1991). De grandes ouvertures peuvent être créées à la suite de chablis ou de feux de forêt. La fragmentation d'origine anthropique, comme celle créée par l'urbanisation, l'agriculture ou l'exploitation forestière, est la plus étudiée pour l'érable à sucre (Young *et al*, 1993a; Young & Merriam, 1994).

Suivant la théorie, la fragmentation à long terme de petites populations entraînerait une réduction de la diversité génétique, une augmentation de la consanguinité intra-population et une augmentation de la différenciation génétique entre les populations comparativement aux grandes populations continues (Young *et al.*, 1996). De plus, dans les coupes forestières telles que pratiquées en Amérique du Nord, les arbres ont souvent été sélectionnés sur la base de certains critères qui mènent souvent à un appauvrissement de la qualité des tiges composant un peuplement (Majcen, 1994; Bouchard & Domon, 1997) et, éventuellement à un écrémage génétique (Nanson, 2004).

Les effets des coupes forestières se superposant aux changements climatiques, nous pouvons nous demander comment ces populations vont réagir. La capacité d'adaptation dépend en partie de la présence d'une grande diversité génétique (Hamrick, 2004).

1.2. L'érable à sucre (*Acer saccharum* Marshall)

1.2.1. Description

L'érable à sucre fait partie du genre *Acer*, de la famille des *Aceraceae* et de l'ordre des *Sapindales* selon l'ancienne classification des angiospermes; et de la famille des *Sapindaceae* et de l'ordre des *Sapindales* selon les classifications phylogénétiques récentes de l'APG II (APG II, 2003). Le genre *Acer* compte 13 essences en Amérique du Nord dont 10 au Canada (Farrar, 1996).

L'érable à sucre, *Acer saccharum* Marsh., tire son nom de l'eau d'érable qui est sucrée et sert à faire le sirop d'érable. *Saccharum* vient du mot grec *sakcharon* qui signifie sucré ou doux et désigne la sève sucrée des noeuds de Bambou (Hosie, 1980). L'abréviation Marsh. vient de Humphry Marshall (1722–1801), botaniste américain rendu célèbre par son ouvrage intitulé « *Arbustrum americanum* », publié en 1785

(Hosie, 1980). L'érable à sucre est aussi appelé érable franc au Canada francophone (Farrar, 1996) et « sugar maple », « rock maple » et « hard maple » au Canada anglophone et aux Etats-Unis d'Amérique (USA) (Godman *et al.*, 1990).

Cette espèce est tolérante à l'ombre (Logan, 1965) et peut vivre jusqu'à 300–400 ans, atteindre jusqu'à 27–30 mètres de haut et 76–91 cm de diamètre à hauteur de poitrine (dhp) (Godman *et al.*, 1990) (Fig. 1.1a). L'écorce des jeunes tiges est grise et lisse (Fig. 1.1b). Elle devient ensuite gris foncé, crevassée, en longues crêtes verticales profondes et irrégulières (Fig. 1.1c) et parfois écailleuse (Fig. 1.1d). Les feuilles sont caduques, simples et opposées (Fig. 1.1e et 1.1f). Elles mesurent de 8 à 20 cm de longueur et sont un peu plus larges que longues. Elles ont cinq (parfois trois) lobes à longues pointes obtuses et ondulées de quelques dents irrégulières. Elles sont vertes et deviennent jaunes, orangé brillant ou rouge vif à l'automne avant de tomber ce qui donne le paysage de carte postale, si typique du Canada (Farrar, 1996). Sa sève est utilisée pour la fabrication du sirop d'érable et son bois pour la fabrication de planchers, pâte à papier et de bois de chauffage (Godman *et al.*, 1990).

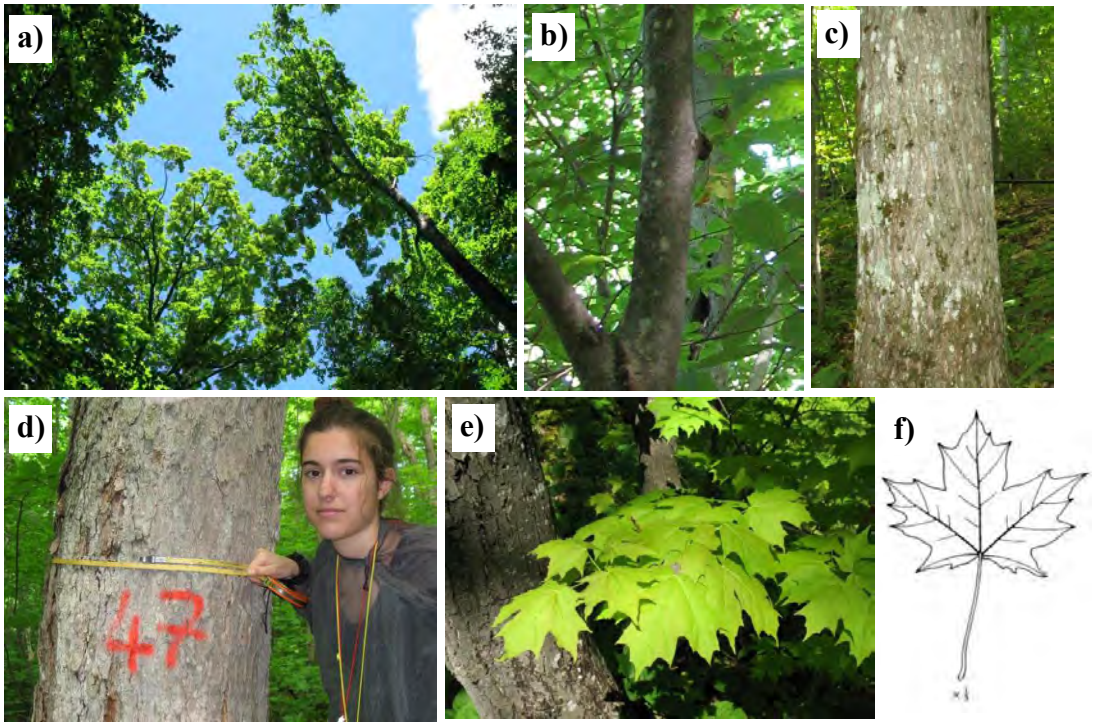

Figure 1.1 Morphologie de l'érable à sucre (*Acer saccharum*). (a) érables à sucre adultes en forêt; (b) écorce grise et lisse d'un jeune érable à sucre d'environ 5 cm de dhp; (c) écorce d'un érable à sucre mature montrant les longues crêtes verticales profondes et irrégulières; (d) écorce écailleuse d'un érable à sucre de 50 cm de dhp; (e) feuilles d'érable à sucre au printemps; (f) schéma d'une feuille d'érable à sucre tiré de Farrar (1996). Photos: a, b, c et e, Noémie Graignic; d, Geneviève Trudeau.

1.2.2. Aire de répartition

L'érable à sucre est établi dans le monde seulement à l'est de l'Amérique du Nord. Son aire de répartition s'étend, pour sa limite nord, au Canada depuis l'extrême sud-est du Manitoba, jusqu'à la Nouvelle-Écosse. La limite sud traverse le centre du New Jersey, jusqu'à l'extrême sud du Tennessee, USA (Fig. 1.2a).

Plus particulièrement, au Québec, la limite nordique de l'érable à sucre se situe entre le domaine bioclimatique de la sapinière à bouleau jaune au sud et celui de la sapinière à bouleau blanc au nord (Saucier *et al.*, 2003) (Fig. 1.2b). Dans le domaine bioclimatique de l'érablière à bouleau jaune et plus au sud, l'érable à sucre est très fréquent. Dans le domaine bioclimatique de la sapinière à bouleau jaune, les

populations d'érable à sucre sont de moins en moins fréquentes, plus isolées les unes des autres jusqu'à la limite nordique; elles sont donc fragmentées.

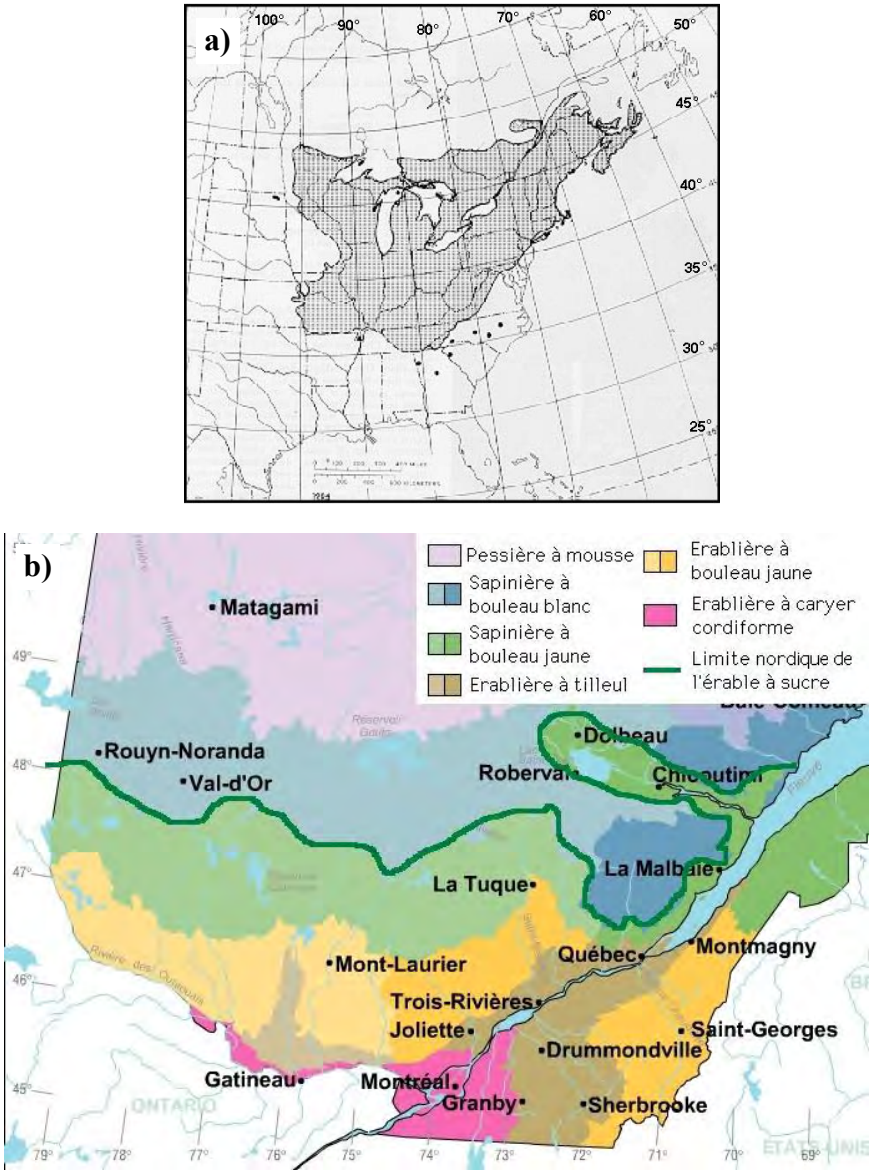

Figure 1.2 Répartition de l'érable à sucre (*Acer saccharum*) (a) en Amérique du Nord (figure tirée de Godman *et al.*, 1990) et (b) au Québec avec les domaines bioclimatiques en légende, ceux de l'est sont représentés par une couleur plus foncée que ceux de l'ouest (Saucier *et al.*, 2003).

1.2.3. Reproduction

La floraison peut commencer après une vingtaine d'années. Cette espèce est monoïque (fleurs mâles et femelles sur le même arbre), les fleurs peuvent porter les deux sexes en même temps, mais généralement un seul des deux organes est fonctionnel (Fig. 1.3a). Les fleurs apparaissent à la fin mars – mi-mai selon la localisation géographique (Godman *et al.*, 1990). Le pollen est disséminé par le vent (anémophile) et les insectes (entomophile) avec une contribution plus importante du vent (Gabriel & Garrett, 1984). L'érable à sucre est dichogame (organes mâles fleurissent avant les femelles, protandrie et inversement, protogynie) créant ainsi une barrière à l'autofécondation (Gabriel, 1968). Dans le cas où une autofécondation a quand même lieu, un mécanisme d'avortement post-zygotique des ovules a été observé 2 semaines après l'autofécondation (Gabriel & Garrett, 1967).

Les fruits ou samares (Fig. 1.3b, c, d) se forment à la fin juin – fin juillet et ils commencent à tomber à la mi-août – fin septembre, habituellement juste avant que les feuilles ne tombent. Généralement, seulement une des deux samares jointes contient une graine (Godman *et al.*, 1990). Les ailes mesurent 30–35 mm de longueur (Farrar, 1996) et les graines, 7–9 mm (Godman *et al.*, 1990). Elles sont dispersées par le vent sur une distance d'une centaine de mètres (Johnson, 1988).

Figure 1.3 (a) fleurs d'érable à sucre (*Acer saccharum*) avec un pistil fonctionnel; (b) disamare: samares d'érable à sucre vertes jointes par deux; (c) samares d'érable à sucre mûres; (d) disamare d'érable à sucre mûre. a et b, photos tirées de Farrar (1996); c et d, photos de Noémie Graignic.

Il existe des périodes de bonnes et de mauvaises années de fructification. Il y a environ une année semencière tous les 1 à 4 ans dans le centre nord du Wisconsin, 2 à 5 ans dans le reste des États-Unis et 3 à 8 ans au Canada (Wang, 1974; Godman *et al.*, 1990) (Fig. 1.4). Au nord du Michigan, jusqu'à 2 200 samares /m^2 ont été produites dans un vieux peuplement (Godman *et al.*, 1990). Dans une forêt du parc provincial du lac Supérieur en Ontario (limite nordique de l'érable à sucre), on a dénombré en moyenne de 16 à 277 graines pleines /m^2 entre 1992 et 1996, avec seulement une bonne année de fructification en 1996 (Kellman, 2004). Dans le centre nord du New Hampshire, des années semencières ont été identifiées en 1998, 2002 et 2006 pendant la période 1998–2008 (Cleavitt *et al.*, 2011).

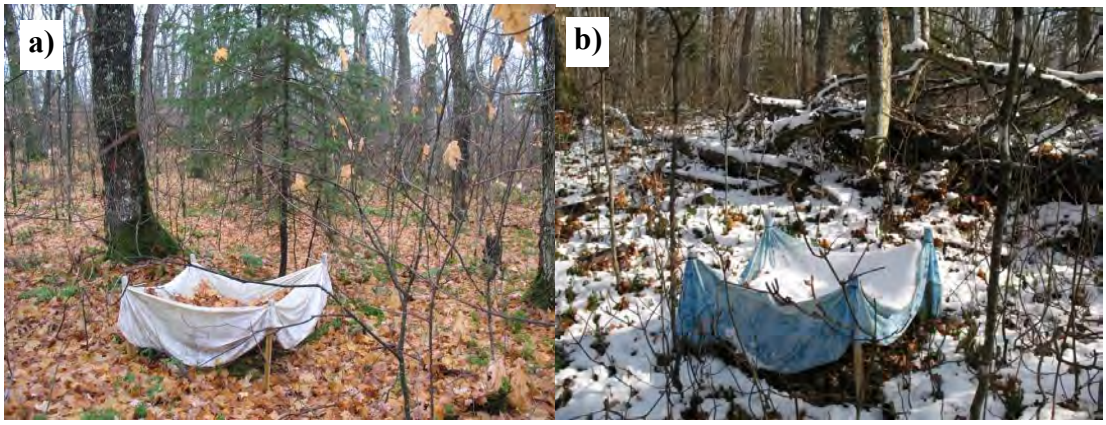

Figure 1.4 Exemple de trappe à graine de 1 m^2. (a) dispositif en Abitibi-Témiscamingue, fin octobre; (b) à la même période, il peut y avoir la première neige de l'année. Photos: Noémie Graignic.

Les samares vont germer le printemps suivant leur dispersion. Il faut une période de froid de 1–3°C (Carl, 1983) et de l'humidité (Janerette, 1979) pour que cette germination soit optimale. Cette température est la plus basse enregistrée pour les feuillus d'Amérique du Nord (Godman *et al.*, 1990). Les tests de viabilités réalisés à l'automne montrent que 80–100% des graines sont viables (Kellman, 2004). Les tests de germination réalisés en laboratoire au printemps suivant la dispersion donnent jsuqu'à 77% de graines germées (Carl, 1983).

1.2.4. Reproduction végétative

L'érable à sucre peut former des rejets de souche à l'occasion. Ce mode de régénération est plus fréquent dans les peuplements situés au nord de son aire de répartition (Godman *et al.*, 1990). Le drageonnement, depuis une racine, est rarement observé (Godman *et al.*, 1990).

1.2.5. Croissance

La période de croissance des plantules (Fig. 1.5a, b) commence à la mi-mai au nord du Michigan, avant que les feuilles de l'étage dominant sortent (Godman *et al.*, 1990). L'érable à sucre est une espèce tolérante à l'ombre (Logan, 1965), ce qui en fait une espèce compétitive. Environ 90% de la croissance en hauteur dans des peuplements denses et ouverts s'effectue respectivement en 18 et 24 jours. Il n'est pas rare d'avoir plus de 37 plantules m^{-2}. Environ 50 % des plantules survivent à la première année, et une forte mortalité est observée les 4 années subséquentes (Godman *et al.*, 1990).

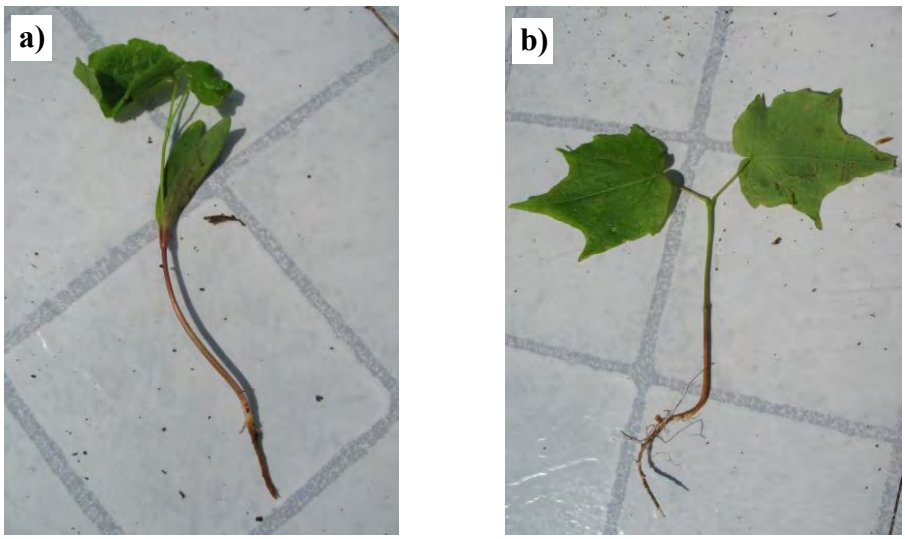

Figure 1.5 Plantules d'érable à sucre (*Acer saccharum*) dans leur première année (issues de graines de l'année précédente) à la mi-juin 2009 avec (a) et sans (b) leurs cotylédons. Photos: Noémie Graignic.

La saison de croissance en hauteur et en diamètre de l'érable à sucre varie selon la localisation géographique et le climat (Godman *et al*., 1990). Pour de nombreuses espèces arborescentes, la limite nord est modulée par un ensemble de conditions climatiques (principalement la température) et phénologiques qui convergent vers la réduction des chances de survie à différents stades du cycle de vie (Chuine & Beaubien, 2001). Par exemple, pour l'érable rouge (*Acer rubrum* L.), on observe une baisse du succès de reproduction sexuée qui entraîne une diminution de la capacité à se maintenir et à coloniser de nouveaux sites (Tremblay *et al.*, 2002).

1.2.6. Les tests de provenances: premières observations des variations génétiques

Un test de provenances consiste à comparer, dans des conditions environnementales similaires, le phénotype de plusieurs exemplaires d'arbres, issus de semences ou de boutures prélevées dans plusieurs régions couvrant l'aire naturelle de répartition de l'espèce (Wright, 1976). L'objectif d'un test de provenances est donc d'identifier les variations génétiques intra-spécifiques en relation avec les conditions environnementales.

Des tests de provenances ont été réalisés pour l'érable à sucre et ils ont montré une variation génétique pour de nombreuses caractéristiques. Kriebel (1957) a utilisé un total de 34 provenances (Fig.1.7), dont il a évalué les différences phénotypiques dans un test localisé en Ohio (USA). Plus précisément, l'auteur a montré qu'il existait (1) une variation clinale est-ouest de la sensibilité des feuilles aux dommages causés par une forte intensité lumineuse, (2) une plus faible résistance à la sécheresse pour les populations du nord par rapport à celles du centre et du sud, (3) une variation clinale nord-sud pour l'initiation de la saison de croissance avec les populations du nord qui débutent leur saison de croissance plus rapidement au printemps et (4) une variation clinale très marquée, nord-sud, avec la coloration des feuilles à l'automne qui est plus rapide pour les provenances du nord (Fig. 1.6). Ledig & Korbobo (1983) ont quant à eux travaillé sur des populations d'érable à sucre provenant d'un gradient

altitudinal au New Hampshire (USA). Ils ont montré que les populations à la limite de répartition altitudinale, ont une photosynthèse et un taux de respiration plus élevés.

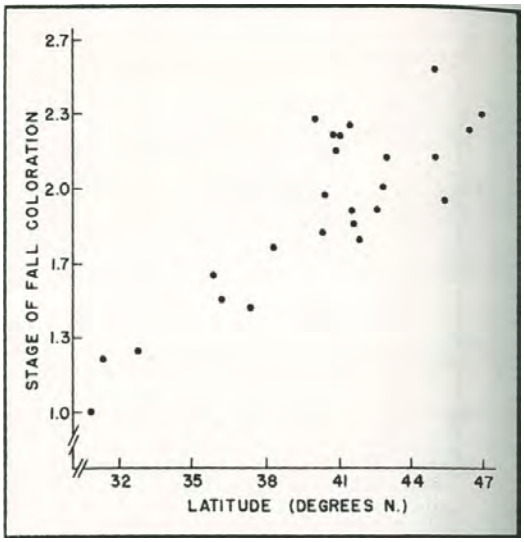

Figure 1.6 Variation clinale du stade de coloration des feuilles d'érable à sucre (*Acer saccharum*) à l'automne selon leur provenance. Figure tirée de (Kriebel, 1957).

L'érable à sucre est diploïde avec 26 chromosomes ($2n = 26$) (Kriebel, 1957). Les espèces du genre *Acer* sont souvent diploïdes avec un nombre de chromosomes multiple de 13 (Darlington & Wylie, 1955). Il existe aussi des érables polyploïdes comme l'érable argenté en Amérique du Nord (*Acer saccharinum*) et un érable européen (*Acer pseudoplatanus*), qui sont tétraploïdes avec 52 chromosomes (Darlington & Wylie, 1955). L'érable à sucre et l'érable noir (*Acer nigrum*) sont compatibles et une hybridation est possible entre ces deux espèces (Kriebel & Gabriel, 1969). Grâce aux nouvelles techniques de génétique, il a pu être montré que les patrons génétiques (RAPD et ADN chloroplastique) sont très similaires entre les deux espèces (Skepner & Krane, 1997; Skepner, 1998).

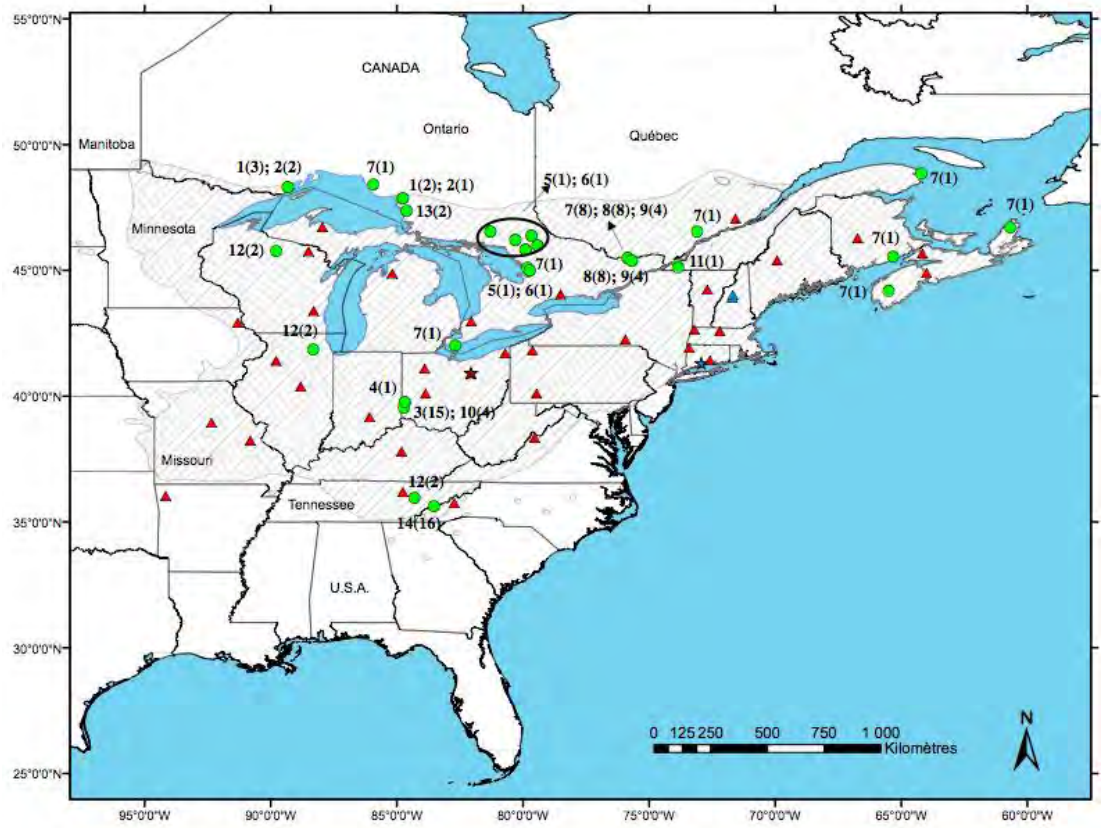

Figure 1.7 Localisation des études génétiques sur l'érable à sucre (*Acer saccharum*). L'aire de répartition de l'espèce est hachurée (Little, 1971). Les populations prélevées pour les tests de provenances sont représentées par un triangle; le site expérimental où le test a été effectué est représenté par une étoile; la couleur rouge a été utilisée pour l'étude de (Kriebel, 1957) et le bleu pour l'étude de (Ledig & Korbobo, 1983). Les études génétiques utilisant les allozymes et RAPD sont représentées par un cercle vert; associé à chaque cercle, le numéro de la référence (voir tableau 1.1 pour la correspondance entre le numéro et la référence) est indiqué et entre parenthèse le nombre de sites étudié à cette localisation géographique.

1.2.7. État des connaissances sur la génétique des populations naturelles

Les premières études sur la diversité et la structure génétique de l'érable à sucre, ont été réalisées dès le début des années 90 grâce à l'étude du polymorphisme des allozymes, un type de marqueur biochimique qui fait appel au polymorphisme des protéines (Tableau 1.1). Puis, depuis la fin des années 90, les marqueurs RAPD, qui analysent directement l'ADN, sont utilisés sur l'érable à sucre.

Beaucoup d'espèces d'arbres forestiers pollinisées par le vent ont une dispersion moyenne efficace ce qui maintient une diversité génétique importante dans les populations et une faible différenciation génétique entre elles (Hamrick *et al.*, 1992; Hamrick & Godt, 1996). La diversité génétique, basée sur l'analyse des allozymes, est modérée chez l'érable à sucre (H_E = 0,148; H_O = 0,150; Tableau 1.1) et est comparable aux autres espèces d'arbres (Foré *et al.*, 1992a).

Il existe une faible différenciation entre les régions dans l'aire de répartition de l'espèce. Elle représente moins de 2 % de la variation totale pour trois régions situées au nord (Wisconsin, USA), au centre (Illinois, USA) et au sud (Tennessee, USA) de l'aire de répartition (Gunter *et al.*, 2000) (Fig. 1.7). Young *et al.* (1993b) ont étudié des régions très éloignées géographiquement au Canada, dont une à la limite nordique en Ontario. Ils n'ont trouvé qu'une faible distance génétique entre les populations. En théorie, les populations situées au centre de l'aire de répartition vont avoir la plus grande diversité génétique et les populations très proches des limites (nord et sud) vont avoir une plus faible diversité génétique (Hampe & Petit, 2005) (Fig. 1.8). Pour l'érable à sucre, la plus grande diversité génétique devrait, donc, se retrouver aux USA (états de l'Indiana, de l'Ohio et du Kentucky). L'étude sur des populations naturelles, basée sur l'analyse des allozymes, dans ce secteur est celle de Foré *et al.* (1992a) (H_E = 0,148) et la diversité génétique n'était pas différente de populations situées plus au nord, au Canada, (H_E = 0,112; Young *et al.*, 1993b), et à proximité des limites nord (H_E = 0,110; Perry & Knowles, 1989) et sud (H_E = 0,133; Baucom *et al.*, 2005, pour les vieux peuplements seulement).

Tableau 1.1 Etudes génétiques sur l'érable à sucre (*Acer saccharum*) classées suivant l'ordre chronologique des publications et selon le type (1) de marqueur utilisé (M; Az, Allozyme; R, RAPD), (2) d'échantillon sur lequel l'étude a été effectuée et (3) de peuplement étudié (LN, limite nordique; PN, population naturelles; FCF, fragmentation du couvert forestier; CF, coupe forestière et A, autres types de peuplements). P, nombre de populations total; I, nombre d'individus total; H_O, moyenne de l'hétérozygotie observée; H_E, moyenne de l'hétérozygotie attendue; F_{IS}, coefficient de consanguinité

n°	M	Cohorte échantillonnée	P	I	LN	PN	FCF	CF	A	H_O	H_E	F_{IS}	Référence
1	Az	Arbre	5	500	×	×				—	0,110	—	(Perry & Knowles, 1989)
2	Az	Arbre	3	302	×	×				—	—	—	(Perry & Knowles, 1991)
3	Az	Juvénile (≤ 1 cm diamètre à la base) et canopée (≥ 30 cm dhp)	15	755			×			0,169	0,171	—	(Foré *et al.*, 1992b)
4	Az	Embryon, semis d'1 an, jeune arbre (dhp ≤ 2 cm), sous-canopée (dhp = 15–25 cm) et canopée (dhp ≥ 40 cm)	1	280		×				0,15	0,148	—	(Foré *et al.*, 1992a)
5	Az	Utilisation de l'index de déclin pour chaque arbre	6	350					×	0,141	—	-0,03	(Geburek & Knowles, 1992)
6	Az	Arbre	6	350		×				—	—	-0,027	(Geburek, 1993)
7	Az	Plantule d'1 an	16	384	×	×				—	0,112	0,042	(Young *et al.*, 1993b)
8	Az	Plantule d'1 an	16	800			×			—	0,115	0,062	(Young *et al.*, 1993a)
9	Az	Plantule d'1 an	8	968			×			—	—	—	(Young & Merriam, 1994)
10	Az	Embryon, juvénile (1 an à ≤ 1,0 cm de diamètre à la base) et canopée (dhp ≥ 30 cm)	4	572			×			0,208	—	0,126	(Ballal, 1994)
11	Az	Juvénile (6–15 ans) et canopée (arbres établi avant 1850)	1	152					×	0,136	0,148	0,077	(Simon *et al.*, 1995)
12	R	Plantules issues d'une récolte de graines	6	547		×				—	—	—	(Gunter *et al.*, 2000)
13	R	Plantules	2	49	×	×				—	—	—	(Diochon *et al.*, 2003)
14	Az	Plantules (dhp ≤ 1 cm), jeunes arbres (dhp > 1–10 cm) et adultes (dhp > 10 cm)	16	567				×		0,113	0,116	0,025	(Baucom *et al.*, 2005)

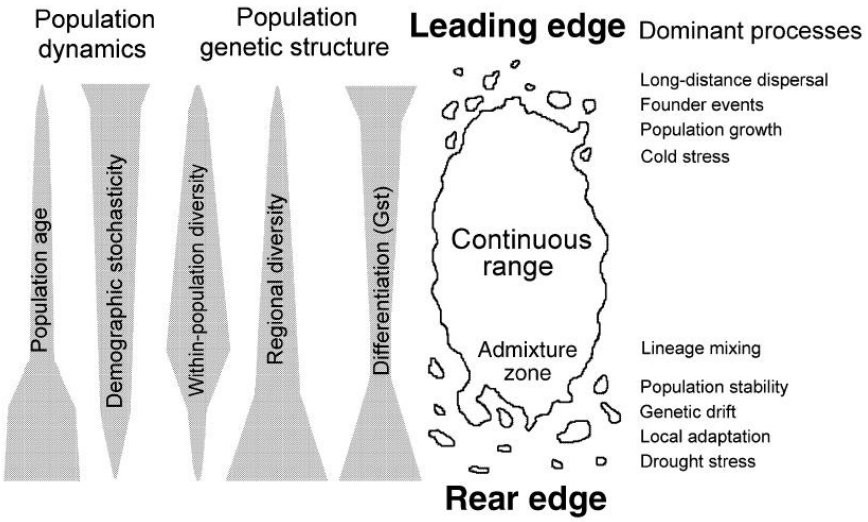

Figure 1.8 Caractéristiques des populations situées au front de migration ("leading edge") et à la zone arrière ("rear edge") de l'aire de répartition des espèces. La largeur des barres grises, à gauche de la figure, indique la variation de chacune des caractéristiques mesurées correspondant à la position des populations dans l'aire de répartition. Figure tirée de Hampe & Petit (2005).

La différenciation génétique entre les populations d'une même région est faible (Young *et al.*, 1993b; Gunter *et al.*, 2000), alors qu'elle est plus importante entre deux populations à la limite sud de l'aire de répartition comparativement à celles situées au centre et au nord de l'aire de répartition (Gunter *et al.*, 2000). En bref, la grande partie de la diversité génétique se retrouverait intra-populations (Foré *et al.*, 1992a; Young *et al.*, 1993b). Les études génétiques sur l'érable à sucre à l'échelle du peuplement ont été effectuées à plusieurs niveaux suivant les familles (graines issues d'un même arbre), l'individu, la topographie (face sud, nord et haut de pente) et selon différents critères (indice de déclin, cohortes de classes d'âge et dhp). La distance génétique est plus grande entre les familles qu'entre les peuplements ou les régions (Gunter *et al.*, 2000). Selon la position de chaque individu dans le peuplement, une structure très faible a été trouvée pour des populations proches de la limite nordique (Perry & Knowles, 1991) et d'autres populations situées un peu plus au sud (Geburek, 1993). Du point de vue topographique, la division en sous-groupe selon la position des individus sur la pente (face sud, nord et haut de pente) n'a pas montré de motif d'association génétique particulier en utilisant la RAPD (Diochon *et al.*, 2003). En

comparant des sous-groupes d'individus en santé et en déclin, aucune différence génétique (allozymes) n'a été détectée (Geburek & Knowles, 1992). Des analyses de la structure allélique de sous-groupes classés suivant des classes d'âge et de dhp n'ont révélé qu'une faible différenciation entre cinq cohortes (Foré *et al.*, 1992a). Une différence (fréquences génotypiques et alléliques) a été observée entre les semis d'un an et les autres cohortes (Tableau 1.1).

1.2.8. Génétique et impacts anthropiques

Plusieurs études se sont intéressées à l'effet, sur la diversité et structure génétique, de la fragmentation du couvert forestier par l'agriculture, l'urbanisation et la récolte du bois qui a ouvert de grands espaces particulièrement depuis les 200 dernières années en Amérique du Nord. L'érable à sucre est utilisé comme bois de chauffage (Godman *et al.*, 1990) et pour la fabrication des planchers, des feuilles de placages et du contreplaqué (Farrar, 1996; Bowyer *et al.*, 2005). Il est très recherché pour la fabrication de meubles haut de gamme, et compte parmi les espèces utilisées pour les dormants de chemin de fer (Bowyer *et al.*, 2005). Une utilisation de l'érable à sucre qui lui confère une valeur économique très importante est la fabrication du sirop d'érable à partir de l'eau d'érable. À cette fin, la culture de cette espèce (l'acériculture) utilise l'éclaircie pour permettre aux érables à sucre de croître en diamètre, car plus l'arbre a un diamètre important, plus il produira d'eau d'érable (Robitaille & Pardé, 1979). Ces différentes utilisations de l'érable à sucre ouvrent le couvert forestier plus ou moins intensivement, elles ont donc été spécifiquement étudiées pour leur impact sur la génétique de cette espèce.

À la suite de l'ouverture du couvert forestier par l'agriculture, une différenciation génétique moins importante de l'érable à sucre se trouvant dans des massifs forestiers résiduels a été observée (Young & Merriam, 1994), de même qu'une augmentation de l'hétérozygotie et du polymorphisme alléliques (Young *et al.*, 1993a) comparativement à ceux se trouvant dans une matrice forestière relativement

continue. Ces résultats s'expliqueraient par l'absence de barrières physiques à la dispersion du pollen et des graines entre des massifs forestiers dans un paysage agricole et l'augmentation conséquente du flux génique entre des populations fragmentées (Saunders *et al.*, 1991; Kramer *et al.*, 2008). Cependant, une perte d'allèles présents à une faible fréquence dans les populations témoins a été détectée dans les peuplements résiduels (Young *et al.*, 1993a). Ces deux études ont été réalisées sur des plantules âgées d'un an. Toutefois, les études utilisant des cohortes d'érable à sucre de différentes classes de diamètres et d'âge ont montré qu'on pouvait observer, occasionnellement, des différences génétiques. Par exemple, la diversité génétique n'était pas différente selon la cohorte analysée dans l'étude de Foré *et al.* (1992b), mais elle était plus faible pour les embryons selon Ballal (1994). La différenciation génétique entre les peuplements fragmentés pour les érables à sucre matures (dhp $\geq$ 30 cm) était plus importante que pour les juvéniles ($\leq$ 1 cm de diamètre à la base; établis après la fragmentation) (Foré *et al.*, 1992b) (Tableau 1.1). Il faut toutefois noter que ces deux dernières études ont été réalisées dans des forêts fragmentées et aucune comparaison n'avait été faite avec une forêt continue proche des peuplements fragmentés. Cette différence entre cohortes pourrait donc être dû à un processus naturel et non l'effet de la fragmentation.

Baucom *et al.* (2005) ont analysé les effets de la coupe forestière (réalisée en 1934) de peuplements d'érable à sucre et non la fragmentation du couvert forestier. Ils ont montré, avec les allozymes, que les peuplements coupés avaient une perte de 40 % de diversité génétique (pourcentage de sites polymorphes) par rapport à une forêt ancienne (non perturbée). Cette perte était moindre pour les classes d'âges des jeunes arbres et arbres matures de ces populations (Tableau 1.1). La différenciation génétique entre les peuplements était faible et elle était plus élevée entre les peuplements coupés (θ_p = 0,093; θ_p est similaire au F_{ST}) comparativement à celle des forêts anciennes (θ_p = 0,060).

Un autre impact de l'activité humaine moins visible à l'échelle du paysage est le problème des pluies acides apparu au cours des années 80. Simon *et al.* (1995) ont étudié l'effet de cette perturbation sur une forêt ancienne d'érable à sucre. L'analyse des isoenzymes a révélé la présence d'une faible différenciation génétique entre le sous-groupe des arbres juvéniles (6–15 ans) et celui des arbres pré-perturbation (établis avant 1850; Tableau 1.1). Certains allèles peu fréquents dans le sous-groupe pré-perturbation étaient encore moins fréquents, voire absents, dans le sous-groupe juvénile. La différence étant peu importante et il en ressort que les pluies acides ne semblent pas avoir eu d'effet sur la structure génétique de l'érable à sucre.

1.2.9. Migration post-glaciaire et phylogéographie

Actuellement, l'aire de répartition de l'érable à sucre s'étend du Tennessee, au sud jusqu'au Québec, au nord (section 1.2.2). Jackson *et al.* (2000) ont montré, par l'étude du pollen fossile, que l'érable (genre *Acer* incluant l'érable à sucre) était localisé dans deux refuges aux USA (refuge 1: environ les états du Mississipi, d'Alabama et du Tennessee; refuge 2: Caroline du Sud et du Nord) pendant la période du maximum glaciaire, soit vers 21 000 ±1 500 ans AA (Fig. 1.9). Les analyses palynologiques des macrorestes d'érable ont permis de confirmer la limite sud du plus grand refuge, le refuge 1 (Fig. 1.9). Une hypothèse suggère que l'expansion de l'érable à sucre vers le nord en suivant le retrait des glaces a été faite suivant deux voies principales (Braun, 1950) soit une direction: (1) nord-est le long des Appalaches et (2) directement vers le nord. L'expansion directement au nord, aurait été retardée en Ohio et en Indiana (USA) par un climat post-glaciaire chaud et sec. L'érable à sucre se trouvant dans la région des Grands Lacs pourrait être issu d'une migration directement vers le nord ou en provenance de l'est (Braun, 1950). L'érable à sucre s'est établi au sud du Québec vers 8 500 ans AA et des analyses polliniques indiquent que dès cette période, des populations disjointes étaient présentes près du lac St-Jean (Richard & Grondin, 2009). D'autres populations disjointes seraient

également apparues au nord de la Gaspésie vers 4 000 ans AA (Labelle & Richard, 1984). L'érable à sucre, comme d'autres espèces (section 1.1.1), aurait subi un recul vers 4 500–3 000 AA des populations les plus nordiques laissant sur place quelques populations qui sont actuellement à proximité de la limite nordique de l'aire de répartition de l'espèce (dans la sapinière à bouleau jaune). Cette possibilité n'a pas encore été validée pour l'érable à sucre (Richard & Grondin, 2009) (preuves trouvées pour le sapin baumier; Ali *et al*., 2008), laissant toujours plausible l'hypothèse de « sauts de puce » importants (Cain *et al.*, 2000).

Figure 1.9 Carte Isopollinique et de macrorestes de l'érable durant le maximum glaciaire (21 000 ±1 500 ans AA). Cercles pleins = présence; vides = absence. Figure modifiée de Jackson *et al.* (2000).

La phylogéographie étudie les liens de parenté, entre des populations d'une même espèce ou des espèces très proches, intégrés dans une dimension spatiale (Avise *et al.*, 1987). Elle permet donc de reconstruire les voies empruntées par les espèces lors de leur migration. Une étude de l'ADN chloroplastique d'une autre espèce d'érable, l'érable rouge, confirme l'hypothèse de deux refuges pour l'érable rouge lors du maximum glaciaire (McLachlan *et al.*, 2005). Le premier refuge serait situé entre les états de Louisiane et Georgie et l'autre, est au sud des Appalaches (McLachlan *et al.*, 2005). Ce sont à peu près les mêmes refuges retrouvés dans l'étude de Jackson *et al.* (2000). De plus, l'analyse de ces haplotypes démontrent que les

individus du refuge au sud-ouest (premier refuge) ont moins contribué à la diffusion de l'érable rouge dans les régions plus au nord contrairement au refuge situé au sud-est (Fig. 1.10). Dans leur revue de littérature, Soltis *et al.* (2006) ont comparé la phylogéographie d'espèces animales et végétales à l'est de l'Amérique du Nord. Les auteurs ont trouvé que la migration ne répondait pas à un patron simple pour tous les organismes. Cependant, deux espèces ayant à peu près la même répartition nordique pourraient avoir rencontré les mêmes barrières géographiques lors de leur migration, comme les Appalaches ou les Grands Lacs dans l'est de l'Amérique du Nord. Dans la perspective où deux voies de migration existeraiennt pour l'érable à sucre et rouge, nous pourrions émettre l'hypothèse que celles-ci se sont rencontrées au nord au Québec ou en Ontario.

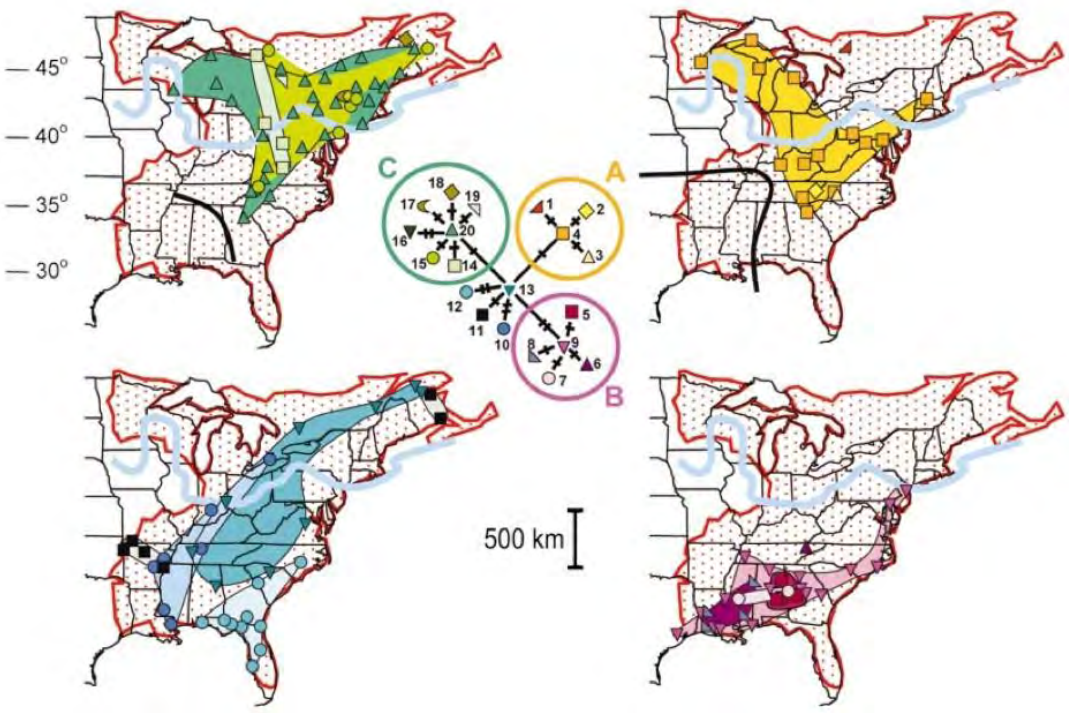

Figure 1.10 Répartition actuelle (pointillé rouge) et des haplotypes d'ADN chloroplastique de l'érable rouge (schéma des clades au centre). La ligne bleue représente le maximum glaciaire. La ligne noire représente en haut à gauche la répartition de l'espèce (pollen) il y a 15 000 ans et en haut à droite il y a 16 000 ans. Figure tirée de McLachlan *et al.* (2005).

1.2.10. Dépérissement, contraction ou expansion?

Au Québec, on observe un certain dépérissement des érablières depuis le début des années 80. Les symptômes sont une perte de coloration des feuilles, une diminution de la vigueur, et de la croissance, une perte prématurée du feuillage et une diminution de la capacité à cicatriser les blessures causées par les entailles pratiquées pour l'acériculture. Différentes études indiquent que ce dépérissement pourrait être dû (1) à la sécheresse et aux insectes défoliateurs (Payette *et al.*, 1996), (2) à la sécheresse et à des déficiences en potassium (K), phosphate (P) et magnésium (Mg) (Bernier *et al.*, 1989) ou (3) encore, plus probablement, à une déficience en nutriments et acidification du sol (Moore *et al.*, 2000; Ouimet *et al.*, 2001; Duchesne *et al.*, 2005).

Dans la région de la ville de Québec, durant le refroidissement du petit âge glaciaire (environ quatre siècles) l'abondance de l'érable à sucre a fortement diminué au profit de l'épinette rouge qui a atteint son maximum au 18^{ième} siècle (Richard & Grondin, 2009). Lors du réchauffement qui a suivi, l'érable à sucre a rapidement repris la même importance qu'avant le petit âge glaciaire. Des travaux réalisés dans la région du Bas St-Laurent à l'est du Québec ont montré que l'érable à sucre et le peuplier faux-tremble (*Populus tremuloides*) étaient moins abondants que les résineux (cèdre blanc de l'est, *Thuja occidentalis* et de l'épinette, *Picea* spp.) avant la colonisation par les Européens (1846–1949) comparativement à l'actuel (1980–2009) (Dupuis *et al.*, 2011). Les auteurs attribuent cet enfeuillement à l'augmentation des coupes forestières (coupes à blanc) et des feux après 1900 (Dupuis *et al.*, 2011). Plus au sud, dans les forêts dominées par le chêne (*Quercus*) et le caryer (*Carya*), on observe également une augmentation de l'érable à sucre et de l'érable rouge qui serait due au contrôle des feux depuis le début des années 20 (Abrams, 1992; Nowacki & Abrams, 2008; Pierce *et al.*, 2008). Par exemple, dans une réserve biologique de

l'Indiana (USA), la valeur d'importance de l'érable à sucre est passée du 12^{ième} rang en 1960 (6,3 tiges/ha) au 2^{ième} rang en 2000 (68,9 tiges/ha) (Pierce et al., 2008).

Dans le futur et dans le contexte des changements climatiques, la plupart des modèles prédisent une migration vers le nord pour l'érable à sucre, comme pour la plupart des espèces, qui serait accompagnée d'une diminution de leur abondance au sud (Goldblum & Rigg, 2005; Iverson *et al.*, 2008).

1.3. Hypothèses, Objectifs et structure de la thèse

Nos travaux s'articulent autour de l'hypothèse que les populations nordiques, fragmentées sont les plus susceptibles d'être à l'origine de l'expansion, vers le nord, de l'aire de répartition de l'érable à sucre dans un contexte de changements climatiques.

Dans cette thèse, nous avons étudié les populations nordiques, situées dans l'aire continue (non fragmentées) et discontinue (fragmentées) de répartition de l'érable à sucre au Québec. Nous avons abordé à la fois les aspects démographiques et génétiques de la dynamique des populations, à l'aide d'une approche multidisciplinaire.

Pour se propager vers le nord, les populations nordiques fragmentées doivent déjà, actuellement, pouvoir se régénérer. Dans le chapitre II, nous avons abordé l'aspect écologique en étudiant la capacité reproductrice des populations nordiques d'érable à sucre dans trois régions (ouest, centre et est) du Québec. Nous avons comparé leur capacité reproductrice à celle des populations qui se situent plus au sud. Pour plus de clarté, nous avons délimité, au Québec, une zone nordique où les populations d'érable à sucre sont fragmentées naturellement, cette zone a été appelée « zone discontinue » et les populations sont ainsi appelées « populations discontinues ». Cette zone discontinue se situe dans les domaines bioclimatiques de la sapinière à bouleau jaune et de la sapinière à bouleau blanc (Fig. 1.2b). Les

populations plus au sud sont incluses dans une zone appelée « zone continue ». Cette zone est comprise exclusivement dans le domaine bioclimatique de l'érablière à bouleau jaune, pour être proche écologiquement de la zone discontinue (Fig. 1.2b). De plus, nous avons comparé les régions entre elles pour savoir si des variations existaient longitudinalement au Québec.

Une population ayant une diversité importante d'un point de vue génétique, aura plus de chance d'avoir, parmi ses individus, des individus adaptés à différentes conditions environnementales. Dans l'hypothèse que ces populations nordiques puissent se propager, il faut aussi qu'elles aient une grande diversité génétique, afin de pouvoir prendre de l'expansion vers des nouveaux milieux. Dans le chapitre IV de cette thèse, nous avons étudié, pour les mêmes populations que celles du chapitre II, le niveau de diversité génétique et le type de structure génétique. Nous avons fait les mêmes comparaisons entre les populations discontinues (nordiques, fragmentées) et continues (sud), et entre les régions.

Dans l'éventualité où les populations nordiques auraient une très faible capacité reproductrice et très peu de diversité génétique, l'expansion nordique pourrait difficilement provenir de ces populations et devrait provenir des populations situées plus au sud. Dans la zone continue (au sud), l'érable à sucre est exploité pour son bois. Cette perturbation d'origine anthropique a-t-elle un effet négatif sur la diversité génétique des populations et sur leur potentiel d'adaptation et d'expansion? Nous avons abordé cette question dans le chapitre V.

Deux points importants sont à mentionner et constituent l'aspect novateur de cette thèse :

L'un des aspects concerne les chapitres III à V; Les études en génétique des populations utilisent de plus de plus un type de marqueur très polymorphe: les marqueurs microsatellites (Li *et al.*, 2002). De tels marqueurs n'étant pas développés

pour l'érable à sucre, nous avons d'abord utilisé des microsatellites développés pour d'autres espèces d'érables. Ce transfert ne s'est pas avéré très fructueux et nous avons utilisé la technique du pyrosequençage pour le développement de marqueurs microsatellites spécifiques à l'érable à sucre. Un article a été publié à partir de ses travaux et fait l'objet du chapitre III.

Un second aspect est le nombre de populations étudiées couvrant une large zone géographique et le fait qu'elles soient étudiées sous les aspects démographique et génétique (chapitres II et IV). Comme nous l'avons vu (Fig. 1.7), les études génétiques sur les populations proches de la limite nordique et sur leur potentiel de régénération sont limitées tant du point de vue du nombre de populations étudiées que de leur répartition. La présente étude couvre trois régions au Québec où les populations d'érable à sucre peuvent prendre de l'expansion au nord.

CHAPITRE II

GEOGRAPHICAL VARIATION IN REPRODUCTIVE CAPACITY OF SUGAR MAPLE (*ACER SACCHARUM* MARSHALL) NORTHERN PERIPHERAL POPULATIONS

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Article publié en 2014 dans *Journal of Biogeography*, vol. 41, p. 145–157

2.1. Résumé

Objectif • L'érable à sucre (*Acer saccharum* Marshall) atteint sa limite de répartition continue nordique dans le nord-est de l'Amérique du Nord au niveau de la transition entre la forêt boréale mixte et la forêt feuillue tempérée. Avec les changements climatiques, plusieurs modèles prédisent la migration vers le nord de cette espèce. Notre objectif était d'évaluer si le potentiel de recrutement de l'érable à sucre diminuait au nord suivant la transition progressive entre les zones continue et discontinue de l'aire de répartition de l'espèce.

Localisation • Le nord-est du Canada, à la limite nordique de l'érable à sucre.

Méthodes • Nous avons analysé la capacité reproductrice des populations d'érable à sucre le long de trois transects latitudinaux (situés dans l'ouest, le centre et l'est du Québec) dans 24 sites situés entre 45°51' – 48°59' N et 70°21' – 79°27' O. Le territoire étudié a été divisé en deux zones, continue et discontinue, sur la base de l'abondance des peuplements d'érable à sucre dans chacune des zones. Nous avons examiné la structure d'âge du peuplement, la production et la germination des graines d'érable à sucre, la densité et la structure d'âge des plantules d'érable à sucre.

Résultats • La régénération de l'érable à sucre était inéquienne et similaire entre la zone continue (sud) et discontinue (nord). Nous avons observé plus de samares pleines et de plantules dans la zone continue par rapport à la zone discontinue sur le transect ouest. La densité des plantules d'érable à sucre était positivement influencée par (1) la surface terrière des érables à sucre matures et celle des jeunes arbres de toutes les espèces, et (2) la température et les précipitations moyennes de juillet. Quatre années semencières ont été identifiées et étaient bien synchronisées dans l'ensemble des sites; les bonnes années semencières variaient significativement avec les températures moyennes et les précipitations moyennes du mois de juillet de l'année précédente.

Conclusions principales • Notre étude a clairement démontré un effet des variables climatiques et des caractéristiques du peuplement sur la régénération de l'érable à sucre. Cependant, ces facteurs n'expliquaient pas le passage de la zone de répartition continue à discontinue pour cette espèce. La plupart de nos sites nordiques montraient un recrutement constant de l'érable à sucre dans le temps. Ces résultats soulignent l'importance d'inclure des facteurs non climatiques dans les modèles visant à prédire des changements dans l'abondance des espèces.

2.2. Abstract

Aim • Several models have predicted that, with climate change, Northern Hemisphere species will migrate northwards from their present distribution ranges. Sugar maple (*Acer saccharum* Marshall) reaches its northern continuous distributional limit in north-eastern North America at the transition between boreal mixed-wood and temperate deciduous forest. Our objective was to determine whether lower sugar maple recruitment potential accounts for this gradual transition between the continuous and discontinuous zones of the distribution.

Location • The northern limit of sugar maple in eastern Canada.

Methods • We analysed the reproductive capacity of sugar maple populations along three latitudinal transects (located in the west, centre and east of Québec) in 24 sites located between 45°51′–48°59′ N and 70°21′–79°27′ W. The study area was divided into two zones, continuous and discontinuous, based on sugar maple stand abundance. We examined stand structure, sugar maple seed abundance and germination, and sugar maple seedling density and age structure.

Results • Sugar maple regeneration was uneven-aged and similar between continuous (south) and discontinuous (north) zones. For the western transect, more filled seeds and more seedlings were recorded in the continuous zone than in the discontinuous zone. Sugar maple seedling density was positively influenced by (1) basal area of mature sugar maple and saplings of all species, and (2) July mean temperature and precipitation. Four mast seed years were identified that were well synchronized across all sites; mast seeding covaried significantly with July mean temperature and July mean precipitation of the previous year.

Main conclusions • Our study clearly demonstrated an effect of climatic variables and stand characteristics on sugar maple regeneration. However, these

factors did not explain the transition from a continuous to a discontinuous distribution for this species. Most of our northern sites exhibited constant sugar maple recruitment over time. These results highlight the importance of including non-climatic factors in models predicting species change in abundance.

2.3. Introduction

Several models suggest that tree populations are capable of rapid migration in the face of climatic variation (Iverson *et al*., 2008; Morin & Thuiller, 2009). Accordingly, the reconstruction of post-glacial vegetation in North America shows several forest tree species reaching their maximum extent in the middle Holocene, followed by contractions that could have been caused by a cooling climate (McLachlan *et al*., 2005). Given ongoing climate changes, many species are expected to expand their ranges, which could be particularly marked for populations located at the limits of their distribution ranges (Iverson *et al*., 2004). For example, the northern limits of many tree species are modulated primarily by climatic factors, mainly temperature and light availability, which constrain the chances of survival at various stages of the life cycle (Woodward, 1987). A progressive decline in reproductive success results in a reduced capacity of these species to sustain themselves and to colonize new sites (Gaston, 2009). Among various natural processes, disturbances (e.g. fire, insect outbreaks and disease) play a major role in regulating species distributions at their latitudinal limits by altering population densities and limiting reproduction capacity (Ali *et al*., 2008). Human activities, such as agriculture and forest exploitation, are superimposed upon these factors and can contribute to habitat fragmentation, thereby accentuating the isolation of populations at a landscape scale (Vranckx *et al*., 2012).

To date, only a few studies have specifically addressed climate effects on species that are present within transition zones between forested areas. Most of these studies have focused on species that are present in northern tree-line ecosystems (i.e. the transition zone between boreal forest and the tundra) that are very sensitive to changes in climatic conditions, and which have shown recent species expansions (Lloyd & Fastie, 2003; Caccianiga & Payette, 2006). However, recent empirical observations in North America have shown that range contraction can also be observed (Zhu *et al*., 2012).

Sugar maple (*Acer saccharum* Marshall) is a widespread and abundant tree in north-eastern North America that reaches its northern continuous distribution range at the transition between boreal mixed-wood and temperate deciduous forests (Saucier *et al*., 2003). It is a deciduous, shade-tolerant species (Logan, 1965) that forms uneven-aged stands (Majcen *et al*., 1984) and has major ecological and economic value in eastern North America (Godman *et al*., 1990). Like other tree species in the Northern Hemisphere, sugar maple is predicted to migrate northwards from its current range. In the United States, models predict decreases in abundance at the southern edge of this species' range (Iverson *et al*., 2008) and a northward expansion that will eventually lead to an increase in sugar maple abundance towards its northern limits in Canada (Goldblum & Rigg, 2005).

Climate controls species distribution in part by affecting recruitment at different phases of sexual reproduction (Walck *et al*., 2011). Sugar maple seeds require high soil moisture levels during germination (Janerette, 1979) and a period of stratification at low temperatures, between 1 and 5 °C, to break embryo dormancy and stimulate germination (Shih *et al*., 1985; Godman *et al*., 1990). Germination of northern seed sources begins one week earlier at 1 °C than at 7 °C, but the cumulative proportion of germination after 90 days is 20% higher at 7 °C than at 1 °C (McCarragher *et al*., 2011). Sugar maple seedlings and mature trees may be affected by early leaf senescence and eventually die due to frost damage (Pilon *et al*., 1994). Sufficient understorey light is limiting during the growing season for seedlings at northern latitudes and may lead to decreased seedling growth because the time period between seedling leaf emergence and canopy closure by mature trees is shorter in northern stands (Kwit *et al*., 2010).

In the present study, we analysed the reproductive capacity of sugar maple populations along a climatic gradient. Our objective was to determine whether or not sugar maple recruitment differs between the discontinuous and continuous zones

within its northern range. We hypothesized that sugar maple had lower recruitment in the discontinuous than in the continuous part of its range, because seed production and seedling survival are reduced by low temperatures. To test this hypothesis, we examined stand structure, seed abundance and germination, seedling density and seedling age structure in populations along latitudinal transects ranging from the southern limit of the continuous sugar maple distribution in the sugar maple–yellow birch bioclimatic domain to its northern limit in the balsam fir–white birch bioclimatic domain.

2.4. Materials and methods

2.4.1. Study area

The study was located at the northern range limit of sugar maple in Québec, eastern Canada (Fig. 2.1). The presence of sugar maple stands along the latitudinal gradient was estimated from the analysis of large inventory databases (‘points d’observations écologiques’, ‘placettes permanentes’ and ‘placettes temporaires’) of the Ministère des Ressources Naturelles du Québec (MRNQ, 2013a). The gradient was divided into two zones based on the proportion of sugar maple stands in the continuous and discontinuous zones (8.5% and 2.2%, respectively).

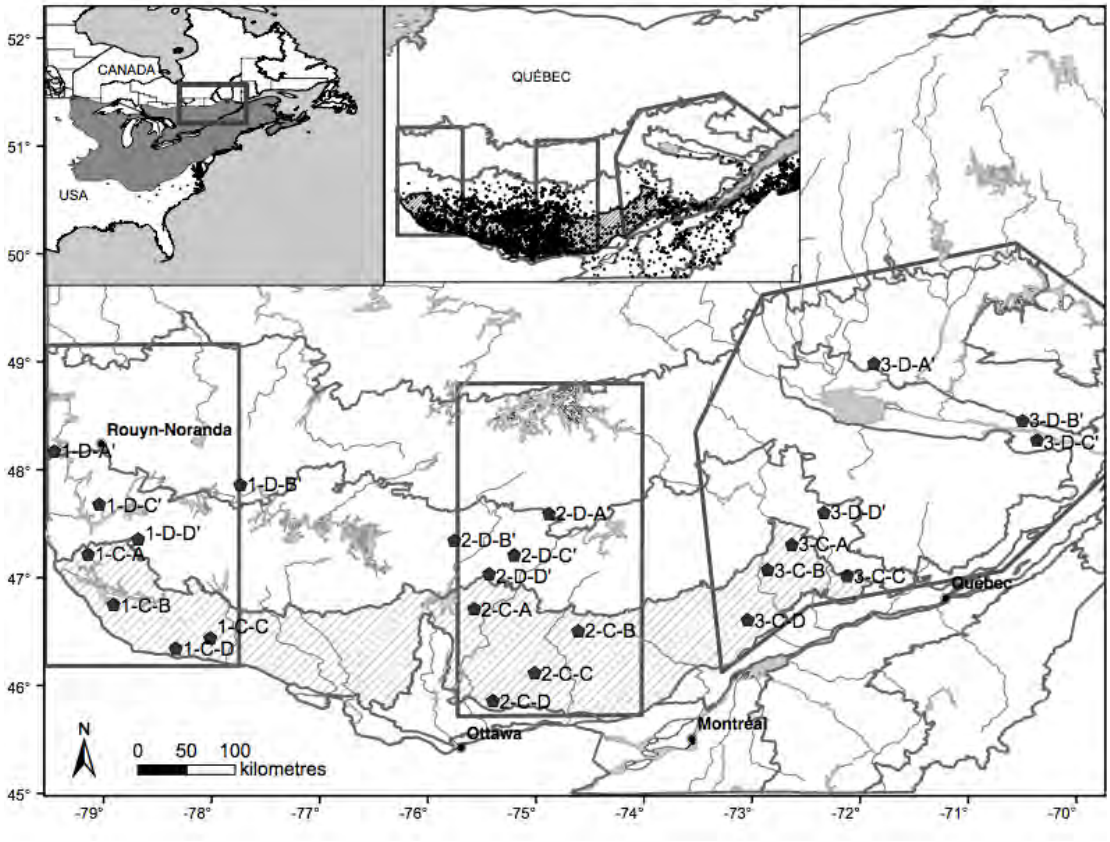

Figure 2.1 Map of the study area at the northern limit of sugar maple (*Acer saccharum*) distribution in Québec, showing the three transects (lines), locations of the 24 study sites (polygons; see Table A2.1 for more details), sugar maple–yellow birch (*Betula alleghaniensis*) bioclimatic domain (hatched), and boundary of all bioclimatic domain limits (thin line) (Saucier *et al*., 2003). In the top middle map panel, points represents sugar maple detected in databases of the Ministère des Ressources Naturelles du Québec ('points d'observation ecologiques', 'placettes permanentes' and 'placettes temporaires').

The continuous zone lay within the sugar maple–yellow birch (*A. saccharum* and *Betula alleghaniensis* Britton) bioclimatic domain where sugar maple is abundant. The discontinuous zone was in the balsam fir–yellow birch (*Abies balsamea* (L.) Miller and *B. alleghaniensis*) bioclimatic domain, and some northern sites were located in the transition with the balsam fir–white birch (*A. balsamea* and *Betula papyrifera* Marshall) bioclimatic domain (Saucier *et al*., 2003). Old-growth, uneven-aged sugar maple stands were selected to be as similar as possible after an analysis of the databases (the ecoforestry maps and tessellation-based forest information system

(Système d'Information FORestière par Tesselle, SIFORT) obtained from MRNQ (2013a,c). The ecoforestry maps are a result of three aerial photographic campaigns and field surveys. SIFORT uses a 14-ha grid overlaid on the ecoforestry maps. In the SIFORT database, sites that had been severely disturbed by fires, insect outbreaks or wind-throw since 1965 were identified (MRNQ, 2013c). In all sites, the diameter structures of sugar maple trees formed a reverse-J shape that is typical of uneven-aged stands (Fig. A2.1).

Sites were distributed along three north–south transects (eight sites per transect) and four sites per transect per zone (Fig. 2.1). Eleven of those sites are old-growth or rare forests that were classified as Exceptional Forest Ecosystems (EFE; MRNQ, 2013b). Data were collected at 24 sites between 45°51′ N and 48°59′ N latitude, and between 70°21′ W and 79°27′ W longitude (Table A2.1), at elevations ranging between 157 and 493 m a.s.l. Climatic data for each zone and transect (1971–2010) are summarized in Table A2.2 and were estimated from the meteorological station nearest to each study site (Environment Canada, 2009).

2.4.2. Field sampling

Data were collected in 2008 and 2009. Quadrats of 0.16 ha (40 m × 40 m) were established at each site. Within each quadrat, the diameter at breast height (d.b.h. at 1.3 m) of every mature tree (d.b.h. ≥ 10 cm) was measured. The five largest (d.b.h.) sugar maple trees were cored in each study plot. Cores were mounted on wooden strips and sanded, and the number of rings was counted to determine their age. The ages of individuals with missing piths were estimated using correlations with trees of the same size of the missing portion of the cores. Data on age and size of trees from the same areas were available in Majcen *et al*. (1984).

The d.b.h. of every sapling (1 cm ≤ d.b.h. < 10 cm) was measured within five circular plots (2 m radius) that were randomly distributed in the larger study plot. The

age of sugar maple seedlings (d.b.h. < 1 cm) was recorded in 15 circular plots of 1 m^2 that were randomly distributed across the study site. Seedlings were excavated to count all scars because sugar maple frequently develops adventitious roots along prostrate portions of stems. Age was estimated for 8822 sugar maple seedlings (total across all sites) using scars that were left each year by the loss of the scales protecting the bud of the terminal leader. Dating may be not precise for older seedlings, but this imprecision should be constant across sites. Five-year age classes were used in subsequent age structure models. When it was not possible to count the number of scars (i.e. due to stem breakage or larger basal diameter), the affected individuals were used to estimate seedling density ('undetermined' class) but were excluded from the age structure analysis.

Three seed traps, which covered a total area of 3 m^2, were randomly distributed within the 0.16-ha sample plot in two sites per zone in the western transect (transect 1 – Lac Labelle, Rémigny, Kipawa and Lac Six Milles; Table A2.1). Traps were installed in July and were removed at the end of October in 2008, 2009, 2010 and 2011. Filled seeds (seeds with kernels) were checked by firmly pressing each seed between the fingers during counting. Unfilled seeds were discarded and the remaining filled seeds were cold moist-stratified at 3 °C (for a maximum of 42 days) and germinated. Germination tests were performed at the Centre de Semences Forestières de Berthier of MRNQ.

2.4.3. Data analysis

Data were analysed using the statistical software package R version 2.13.1 (R Development Core Team, 2011).

2.4.3.1. Forest composition

Tree species composition (presence/absence) in the 24 sites was analysed using correspondence analysis (CA, using the *cca* function in the VEGAN library; Oksanen

et al., 2011). Mature sugar maple trees and sugar maple saplings were excluded from this analysis because they were present in all sites.

2.4.3.2. Recruitment between zones

Variation in mature tree density and basal area was tested for every tree species (across all plots) and for sugar maple alone, using two-way analysis of variance (ANOVA) with zone, transect and their interaction as fixed effects. Density and basal area for all tree species (total) and sugar maple saplings, seed abundance and sugar maple seedling density were tested using a linear mixed-model analysis (LMM, using the *lme* function in the NLME library; Pinheiro *et al*., 2011). For saplings, zone, transect and their interaction were treated as fixed effects in the analysis. For seed abundance, zone, year and their interaction were the fixed effects. For sugar maple seedling density responses, the fixed effects were seedling emergence year, zone, transect and their three-way interaction (seedling emergence year × zone × transect). Random effects included site for saplings and seed abundance, and site and circular plot for sugar maple seedling density. Year of seedling emergence was estimated on the basis of seedling age for the period from 1970 to 2008, plus one 'undetermined' class. The assumption of normality and homoscedasticity was verified graphically; seed abundance and seedling density data were log-transformed to respect these assumptions. ANOVA and linear mixed models were simplified by stepwise backward elimination of non-significant fixed-effect terms to produce the most parsimonious models.

2.4.3.3. Filled seeds and germination

We used generalized linear mixed-effects models (GLMM, using the *glmer* function in the LME4 library; Bates et al., 2011) with a logit link function and binomial error distribution to analyse the filled seed ratio (the proportion of filled seeds to total seeds) and the germination ratio (the proportion of germinated seeds to

filled seeds). In order to avoid problems in estimation, year and zone were considered to be fixed effects in two different models for each seed ratio analysis, and in one model for germination ratio; seed trap was considered a random effect. The germination ratio model was simplified by backward elimination.

2.4.3.4. Age structure

To compare sugar maple recruitment across the study area, seedlings (1–40 years old) were grouped into 5-year age classes. Sugar maple seedling age structures can be described either by a negative exponential function with constant mortality, or by a power function with a higher mortality rate in early years (Hett & Loucks, 1971). We used the Akaike information criterion (AIC; *aictab* in the AICcmodavg library; Mazerolle, 2011), corrected for small sample sizes (AIC_c), and AIC_c weights (ω) for model evaluation (Burnham & Anderson, 2004). The power function was the best model ($\Delta AIC_c \leq 4$) for most of the 24 sites (Table A2.3). It was used to estimate R (initial recruitment) and M (mortality rate) with the function $\ln(\text{stem m}^{-2} + 1) = \ln(R + 1) - M \times \ln(\text{age})$. We then used R and M to assess the effects of zones on sugar maple abundance.

The age-structure data set ($n = 24$) was not large enough to include all stand and climate variables in one model. Sugar maple seedling $\ln(R)$ was analysed using one-way, two-way or three-way ANOVA. We determined five candidate models: model 1 considered the effect of mature sugar maple basal area; model 2, mature sugar maple density; model 3, transect, zone and transect × zone; model 4 included models 1 and 3; and model 5 included models 2 and 3. We ranked each model based on AIC_c. We then computed ΔAIC_c and ω to determine the strength of evidence for each model (Burnham & Anderson, 2004). Following model fitting, we performed multimodal inference (*modavg* function in AICcmodavg library) when required ($\Delta AIC_c \leq 4$) to assess variable effects on the initial recruitment of sugar maple. Variation in M for

sugar maple seedlings was tested using two-way ANOVA with zone, transect and their interaction as fixed effects. Assumptions of normality and homoscedasticity were verified prior to analysis of ln(R) and M.

2.4.3.5. Relationships with climate

Sugar maple seedling density was compared using LMM analysis for transect × zone, or stand and/or meteorological fixed effects, with site as a random effect. Meteorological data for all sites (monthly means for 1930–2010) were obtained using the simulation software BIOSIM 9 (Régnière, 1996). We constructed different models to test the following effects: transect × zone; stand characteristics, which included total density and basal area (density and basal area included mature tree, mature sugar maple, total saplings and sugar maple saplings); climatic conditions, which included average annual temperature and precipitation, monthly average temperature and precipitation from April to October; and global models with a combination of one model of stand characteristics and one model of climate conditions. Correlations between variables were examined; total sapling density was therefore excluded from the model, because it was strongly correlated with sugar maple sapling density (r^2 = 0.80). Assumptions of normality and homoscedasticity were tested on all 16 global models and seedling density was log-transformed. Fits of the 27 models were compared using AIC_c. Model averaging was performed to calculate parameter estimates and unconditional 95% confidence intervals (CI).

Mast years were compared for transect 1 using GLMM. We constructed a model based on the hypothesis that high seed production was related to warm, dry conditions in the spring of the previous year (Houle, 1999).

2.5. Results

2.5.1. Stand characteristics

The first and second axes of the correspondence analysis (CA) accounted for 35.0% of the variation in tree species composition among sites. The first CA axis explained 22.8% of the variance (eigenvalue $\lambda_1 = 0.68$) and clearly highlighted a difference in tree stand composition between zones (Fig. 2.2). Towards the left-hand end of CA axis 1, most species were found only in the continuous zone (transects 1 and 2), except for mature ironwood (*Ostrya virginiana* (Mill.) K. Koch), which was also present in one site from the southern discontinuous zone (2-D-D′, Lac des Polonais). Towards the right-hand end of the first CA axis, species that were observed in the discontinuous zone are characteristic of the balsam fir–white birch bioclimatic domain (i.e. white or paper birch and trembling aspen, *Populus tremuloides* Michx.). One exception was white or American elm (*Ulmus americana* L.), which was also observed in the continuous zone. A second CA axis of variation ($\lambda_2 = 0.37$, 12.2% of the variance) distinguished sites within zones. Variation in species composition was greater within the continuous zone. For example, in continuous zone transect 2, variation was due to one species being present only once in three of the four sites sampled; this included saplings of bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) at site 2-C-D (Lac de l'Ecluse), mature red spruce (*Picea rubens* Sarg.) at site 2-C-A (Montagne du Diable), and mature white elm at site 2-C-B (Lac Ecuyer).

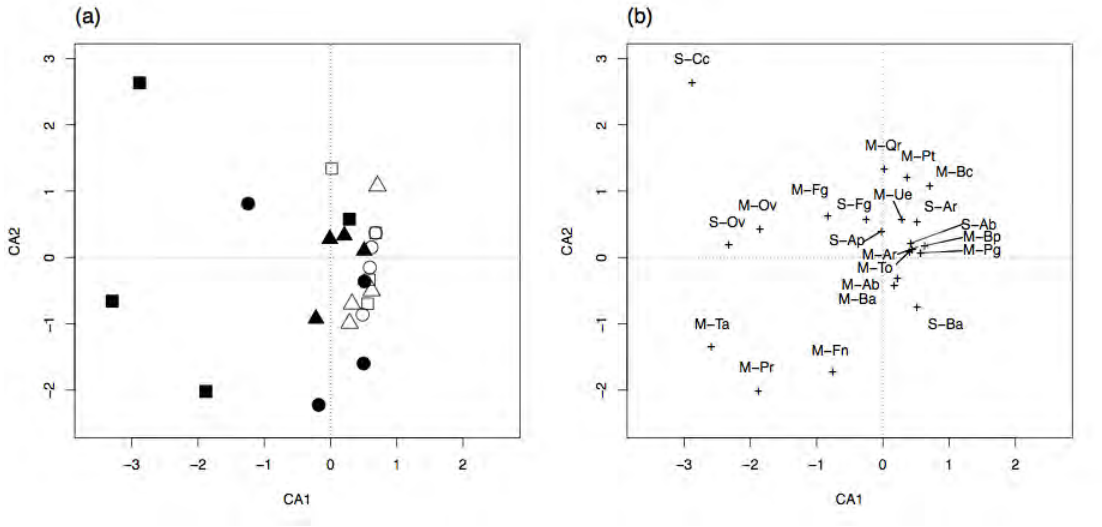

Figure 2.2 Ordination diagram of species presence/absence (except sugar maple, *Acer saccharum*) by site for mature trees (M; $n = 24$) and saplings (S; $n = 24$) obtained by correspondence analysis (CA) in Québec. (a) By site: Circles, transect 1; squares, transect 2; triangles, transect 3; open symbols, discontinuous zone; black symbols, continuous zone; (b) by species. CA1, correspondence analysis axis 1; CA2, correspondence analysis axis 2. Species label abbreviations: Ab, balsam fir, *Abies balsamea* (L.) Mill.; Ap, striped maple, *Acer pensylvanicum* L.; Ar, red maple, *Acer rubrum* L.; Ba, yellow birch, *Betula alleghaniensis* Britt.; Bc, mountain paper birch, *Betula cordifolia* Regel; Bp, white birch, *Betula papyrifera* Marshall; Cc, bitternut hickory, *Carya cordiformis* (Wangenh.) K. Koch; Fg, American beech, *Fagus grandifolia* Ehrh.; Fn, black ash, *Fraxinus nigra* Marshall; Qr, red oak, *Quercus rubra* L.; Ov, ironwood, *Ostrya virginiana* (Mill.) K. Koch; Pg, white spruce, *Picea glauca* (Moench) Voss; Pr, red spruce, *Picea rubens* Sarg.; Pt, trembling aspen, *Populus tremuloides* Michx.; Ta, basswood, *Tilia americana* L.; To, eastern white-cedar, *Thuja occidentalis* L.; Ua, white elm, *Ulmus americana* L.

Total mature tree density was higher along all transects ($F_{1,18} = 8.9691$, $P = 0.0078$) in the discontinuous zone than in the continuous zone (means of 519 stems ha^{-1} and 390 stems ha^{-1}, respectively; Fig. 2.3a). Total basal area was not significantly different (zones, transects or interaction zone × transect), except for total sapling basal area (Table A2.4).

Significantly or marginally significant differences were apparent among transects but not between zones (Table A2.4) for total sapling density ($F_{2,99} = 5.8395$, $P = 0.0040$), total sapling basal area ($F_{2,99} = 2.9039$, $P = 0.0595$) and mature sugar maple density ($F_{1,18} = 3.9380$, $P = 0.0381$). Indeed, sapling densities and sapling basal area

were significantly higher along transect 1 (Fig. 2.3c, 3209 stems ha^{-1}; Fig. 2.3e, 7.02 m^2 ha^{-1}) than along transect 3 (Fig. 2.3c, 1691 stems ha^{-1}; Fig. 2.3e, 3.29 m^2 ha^{-1}). Mature sugar maple density was lower in transect 1 (223 stems ha^{-1}) than in transect 2 (356 stems ha^{-1}). No differences were observed between transect 3 (305 stems ha^{-1}) and transects 1 and 2 (Fig. 2.3b). Sugar maple sapling densities differed among transects, but this response depended upon zone (zone × transect interaction: $F_{2,99}$ = 3.1813, P = 0.0458; Table A2.4). The highest sugar maple sapling density was encountered in transect 1 of the continuous zone (Fig. 2.3d, 3024 stems ha^{-1}), while no differences were found between zones within each transect.

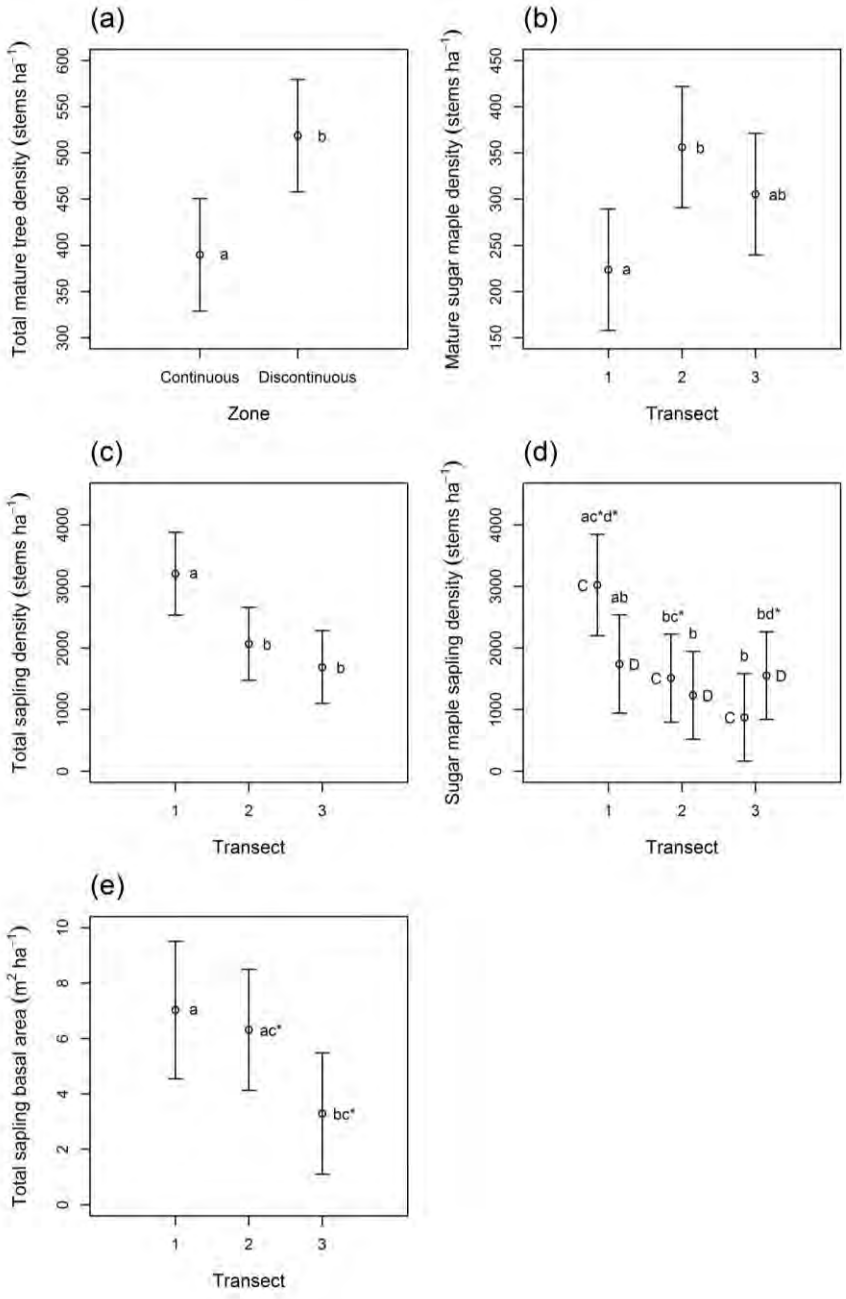

Figure 2.3 Predicted means (± 95% confidence intervals) of (a) total mature tree density (stems ha^{-1}; n = 24), (b) mature sugar maple (*Acer saccharum*) density (stems ha^{-1}; n = 24), (c) total sapling density (stems ha^{-1}; n = 111), (d) sugar maple sapling density (stems ha^{-1}; n = 111) and (e) total sapling basal area (m^2 ha^{-1}; n = 111) in two zones (C: continuous and D: discontinuous) or three transects (1, 2 and 3) or zones and transects in Québec. Means with the same letter do not differ at $\alpha = 0.05$ but differ (with an asterisk) at $\alpha = 0.10$.

2.5.2. Sugar maple seed production

Sugar maple seed production differed between years, depending upon zone (zone × year interaction: $F_{3,30} = 24.1483$, $P < 0.0001$). In 2008, seed production was higher in the continuous zone (mean 34.0 seeds m^{-2}) than in the discontinuous zone, where almost no seeds were produced (Fig. 2.4a). In 2009 and 2010, the seed crop was very low in both zones (mean range 0–1.8 seeds m^{-2}). In 2011, very high mean seed production was observed within the continuous zone (471 seeds m^{-2}) but did not significantly differ from that of the discontinuous zone (211 seeds m^{-2}).

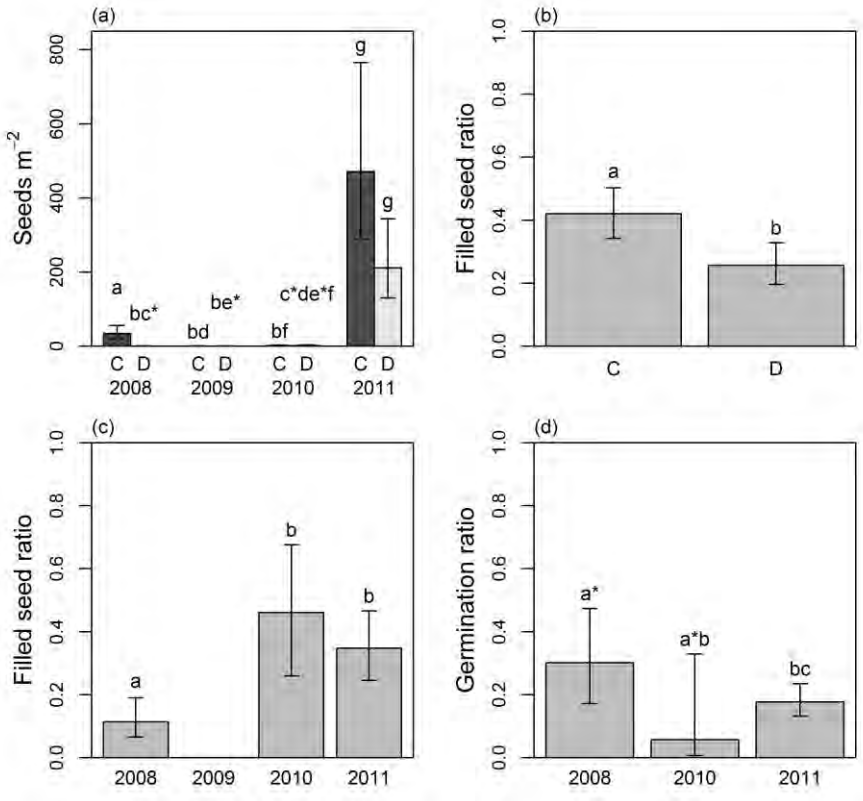

Figure 2.4 Predicted mean (± 95% confidence intervals) of (a) sugar maple (*Acer saccharum*) seed production (seeds m^{-2}) in C (continuous) and D (discontinuous) zones over four years (2008 to 2011; $n = 48$); (b) sugar maple filled seed ratio in two zones ($n = 5234$); (c) sugar maple filled seed ratio over 4 years ($n = 5234$); (d) sugar maple germination ratio over 3 years (2008, 2010 and 2011; $n = 1866$). Seed study was conducted only in transect 1 (Abitibi-Témiscamingue, Québec). Means with the same letter do not differ at $\alpha = 0.05$ but differ (with an asterisk) at $\alpha = 0.10$.

The filled seed ratio varied significantly between zones and years (Fig. 2.4b,c). The mean ratio was higher in the continuous (0.42) than in the discontinuous zone (0.26). It was also higher in 2010 and 2011 (0.46 and 0.35, respectively) than in 2008 (0.11) or 2009 (0.00). Significant differences in germination ratios were apparent between years (2008, 0.30; 2011, 0.18) but not between zones (Fig. 2.4d).

2.5.3. Natural recruitment of sugar maple seedlings

Sugar maple seedling density varied significantly across years, zones and transects (seedling emergence year × zone × transect interaction: $F_{78,13761} = 12.23615$, $P < 0.001$). The age structure exhibited an inverse J shape, suggesting sustained seedling recruitment, especially along transect 1 (Fig. 2.5). In transect 1, the years 1996, 2002 and 2006 were identified as mast seed years in both the continuous and discontinuous zones (here, we assumed that higher seedling recruitment was synchronized with higher seed production during the previous year; Kelly & Sork, 2002). For each mast seed year in this transect, the continuous zone had higher seedling densities. For transect 2, 2002 and 2003 were mast years, whereas only 2003 was a mast year in transect 3. Mast seed years 1996 and 2006 were apparent in transects 2 and 3, but 1996 was not observed as a mast year in the continuous zone of transect 2.

Using a power function (Fig. 2.6; Fig. A2.2), estimated initial recruitment (R) ranged from 4.6 to 119.6 seedlings m^{-2} in the discontinuous zone, and from 2.9 to 436.0 seedlings m^{-2} in the continuous zone. As with recruitment, the range for mortality rate (M) was lower in the discontinuous zone [0.47–1.41 ln(stems m^{-2} + 1) ln(years^{-1})], but it overlapped estimates for the continuous zone [0.31–1.70 ln(stems m^{-2} + 1) ln(years^{-1})] (Fig. 2.6; Fig. A2.2). The model that tested the effects of transect and zone upon R was not the best model. Models that tested the effects of mature sugar maple basal area (model 1) or mature sugar maple density (model 2) on R ranked the highest among our candidate models ($\Delta AIC_c \leq 4.0$), with ω of 0.81 and

0.16, respectively. Nonetheless, multi-model inference showed no influence on *R* of either sugar maple basal area (model-averaged estimate: 0.043; 95% CI: –0.003, 0.089) or density (model-averaged estimate: –0.001; 95% CI: –0.006, 0.004). In brief, none of the explanatory variables that we considered could explain the variation in *R*. *M* was weakly associated with geographical location (zone × transect interaction: $F_{2,18}$ = 3.1340, P = 0.0679), with a marginally significant difference between transects 1 and 3 in the continuous zone (Fig. A2.3).

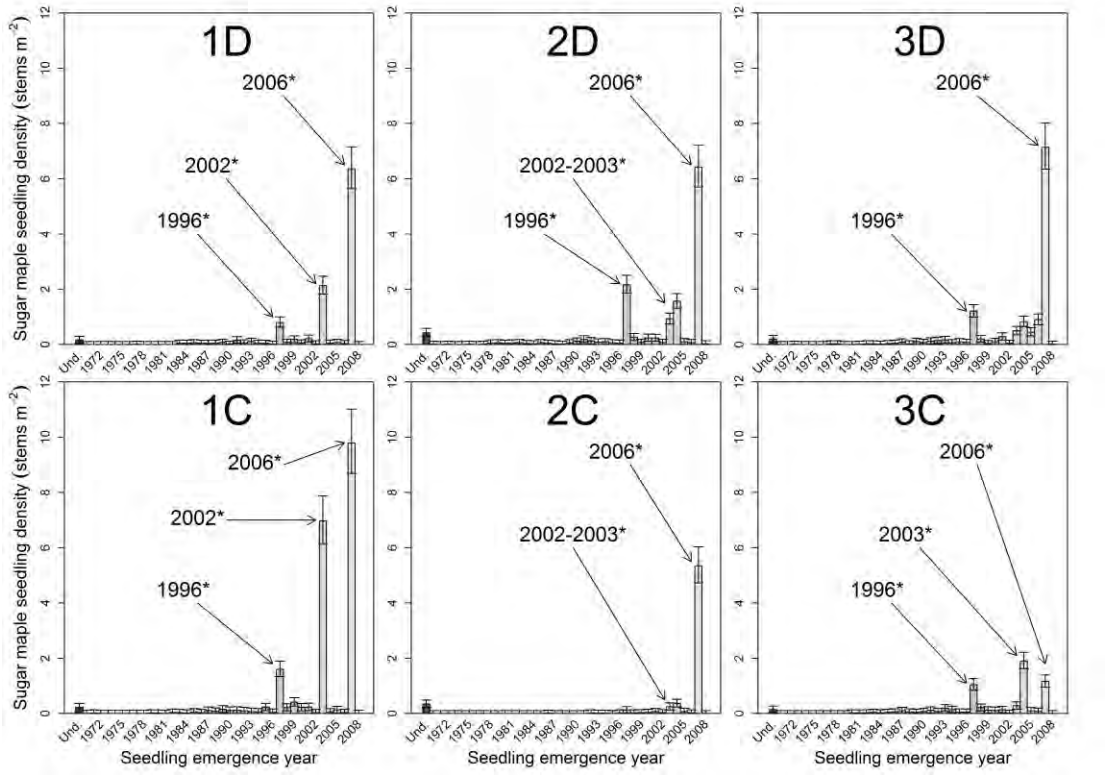

Figure 2.5 Predicted mean (± 95% confidence intervals) of sugar maple (*Acer saccharum*) seedling density (stems m^{-2}) for each year (Und. (undetermined) and 1970 to 2008) of C (continuous) and D (discontinuous) zones (n = 14119) in Québec. Three transects were established in each zone, e.g. 1D = discontinuous zone in transect 1. * Potential mast seed year assigned one year before seedling emergence.

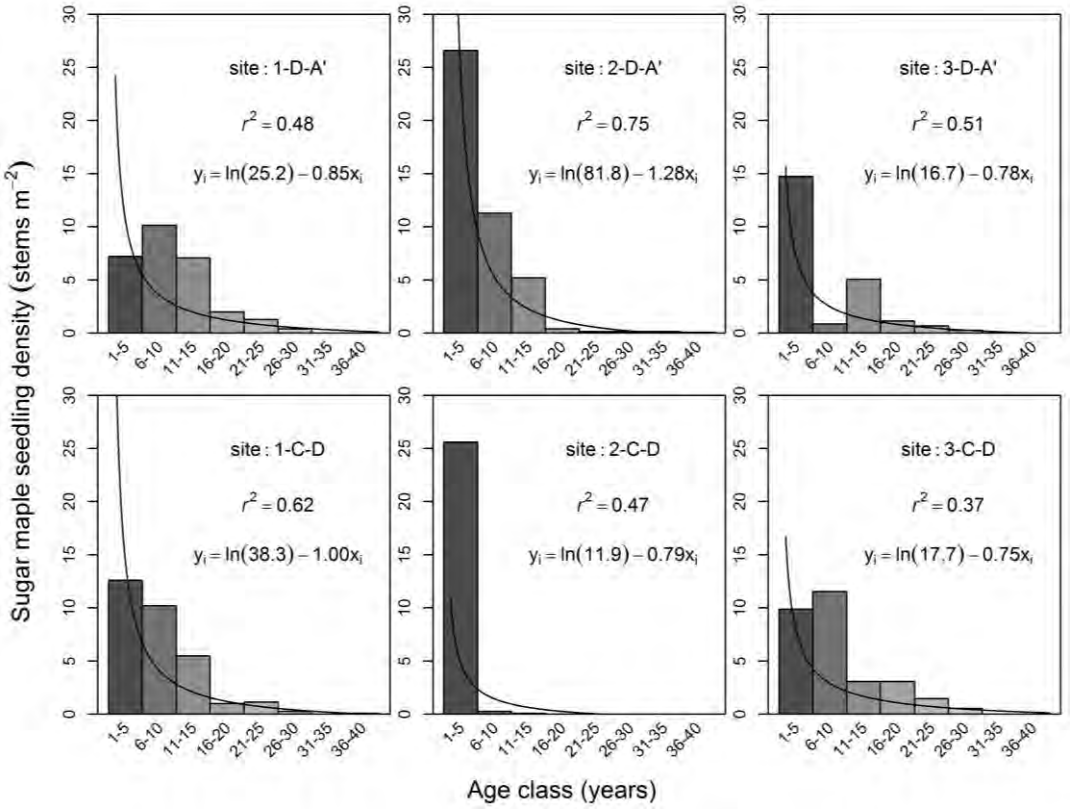

Figure 2.6 Sugar maple (*Acer saccharum*) age structures of the most northern and southern sites of each transect [n = 720; for all 24 sites, see Fig. A2.2 (n = 2880)]. For each population, the linearized form of power function is included, together with its coefficient of determination. $y_i = r - M \times x_i$; y_i is ln(stems m^{-2} + 1); r is the intercept of the curve, ln(R), where R is initial recruitment; M is the slope of the curve, mortality rate and x_i is ln(age).

2.5.4. Relationships with climate

Sugar maple seedling density ranged from 0.0 to 191.8 seedlings m^{-2}, with a mean of 25.5 seedlings m^{-2} in the 1-m^2 circular plots. Only 6% of the plots lacked sugar maple seedlings (4% in the discontinuous zone; 9% in the continuous zone). According to the AIC$_c$, the best model for predicting sugar maple seedling density included basal area, July mean temperature, and July mean precipitation (ΔAIC$_c \leq$ 4.0; Table A2.5). The model including the zone × transect interaction ranked lowest.

Parameter estimates derived from multi-model inference suggested that sugar maple seedling density increased with average July temperature and, to a lesser extent, with sapling basal area, mature sugar maple basal area and mean July precipitation (Fig. 2.7a,b,d,e, Table 2.1). Sugar maple sapling basal area had a negative effect on sugar maple seedling density (Fig. 2.7c, Table 2.1), while total mature tree basal area exerted no influence (Table 2.1).

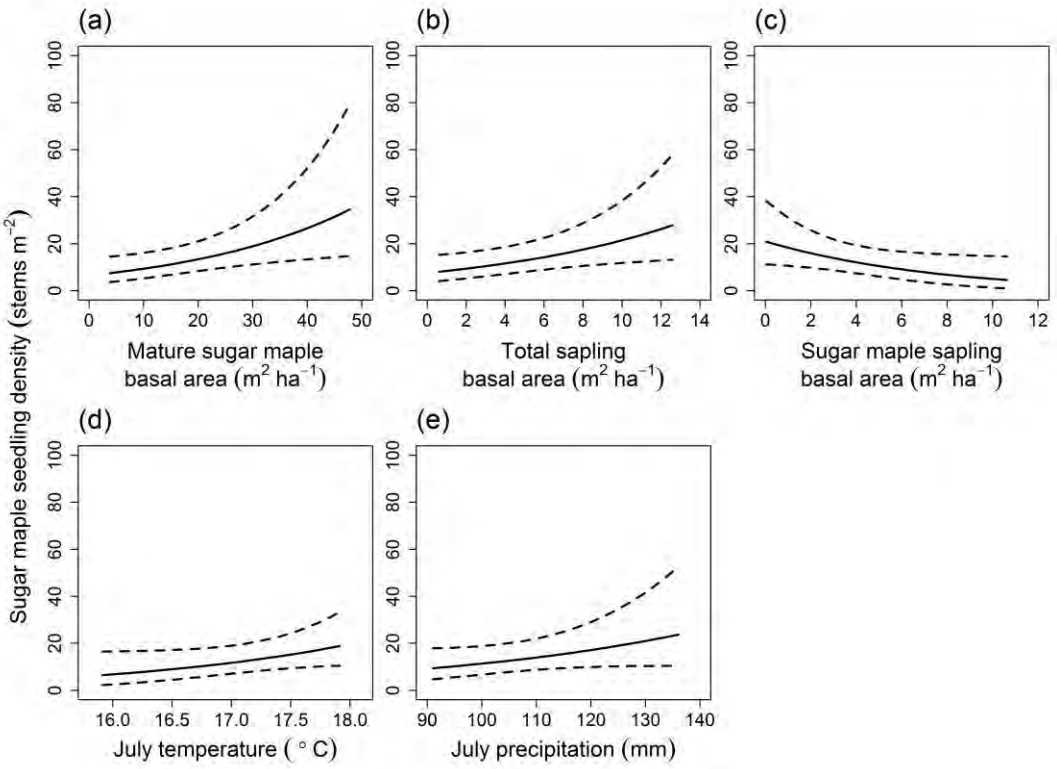

Figure 2.7 Predicted sugar maple (*Acer saccharum*) seedling density (stems m^{-2}) in response to all explanatory variables in the best supported model (model 21), based on multi-model averaging of all candidate models (n = 353) in Québec. Dashed lines show 95% confidence intervals.

Table 2.1 Parameter estimates and unconditional confidence intervals from multi-model inference of sugar maple (*Acer saccharum*) seedling density (ln(data + 1)) in Québec. Term abbreviations: m_BA, mature tree basal area; m_ers_BA, mature sugar maple basal area; s_BA, sapling basal area; s_ers_BA, sugar maple sapling basal area; July_T, July mean temperature; July_P, July mean precipitation.

Explanatory variables	Model-averaged estimate	95% confidence interval	
		Lower	Upper
m_BA [ln(m^2 ha^{-1} + 1)]	0.023	−0.008	0.055
m_ers_BA [ln(m^2 ha^{-1} + 1)]	0.035	0.015	0.055
s_BA [ln(m^2 ha^{-1} + 1)]	0.103	0.037	0.169
s_ers_BA [ln(m^2 ha^{-1} + 1)]	−0.139	−0.250	−0.028
July_T [ln(°C + 1)]	0.578	0.211	0.946
July_P [ln(mm + 1)]	0.023	0.004	0.041

The relationship between mast years and climatic variables was tested for transect 1. Mast seeding varied significantly with July mean temperature (Fig. 2.8a) and July mean precipitation (Fig. 2.8b) of the previous year. Predictions were valid and more than 50% probability of masting was observed when July mean temperature was > 19.5 °C and July mean precipitation was < 35 mm.

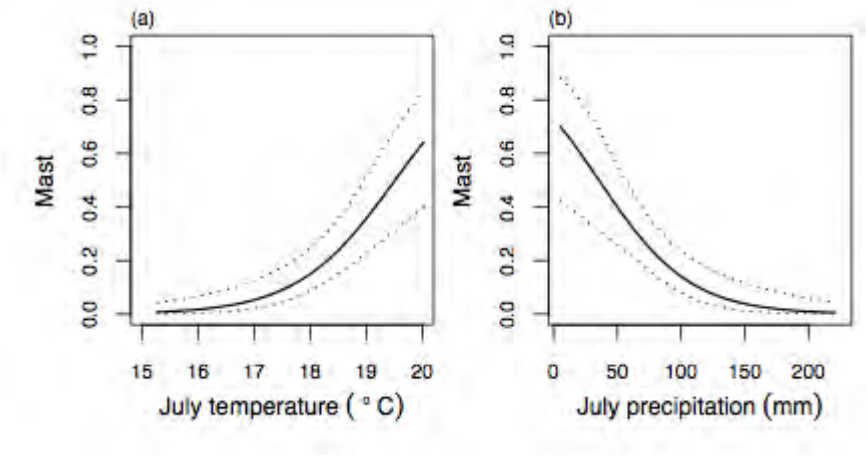

Figure 2.8 Predicted probability of mast seeding in sugar maple (*Acer saccharum*) for transect 1 (Abitibi-Témiscamingue, Québec; *n* = 136) based on (a) July mean temperature of the previous year and (b) July mean precipitation of the previous year. Dashed lines show 95% confidence intervals.

2.6. Discussion

Our results indicated that sugar maple regeneration was globally similar across the discontinuous and continuous parts of its distributional range. Seedling age structures was also similar across its range with high recruitment, higher mortality at early stages, and decreasing mortality rates over time in most sampled sites. However, seedling density varied significantly among year (seedling emergence year), transects (west–east), and bioclimatic domains (zones). Variation in sugar maple seedling density was best explained by stand characteristics (mature tree species, mature sugar maple, tree species saplings, and sugar maple sapling basal areas) and climate conditions (July average temperature and precipitation), rather than by zonation.

Sugar maple seedling density was estimated to be 25.5 stems m^{-2}, when averaged over the 24 stands, and 32.6 stems m^{-2}, when we considered only the three northernmost sites (1-D-A′, Lac Labelle; 2-D-A′, Lac Pénobscot; 3-D-A′, Lac Patrick). These values were higher than those reported by Caspersen & Saprunoff (2005) for central Ontario (i.e. 11.1 stems m^{-2}; Haliburton Forest and Wildlife Reserve, located south of our study area), and the range of values (14.7–29.9 stems m^{-2}) that are reported by Goldblum & Rigg (2002, 2009) on the north-eastern shore of Lake Superior (Lake Superior Provincial Park; 47°45′ N, 84°42′ W). Variation in recruitment was low in our study area, in that sugar maple seedlings were absent from only 9% of circular plots in the continuous zone, which was consistent with a value of 20% for all quadrats measured by Caspersen & Saprunoff (2005). Multi-model inference indicated that five of our six first models included mature sugar maple basal area and that this variable was positively related to sugar maple seedling density (Table 2.1, Fig. 2.7, Table A2.5). This result was also consistent with Caspersen & Saprunoff (2005), who showed that sugar maple seedling density is correlated with higher sugar maple basal area, and with Garrett & Graber (1995), who showed that

larger sugar maple trees generally producing more seeds than did smaller individuals. In contrast, Houle (1992) reported a negative relationship between sugar maple basal area versus sugar maple seed and seedling abundance, within a stand located south-east of our study area. This difference could be related to a different bioclimatic domain (sugar maple–basswood; Houle, 1992) or to stand characteristics that are not representative of a general pattern for sugar maple (Houle, 1992).

Like seedling density, basal area for mature trees (total and sugar maple) did not vary among transects and between zones. Mature sugar maple trees in transect 1 (western region, Abitibi-Témiscamingue) were larger but occurred at lower densities than those in the central region of Québec (transect 2; Fig. 2.3). We had expected to find larger sugar maple trees in the continuous zone where climatic conditions are more favourable to the growth of this species. Our results showed a negative influence of sugar maple sapling basal area on seedling density. The negative effect of saplings may be attributed to the shade produced by sugar maple leaves. This closed shade-cover (compared to mature trees) may induce higher sugar maple seedling mortality, even though sugar maple is a shade-tolerant species (Logan, 1965). This hypothesis of light limitation is supported by Kellman (2004), who found that sugar maple seedling mortality is lower in boreal stands than in sugar maple stands at the same latitude.

In transect 1 (west), differences between the continuous and discontinuous zones were very clear with respect to seed abundance and seedling density. In 2008, seeds were produced only in the continuous zone (34.0 seeds m^{-2}; Fig. 2.4). However, this trend was not observed in 2009 and 2010, where very few seeds were produced in either zone, or in 2011, where high production was observed in both zones. Only 2.5 seeds m^{-2} germinated in 2008, which was not consistent for a mast seed year, while 43.0 seeds m^{-2} germinated in 2011. On the basis of seedling density structure (Fig. 2.5) and seed collections, we identified four mast seed years in transect 1 (1996,

2002, 2006 and 2011). Overall, mast years were well synchronized in all sites, if we excluded 2002–2003. There was a mast year in 2002 in transect 1 (west), 2002 and 2003 in transect 2 (centre), and 2003 in transect 3 (east), which suggested a 'west–east gradient'. Four to 6 years separated each mast, which is consistent with the 3–8 years reported for Canada (Wang, 1974). Cleavitt *et al*. (2011) identified 1998, 2002 and 2006 as mast years in north-central New Hampshire. This synchronized and intermittent reproduction across the range of sugar maple could be due to endogenous rhythms (Kelly, 1994), climate conditions (Houle, 1999; Kelly & Sork, 2002), or seed predators (Tachiki & Iwasa, 2010). With respect to climate conditions, our data suggested that a warm and dry July in the previous year can induce mast seeding (Fig. 2.8). If some seedlings survived for several years, the presence of a seedling bank on the forest floor could compensate for the disadvantage of intermittent reproduction.

Model selection identified July mean temperature and precipitation (Table A2.5) as variables positively influencing sugar maple seedling density (Fig. 2.7). Sugar maple seeds have high soil moisture requirements during germination (Janerette, 1979). Our results showed that precipitation during April and May did not influence seedling density. This suggested that moisture during germination was not a limiting factor. We could hypothesize that warm July temperature, combined with high precipitation, might reduce seedling mortality. However, more studies are needed to identify the direct effect of climate conditions on seedling survival in sugar maple.

Climatic models for eastern North America have predicted a mean increase of +3.3 °C (minimum, 2.1 °C; maximum, 5.4 °C) and +1% in precipitation (min. –17%, max. +13%) in June, July and August for the decade 2080–2099 compared to 1980–1999 (Christensen *et al*., 2007). Applying these mean values with our model for the northernmost site of transect 1 (1-D-A′, Lac Labelle), our model predicted a mean increase of 5.3% (min. 2.1%, max. 18.4%) in sugar maple seedling densities for 2080–2099 compared to 1980–1999. However, the uncertainties around these

estimates progressively increased as temperature and precipitation increased (Fig. 2.7). Therefore, our predictions are limited by these uncertainties, but an increase in sugar maple seedling density is predicted to occur with climate change.

Species distributional range-shift predictions are based on niche models, climatic envelopes, and process-based models (McKenney *et al*., 2007; Morin & Thuiller, 2009). All of these approaches have more or less emphasized the influence of climate in predicting future species distributions, in part because other predictors are frequently unavailable. Our sugar maple seedling density model and habitat distribution models showed that the sugar maple limit was not controlled exclusively by the effect of tested climatic variables on regeneration. Therefore, northward expansion could possibly occur under different climatic scenarios (Iverson *et al*., 2008; Morin & Thuiller, 2009). All of the sites from the discontinuous zone showed very good sugar maple regeneration. For example, the northernmost site in transect 2 (2-D-A′, Lac Pénobscot; Fig. 2.6) showed high sugar maple seedling densities and a typical J-shaped age structure, which indicates continuous recruitment over time. It is possible that soil characteristics (type and nutrients) could serve as explanatory factors. For example, a lack of rotten wood and leaf litter can represent a barrier to seedling establishment (Caspersen & Saprunoff, 2005), while an increase in calcium availability and a thinner litter layer are important for improving early sugar maple seedling survival (Cleavitt *et al*., 2011). The inclusion of soil characteristics may increase the predictive power of our sugar maple seedling density model. Sugar maple regeneration could also be influenced by factors such as herbivore grazing (Salk *et al*., 2011), seed predation (Hsia, 2009), disease (Cleavitt *et al*., 2011), and interspecific competition (Gravel *et al*., 2011). Accumulating evidence has shown that important non-climatic factors must be included to increase model predictive power for actual and future tree species range shifts (McMahon *et al*., 2011).

2.7. Acknowledgements

We thank Normand Villeneuve, Claude Poulin and Renaud Dostie of MRNF du Québec who found many potential sites. Michèle Bettez and Jean-Pierre Faust of the Centre de Semences Forestières de Berthier (MRNF du Québec) performed the seed germination tests. Geneviève Trudeau, Elizabeth Turcotte, Sylvain Larouche, Chelsea Archambault, Emilie Tarroux, Manuella Strukelj-Humphery, Hedi Kebli and Dave Gervais provided invaluable field assistance. We are grateful to Marc J. Mazerolle for statistical advice, Igor Drobyshev for his help with BIOSIM, Osvaldo Valeria for his help with geographic analysis, and William F. J. Parsons for careful language editing. We are thankful for the referees' comments, which greatly improved the manuscript. This work was funded by an NSERC (Natural Sciences and Engineering Research Council of Canada) strategic grant (STPGP 336871) to Francine Tremblay.

2.8. Biosketches

Noémie Graignic is a PhD student in environmental sciences at the University of Québec in Abitibi-Témiscamingue (Canada). Her project consists of identifying factors that are influencing northward migration of sugar maple.

Francine Tremblay is a professor at the University of Québec in Abitibi-Témiscamingue (Canada). Her laboratory research interest focuses on population and conservation genetics of forest ecosystems.

Yves Bergeron is a professor of forest ecology at the University of Québec in Abitibi-Témiscamingue and University of Québec at Montréal (Canada). He is interested in forest dynamics at both the stand and landscape scales.

Author contributions: N.G., F.T. and Y.B. conceived the ideas; N.G. collected and analysed the data and led the writing of this paper.

CHAPITRE III

DEVELOPMENT OF POLYMORPHIC NUCLEAR MICROSATELLITE MARKERS IN SUGAR MAPLE (*ACER SACCHARUM* MARSHALL) USING CROSS-SPECIES TRANSFER AND SSR-ENRICHED SHOTGUN PYROSEQUENCING

Noémie Graignic, Francine Tremblay et Yves Bergeron

Note technique publiée en 2013 dans Conservation Genetics Ressources, vol. 5, p. 845–848

3.1. Résumé

Un ensemble de 23 microsatellites polymorphes a été testé avec succès pour *Acer saccharum*. Dix-huit de ces nouveaux marqueurs polymorphes ont été développés en utilisant le séquençage de nouvelle génération et cinq ont été transférés à partir d'autres espèces d'*Acer*. Un total de 68 individus de deux populations a été génotypé pour tous les marqueurs à l'aide de multiplex. La diversité allélique moyenne observée était de 7,7, le polymorphisme variait de 2 à 16 allèles par locus. L'hétérozygotie globale était élevée, avec une hétérozygotie moyenne observée de 0,644. Deux loci, obtenus à partir de transfert entre espèces, et un locus obtenu par pyroséquençage, ont montré un déficit d'hétérozygotes, une déviation de l'équilibre d'Hardy-Weinberg, et une fréquence importante d'allèles nuls pour une ou deux populations. Aucune preuve de déséquilibre de liaison n'a été détectée. Enfin, 20 des 90 marqueurs pourraient être utilisés dans le futur pour des études de génétique des populations d'*Acer saccharum*.

3.2. Abstract

A set of 23 polymorphic microsatellites was successfully tested for *Acer saccharum*. Eighteen of these new polymorphic markers were developed using nextgeneration sequencing and five were transferred from other *Acer* species. A total of 68 individuals from two populations were genotyped at all markers using a multiplex approach. Mean allelic diversity was 7.7, polymorphism ranged from 2 to 16 alleles per locus. Overall heterozygosity was high, with an average observed heterozygosity of 0.644. Two loci that were obtained from cross-species transfer and one from shotgun pyrosequencing showed heterozygote deficiencies, deviations from Hardy–Weinberg equilibrium, and high frequencies of null alleles for one or both populations. No evidence for linkage disequilibrium was detected. Finally, 20 of the 90 markers could be used in future population genetics studies of *A. saccharum*.

3.3. Introduction

Sugar maple (*Acer saccharum* Marsh.) is a widespread and abundant tree in Northeastern North America (Godman *et al*. 1990). With anticipated climate change, models are predicting a decrease in abundance at the southern edge of its range (Iverson *et al*. 2008). This range contraction could lead to population fragmentation, progressive genetic erosion, and loss of genetic diversity in the most southern populations. Consequently, preservation of the original genetic diversity in marginal populations is a major issue in conservation biology (Hampe & Petit 2005). The aim of the present study was to develop nuclear microsatellite markers for sugar maple to enable future population genetic studies. Here, we report the isolation and characterization of novel microsatellite markers in *A. saccharum* using both cross-species transfer and next-generation sequencing.

3.4. Results & discussion

Total genomic DNA was extracted from dry leaf tissues of sugar maple from different sites in Québec, Canada, using DNeasy Plant Mini Kit (QIAGEN). A set of 9 polymorphic microsatellites has been developed for *Acer yangbiense* (Zhao *et al*. 2011), 8 for *Acer opalus* (Segarra-Moragues *et al*. 2008), 13 for *Acer mono* Maxim. (Kikuchi & Shibata 2008), and 8 for *Acer pseudoplatanus* (Pandey *et al*. 2004). Thirty of these markers were tested with *A. saccharum* and only five were transferable.

One DNA sample of sugar maple was sent to Genoscreen (Lille, France) for the construction of an enriched library. The library was sequenced using pyrosequencing on 454 GS-FLX Titanium (Roche Applied Science) and automated primer pairs were subsequently designed as follows Malausa *et al*. (2011). This provided 103,331 raw reads, 14,718 raw reads with microsatellite motifs, and 9,322 primer pairs, which

flanked 1,269 unique microsatellites. A total of 63 primers pairs were tested. Markers with sequences size that were evenly distributed between 90 and 320 bp, were selected to optimize chances of homogeneously distributed PCR product sizes among the selections that were available for PCR multiplex design. To ensure that we had polymorphic markers, we selected mostly di- and tetra-nucleotide microsatellite motifs and loci with the highest number of repeats (10–25). Since, only few primer pairs were designed for 200–300 bp size products, we downsized our selections to loci with six repeats.

Primer pairs were initially tested for amplification with unlabelled primers on five geographically separated individuals. Amplifications used 10 μL PCRs that contained 1× QIAGEN Multiplex Master Mix, 0.1 μM of each primer, and 2–5 ng of genomic DNA. The thermal profile began with initial denaturation at 95 °C (15 min), followed by 35 cycles of denaturation at 94 °C (1 min), annealing at 54 °C (1 min 30 s) and extension at 72 °C (1 min), and ended with final extension at 72 °C for 45 min. Amplification products were visualized on agarose gel. Twenty-six loci were successfully amplified. They were further tested for polymorphisms using 11 individuals from 7 populations, following the same protocol with labelled primers (Table 3.1). Fragments were separated using an ABI 3730xl Sequencer (Applied Biosystems) at McGill University and Génome Québec Innovation Centre (Montréal, Canada). The resulting microsatellite profiles were examined using GENEMAPPER 3.7 (Applied Biosystems). A total of 23 polymorphic and unambiguous genotype profile markers were then combined into six PCR multiplex sets and two simplex PCR reactions, which were subsequently tested on 28 and 40 individuals from two populations located in western Québec (WQc; 46°45'0.40"N, 78°54'20.16"W) and eastern Québec (EQc; 46°36'34.34"N, 73 2'27.67"W), respectively (Table 3.1).

Table 3.1 Primer sequences and characteristics of 23 microsatellite loci in two populations of *Acer saccharum*.

Locus	Primer sequences (5'-3')	Repeat structure	Size range (bp)	5' dye	M	WQc (n = 28)			EQc (n = 40)			GenBank Accession no.
						N_A	H_O	H_E	N_A	H_O	H_E	
Am096	F: TAAGCTTCATACGCCATCAACCT R: GGCATCACCAAATCCAGACAC	(AG)9	133–152	6-FAM	1	5	0.192‡	0.305	4	0.205*§	0.417	AB303348
Am116	F: AACGCTACCGACTTCGCCAACT R: TGGAGGTCAAGTGCTGGAAACAA	(AG)6	230–273	PET	1	8	0.679	0.644	12	0.744	0.712	AB303350
Am607	F: CACACATGGGCTTCTCTATGAGT R: CATCCGCCAGTTGGTGAAT	(AG)11	133–160	PET	a	9	0.696‡	0.828	12	0.675‡	0.848	AB303355
Aop122	F: TCCCTCGTTAGATTTACGGTGGTTT R: TTCTTGATGACGATGATGACGATG	(TC)12	184–213	6-FAM	a	8	0.227*§	0.645	14	0.436*§	0.844	EF531293
Aop943	F: ACTGTGTAGGAGAGTGAGTGTGAA R: CTTCCCAAAGGTAGGAACCA	(GA)11	143–158	VIC	1	4	0.385	0.456	5	0.641	0.600	EF531298
SM11	F: AAGTTGCAGGAGGAGATTGC R: CACAATAACATGACCTTATGCCA	(CA)17	181–191	NED	4	5	0.667‡	0.622	3	0.575	0.581	KC731552
SM14	F: TTTTATGTAGAGCAACTCAACCCA R: TATCTGCTGCTTGACATGAACTT	(GA)15	72–112	NED	6	14	0.846	0.877	15	0.769	0.886	KC751436
SM21A	F: TAGTTGTGCACCAACCATGC R: TCCATCAAAACGCTGCTATG	(GAT)14	179–243	VIC	6	12	0.889	0.882	15	0.923	0.836	KC751437
SM22	F: CCAGAGCTTGAAGAAAATGTACG R: GGTAAGGGGTTGTTTATGCAAT	(GA)13	295–323	PET	3	14	0.917	0.895	12	0.872	0.888	KC751438
SM26	F: AAATCAAACAATTTCGCGCC R: GATTGATGCAAAGGCAGTGA	(GA)11	277–302	VIC	2	6	0.370*§	0.707	8	0.275*§	0.759	KC751439
SM27	F: TTTCTACTTTAGAGATGGAAACGG R: CCCTAAATCCCAAATCAGTGAA	(TC)10	242–260	PET	6	7	0.760	0.745	6	0.769	0.717	KC751440
SM29	F: TTAAACAAGCTGAACAACCCAA R: TCACACGGAAAGACATCAGC	(CTT)10	281–301	NED	6	6	0.815	0.730	5	0.692	0.667	KC751441
SM34	F: TGTGAAAATTCATAGATTTCTCAGTC R: ATACCACTTCAAAGCAACAAAACA	(GA)14	118–171	6-FAM	4	13	0.926	0.857	16	0.875	0.834	KC751442
SM36	F: GATGCTGATAAAGAAATGGAAACA R: GGCCCTCCCTGTTCTAAAGT	(AG)14	150–176	PET	2	9	0.963	0.814	10	0.950	0.833	KC751443
SM37	F: TGGGAGAAAATTAACATAGGATTT R: AGACTTGACTCTCCTAATCTTGGTG	(AG)14	174–198	NED	3	8	0.731	0.611	9	0.744	0.722	KC751444
SM42	F: ATTGCAGACGCACTCGTAAG R: CAACTCACTTGTGTTGGAATGC	(CT)12	96–128	NED	5	6	0.593	0.761	7	0.650	0.735	KC751445

Table 3.1 (*to continued*)

Locus	Primer sequences (5'-3')	Repeat structure	Size range (bp)	5' dye	M	WQc (n = 28)			EQc (n = 40)			GenBank Accession no.
						N_A	H_O	H_E	N_A	H_O	H_E	
SM47	F: TAAAGAGAAAACCTAGAAATCACTCTG R: CAACCAACTCGCATCAAGAA	(GA)10	201–219	PET	3	6	0.529‡	0.664	6	0.538‡	0.709	KC751446
SM51	F: GCCAAGTAACCACAGGCAAT R: CAAGAACCAGATCACAGATGTC	(TC)9	169–290	NED	5	5	0.481	0.474	6	0.625	0.609	KC751447
SM53	F: TTGGAAAGGATATTTGCATACG R: ATTTTTCTCCGAGCCATTGA	(AG)9	294–301	6-FAM	2	2	0.556	0.497	2	0.600	0.499	KC751448
SM55	F: ATGAGGGAGTAGAGGAGGCG R: TCAACAGATCCAAAACACGC	(TC)8	255–274	6-FAM	3	7	0.769	0.636	11	0.641	0.748	KC751449
SM56	F: GTTGTGGTCGTGAGACTTTAGG R: TAAACCGCTTGAGGACAACTT	(AG)8	287–299	PET	4	6	0.560	0.696	4	0.700	0.648	KC751450
SM57	F: ACTGCCACCAAAAGCAAAAG R: CCAAATCGAACACAAACCCT	(AAG)7	203–218	NED	2	6	0.667	0.663	3	0.425	0.535	KC751451
SM60	F: CTTTAGAGCGGCCCAAGTTA R: GAGGGCCATTTTCAGTTGAG	(AAC)6	231–237	VIC	4	2	0.519	0.494	3	0.575	0.493	KC751452

Repeat structures of Am096, Am116, Am607, Aop122 and Aop943 were obtained from one individual over six sequenced individuals of *Acer saccharum*.

M, letter for simplexes and number for multiplexes; n, number of individuals analyzed; N_A, number of alleles observed; H_O, observed proportion of heterozygous individuals; H_E, expected heterozygosity; PHW, Hardy-Weinberg P-value.

***** Loci significantly deviating from HWE following Bonferroni correction (adjusted critical $P \leq 0.001$)

‡ Loci in HWE following Bonferroni correction

§ Presence of null alleles

The number of alleles per locus (N_A), and observed (H_O) and expected heterozygosities (H_E) were calculated in GENALEX 6.5 (Peakall & Smouse 2006). Deviations from Hardy–Weinberg equilibrium (HWE), linkage disequilibrium (LD) and heterozygote deficiencies were estimated using Genepop v. 4.2 (Rousset 2008). A sequential Bonferroni test for multiple comparisons was used to adjust *P* values to a predetermined experiment-wise error rate of 0.05 (Rice 1989). Null allele frequencies were estimated using FREENA (Chapuis and Estoup 2007).

Mean N_A was 7.7, with a range of 2–16 alleles per locus. Mean H_O and H_E were 0.644 and 0.687, respectively (ranging from 0.192 to 0.963, and from 0.305 to 0.895, respectively). Two of the 23 loci (Aop122 and SM26) in both populations and one locus (Am096) in one population failed to meet HWE (Table 3.1). All deviations from HWE were due to heterozygote deficiencies. Similar results have been previously reported for two loci (Aop122, Am096) in *A. opalus* and *A. mono* (Segarra-Moragues *et al*. 2008; Kikuchi & Shibata 2008). FREENA estimated zero to low (< 10 %) frequencies of null alleles for all of the loci, except Aop122, SM26 and Am096. There was no evidence of linkage disequilibrium between pairs of loci. Finally, 20 highly polymorphic microsatellite markers are now valuable resources for future landscape population genetics studies of *A. saccharum*.

3.5. Acknowledgments

This research was carried out as part of the doctoral research of the first author, with support from an NSERC (Natural Sciences and Engineering Research Council of Canada) strategic grant (STPGP 336871) to Francine Tremblay. We would like to thank Stephanie Ferreira, Stéphanie Duthoy and all team at GenoScreen, France (www.genoscreen.fr), and Valérie Catudal and Alexandre Belisle from Génome Québec (gqinnovationcenter.com) for their work. We are grateful to William F.J.

Parsons from the Centre for Forest Research (www.cef-cfr.ca) for careful language editing.

CHAPITRE IV

GENETIC DIVERSITY AND STRUCTURE AT THE NORTHERN LIMIT OF A WIDESPREAD NORTH-AMERICAN TREE, SUGAR MAPLE (*ACER SACCHARUM* MARSHALL)

Noémie Graignic, Francine Tremblay et Yves Bergeron

4.1. Résumé

Les modèles prédisent une expansion de nombreuses espèces d'arbres nord-américains au nord de leur limite actuelle de répartition avec l'influence des changements climatiques. L'érable à sucre (*Acer saccharum* Marshall) atteint sa limite de répartition continue nordique dans le nord-est de l'Amérique du Nord, à la transition entre la forêt boréale mixte et la forêt feuillue tempérée. Notre travail s'articule autour de l'hypothèse que les populations nordiques fragmentées et marginales de la zone discontinue de répartition ont un patron distinct de structure et de diversité génétique. Nous avons analysé 18 marqueurs microsatellites dans 23 populations réparties le long de trois transects latitudinaux (situés à l'ouest, le centre et l'est du Québec). Chaque transect a été divisé en deux zones, continue et discontinue, sur la base de l'abondance des populations d'érable à sucre. Dans l'ensemble du Québec, la diversité génétique de cette espèce est élevée. Les populations d'érable à sucre situées dans la zone discontinue (nord) ont montré une plus faible diversité génétique comparativement aux populations de la zone continue (sud) - notamment pour les populations du transect ouest. L'analyse de la structure génétique révèle un patron défini avec un groupe au nord formé des populations d'érable à sucre les plus nordiques (1-D-A, 1-D-B, 2-D-A et 3-D-A). Nous avons observé un flux génétique asymétrique entre les populations, avec les populations du nord qui reçoivent un flux génétique plus élevé en provenance des populations du sud. Les populations du sud du Québec semblent provenir de deux voies de migration distinctes ; la première venant de l'est et la seconde, plus tardive, venant de l'ouest. Les populations du nord-ouest ont montré une diversité génétique réduite et une différenciation entre les populations plus élevée. Nous avons par ailleurs observé une baisse de recrutement dans ces mêmes populations lors d'une précédente étude. Nous en arrivons à la conclusion que les populations d'érable à sucre du nord-ouest du Québec pourraient être plus à risque dans un contexte de changements climatiques.

4.2. Abstract

Due to climate change, the ranges of many North-American tree species are expected to shift northward. Sugar maple (*Acer saccharum* Marshall) reaches its northern continuous distributional limit in north-eastern North America at the transition between boreal mixed-wood and temperate deciduous forest. We hypothesized that marginal fragmented populations from the discontinuous zone (northern populations) would have a distinct pattern of genetic structure and diversity. We analyzed 18 microsatellite loci variation in 23 sites distributed along three latitudinal transects (located in the west, centre and east of Québec). Each transect was divided into two zones, continuous and discontinuous, based on sugar maple stand abundance. Sugar maples showed a high level of genetic diversity in Québec, and a lower diversity in populations from the discontinuous zone (north) compared to those from continuous zone (south) - especially in populations in the western transect. North-western populations showed lower genetic diversity and higher population differentiation. These populations may be more at risk in a context of climate changes. The STRUCTURE analysis revealed the presence of 4 clusters with the presence of a high level of admixture. The four most northerly populations received a higher level of gene flow from the southern populations. Southern populations in Québec may have originated from two migration routes (from eastern first and then later from western routes). We concluded that north-western sugar maple populations in Québec need to be protected, due to there lower level of genetic diversity.

4.3. Introduction

The Last Glacial Maximum (LGM) occurred approximately 21 000 years before present (-yr BP) and was the coldest period in recent climatic history (Jackson *et al.*, 2000). At that time, North American species were located south of the Laurentian Ice Sheet. After the ice retreated, postglacial vegetation ranges expanded and contracted repeatedly following climatic oscillations (McLachlan *et al.*, 2005). Given anticipated climate changes, we foresee the northern range expansion of several species (Iverson *et al.*, 2008).

This shift in range could be particularly marked in peripheral populations located along their distribution edge (Iverson *et al.*, 2004). Generally isolated and smaller in size (effective population sizes) than core populations (Vucetich & Waite, 2003), these peripheral populations are expected to have a lower level of genetic diversity and a higher level of genetic differentiation among populations following genetic drift or bottlenecks (Eckert *et al.*, 2008; Waters *et al.*, 2013). In theory, bottlenecked populations are expected to experience a reduction of allelic richness and a limited decrease in heterozygosity. The consequence of this drift would be a reduction in the number of rare alleles (Nei *et al.*, 1975). The central–marginal hypothesis expected that those patterns of diversity structure were link to the ecological marginality of the populations found at the periphery of the species distribution compared to core populations (Eckert *et al.*, 2008). Whereas, "range shift following the last glacial maximum" hypothesis according more link to the influences of the migration during the last glacial maximum (Hampe & Petit, 2005). This range–shift hypothesis expected a lower within population diversity in peripheral populations located along the colonizing front (leading edge) and the low-latitude limit (rear edge) of the species' range, and contrary to the central–marginal hypothesis, a higher regional diversity at rear edge compare to core and leading edge (Hampe & Petit, 2005).

In the Northern Hemisphere, northern peripheral populations often exhibit local adaptations to cold stress (cold hardiness and earlier bud set in fall), and can potentially be maladapted to climate warming. Lower chilling requirements can result in early bud flush in spring under milder environments and higher susceptibility to spring frost damages (Howe *et al.*, 2003). On the other hand, climate warming could also improve their survival and increase the success of sexual reproduction (Alberto *et al.*, 2013). Wind-pollinated tree species may also be buffered against the effect of fragmentation on the genetic structure of peripheral populations due to long-distance gene flow that contributes to a decrease in differentiation among populations (Kremer *et al.*, 2012).

Sugar maple (*Acer saccharum* Marshall) is a widespread, abundant and long-lived (300–400-yr) deciduous north-eastern American tree (Godman *et al.*, 1990). This species is a monoecious, dichogamous, wind-pollinated and shade-tolerant broadleaf tree (Logan, 1965; Gabriel, 1968; Gabriel & Garrett, 1984) that forms uneven-aged stands (Majcen *et al.* 1984). It has major economic value for saw timber and syrup production in Canada and the United States (Godman *et al.*, 1990). Sugar maple reaches its northern range at the transition between the temperate deciduous and boreal mixed-wood forests (Saucier *et al.*, 2003). Stands present in the boreal mixed-wood forest may possibly be remnants of formerly larger populations. Palynological reconstruction supports the idea that many species had migrated farther north of their current range after the retreat of ice sheet (Liu, 1990; Richard, 1993). Richard & Grondin, (2009) reported the establishment of disjointed sugar maple stands around 8500-yr BP in northern Québec. The decline of several tree species in the coniferous forest was concurrent with a climatic shift observed at the beginning of the Neoglacial period. This period was characterized by cooler and drier summers and an increase in fire frequency around 3000-yr BP (Carcaillet & Richard, 2000; Ali *et al.*, 2008). Like many other tree species in the Northern Hemisphere, sugar maple is

predicted to migrate north of its current range (Goldblum & Rigg, 2005; Iverson *et al.*, 2008).

Earlier studies of sugar maple genetic variation were conducted with provenance tests. These studies revealed clinal variations in response to temperature and moisture stresses (Kriebel, 1957). Sugar maple provenances also showed an adaptation to altitudinal gradients for respiration, photosynthesis and specific leaf weight (Ledig & Korbobo, 1983). Analysis of neutral markers (allozymes and RAPD) revealed weak or no genetic differentiation among sugar maple populations in Canada (Perry & Knowles, 1989; Young *et al.*, 1993b) and across its range (Gunter *et al.*, 2000). On a regional scale (20 km in southern Québec), Young *et al.* (1993b) reported the presence of moderate levels of genetic structure among populations, while Diochon *et al.* (2003) found no structure among two populations (distance of 45 km in Ontario, Canada). No relationship between genetic and geographic distances was found between five northern populations (Perry & Knowles, 1989).

In this work, highly polymorphic microsatellite makers recently developed for sugar maple (Graignic *et al.*, 2013) were used to study the genetic diversity and structure of 24 sugar maple populations. Sugar maple populations were selected along three transects (west, central and east) that encompass the continuous-discontinuous species' range at the transition between the temperate deciduous and boreal mixed-wood forests in Québec. We hypothesized that marginal fragmented populations from the discontinuous zone (northern populations) would have; (1) a lower level of genetic diversity and higher genetic structure than populations from the continuous zone (southern populations), (2) the northernmost peripheral populations would have a lower number of rare alleles, and we predicted (3) a higher correlation between genetic and geographic distances in marginal populations. Two cohorts of mature trees ($\geq$ 10 cm d.b.h.) and saplings (1 $\leq$ d.b.h. $<$ 10 cm), were sampled because temporal variations in genetic differentiation may be present between different

cohorts of regeneration (Mulcahy, 1975; Foré *et al*., 1992). We tested the hypothesis that (4) mature trees would be more diverse than saplings; particularly for populations sampled in the discontinuous zone. Sugar maple is wind-pollinated and earlier studies reported a low level of genetic structure between populations, therefore we expected to find (5) high gene flow between populations and a weak signal of migration routes in Québec.

4.4. Materials and methods

4.4.1. Study area and sampling

The study area was located at the northern range limit of sugar maple in Québec (eastern Canada; Fig. 4.1). The climatic gradient was divided into two zones based on the proportion of sugar maple stands in the continuous and discontinuous zones. The presence of sugar maple stands along the latitudinal gradient was estimated from an analysis of large inventory databases (for more details see Graignic *et al.*, 2014). The continuous zone lies within the sugar maple–yellow birch (*A. saccharum–Betula alleghaniensis* Britton) bioclimatic domain where sugar maple is abundant. The discontinuous zone was in the balsam fir–yellow birch (*Abies balsamea* (L.) Miller–*B. alleghaniensis*) bioclimatic domain and some northern sites were located in the transitional area of the balsam fir–white birch (*A. balsamea–Betula papyrifera* Marshall) bioclimatic domain (Saucier *et al.*, 2003).

Sites were distributed along three north–south transects (1, western; 2, center; 3, eastern) with eight sites per transect (four sites per transect per zone) (Fig. 4.1). Eleven of the sites selected were old-growth or rare forests that are classified as Exceptional Forest Ecosystems (EFE) by the ministère des Ressources naturelles du Québec (MRNQ, Québec Ministry of Natural Resources). All the sites were old-growth, uneven-aged stands, selected to be as similar as possible (for more details see Graignic *et al.*, 2014). Data were collected at 24 sites located between 45°51'N and

48°59' N latitude, and 70°21'W and 79°27' W longitude, at elevations ranging between 157 m and 493 m a.s.l.

Tissue samples (usually leaves or bark) were collected from 953 individual sugar maples in 2008 and 2009. Two cohorts were sampled per site: mature trees (≥ 10 cm d.b.h.; *N*=12–22) and saplings (1 ≤ d.b.h. < 10 cm; *N*=20). Samples were frozen (-80° C) or dried (using silica-gel) until needed for genetic analyses.

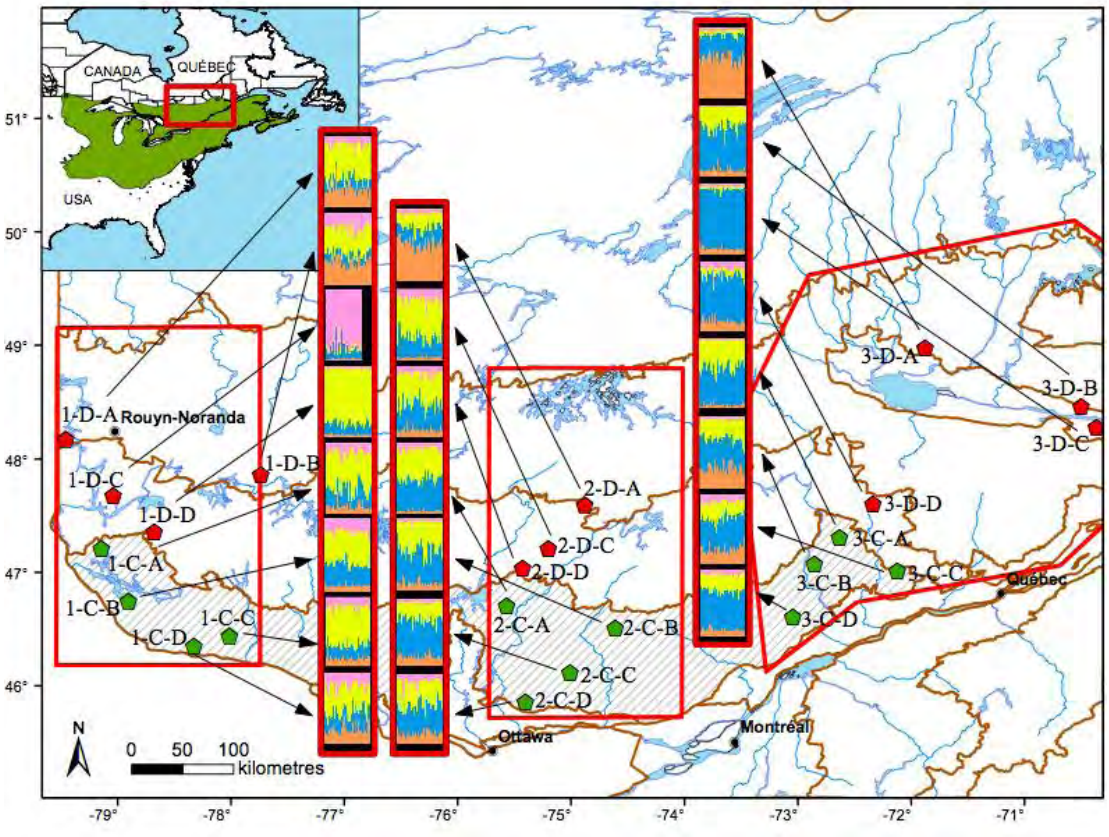

Figure 4.1 Map of the study area at the northern limit of sugar maple (*Acer saccharum* Marsh.) distribution in Québec showing the three transects (red lines), locations of the 23 study sites (2-D-B was remove) that show genetic results (red polygons, sites in discontinuous zone, and green polygons, sites in continuous zone; see Graignic *et al*. (2014) for more details on site characteristics), sugar maple–yellow birch (*Betula alleghaniensis*) bioclimatic domain (gray hatch), boundary of all bioclimatic domain limits (thin brown lines) (Saucier *et al.* 2003), and proportional membership of each sugar maple sample in clusters for five genetic groups (*K* = 4) inferred by STUCTURE analysis. For structure results, each individual was represented as a vertical line segment, and bottom-to-top clusters were: cluster 1, orange; cluster 2, blue; cluster 3, yellow and cluster 4, pink respectively.

4.4.2. Molecular methods

DNA was extracted using Extract-N-Amp™ Plant PCR Kits (Sigma-Aldrich, Oakville, Ontario, Canada). All samples were genotyped for 18 variable microsatellite loci using PCR and genotyping protocols as previously described by Graignic *et al.* (2013) with the following modifications. Five different multiplex PCR sets and 37 cycles in the PCR amplification were used (see Table A4.1).

4.4.3. Markers genetic diversity

The 2-D-B population, Lac aux Cèdres, had to be removed from the analysis due the low number of successful amplifications likely caused by poor sample conservation. Accordingly, a total of 913 individuals were selected for the subsequent analysis. For each locus, the total number of alleles (A_T), mean number of alleles (A), mean observed (H_O) and expected (H_E) heterozygosity, and inbreeding coefficient (F_{IS}) were estimated using FSTAT 2.9.3.2 (Goudet, 2001). Departure from Hardy–Weinberg equilibrium (HWE) per locus in each population, and linkage equilibrium between all pairs of loci in each population were calculated using an exact test implemented in GENEPOP 4.2.1 (Rousset, 2008). Markov chain parameters for HWE were 10 000 dememorizations, followed by 500 batches of 5000 iterations per batch. We corrected for multiple comparisons using a sequential Bonferroni adjustment of *P*-values to a predetermined experiment-wise error rate of 0.05 (Rice, 1989). Null allele frequencies were estimated using FREENA (10 000 replicates; Chapuis & Estoup, 2007). This software was chosen because it uses the Dempster *et al.* (1977) algorithm which provided the most accurate estimate of several algorithms tested in Chapuis & Estoup (2007). When populations are significantly differentiated the presence of null alleles overestimated fixation index (F_{ST}) and genetic distances (Chapuis & Estoup, 2007). We performed a Mantel test (1000 permutations; using the *mantel* function in the VEGAN library from the software R 2.13.1; Oksanen *et al.*,

2011; R Development Core Team, 2011) between pairwise F_{ST} values with and without correction for null alleles calculated with FREENA.

4.4.4. Genetic diversity and differentiation between populations and groups

The mean number of alleles per locus (A), mean allelic richness (A_R), mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), pairwise F_{ST}, mean pairwise F_{ST} and inbreeding coefficient (F_{IS}) were estimated using FSTAT. The indices were estimated for each population and on mature trees and saplings for each population separately. To assess whether population diversity parameters differed between zones and transects, A_R, H_O, H_E, F_{ST} and F_{IS} were calculated by population (all individuals pooled, mature trees and saplings) within each zone (discontinuous and continuous), transects (1, 2 and 3) and zone in each transect separately using FSTAT (tested for significance using 1000 permutations).

4.4.5. Quantitative relationship

Data were analysed using version 2.13.1 of R package statistical software (R Development Core Team, 2011). Genetic indices *(*A_R, H_O, H_E and F_{IS}) were compared using a linear mixed-model analysis (LMM, using the *lme* function in the NLME library; Pinheiro *et al.*, 2011), and a linear model for F_{ST}. Random effect included microsatellite marker for LMM. Different models were run to test the effects of: (1) stand characteristics such as basal area of mature sugar maple or/and sugar maple sapling (m^2 ha^{-1}), density of mature sugar maple or/and sugar maple sapling (stems ha^{-1}), population size of mature sugar maple or/and sugar maple sapling (stems), (2) distance of each population to the northern limit (km) (see below), and (3) global models with a combination of one model of stand characteristics and its distance from the northern limit. Basal area and density were calculated in a quadrat of 0.16 ha at each site (see Graignic *et al.*, 2014). The population size of sugar maple was calculated separately for mature tree and sapling using their densities within the

quadrat and stand surface areas. For stand surface areas, we used data from EFE and ecoforestry maps that were obtained from MRNQ (MRNQ, 2013a, b). We fixed the northern limit between balsam fir–white birch (*A. balsamea–B. papyrifera*) and balsam fir–yellow birch (*A. balsamea–B. alleghaniensis*) bioclimatic domains and the distance of each sampled population to this limit was estimated with ARCMAP™ 10.0 (Environmental Systems Research Institute (Esri), Toronto, Ontario, Canada); negative values were assigned to sites located to the north of the northern limit, i.e. in the balsam fir–white birch (*A. balsamea–B. papyrifera*) bioclimatic domain. Correlations between variables were examined, and assumptions of normality and homoscedasticity were graphically tested on global models. Where needed, the data were squared-root transformed to fit the assumptions. Fits for the 19 models were compared using the Akaike information criterion (AIC; *aictab* in the AIC_CMODAVG library; Mazerolle, 2011), corrected for small sample sizes (AIC_C). We computed AIC_C and ΔAIC_C weights (ω) to determine the strength of evidence for each model (Burnham & Anderson, 2004). We then performed multimodal inference (*modavg* function in AIC_CMODAVG library), where required ($\Delta AIC_C \leq 4$), to calculate the parameter estimates and unconditional 95% confidence intervals (CI).

4.4.6. Correlation with sample size

Spearman's rank correlation coefficients were calculated between the sample size of each population and H_O, H_E, F_{IS} and F_{ST} using the *rcorr* function in the HMISC library from R (Harrell, 2013). As A_R was calculated using rarefaction method, a method that standardizes *A* on the basis of the size of the smallest number of samples, this parameter was already adjusted for sample size.

4.4.7. Proportions of rare alleles

We classified alleles, for each population with all individuals, on the basis of frequency (both common and rare, with two rare allele frequencies (*f*) < 0.05 and

0.02) and distribution (widespread and localized; with localized restricted to < 25% of the number of population that fixed localized at 5 populations and widespread at ≥ 6). This classification was based on Marshall & Brown (1975). Eight classes of alleles emerged from this classification and we considered four additional classes with private alleles (restricted to a single population). The same classification was used for each population for each cohort separately, except that only $f < 0.05$ was used because the lower allele frequency ($f < 0.02$) did not occur. Variation in the percentage of allele in the rare and private ($f < 0.02$; RP2), common and localized ($f \geq 0.05$; CL5) categories was compared in the R software using two-way analysis of variance (ANOVA) with zone, transect and their interaction considered as fixed effects and a three-way ANOVA with zone, transect, cohort and their interaction considered as fixed effects respectively. The assumption of normality and homoscedasticity was verified graphically; CL5 data was log-transformed. Global models were simplified by stepwise backward elimination of non-significant fixed-effect terms to produce the most parsimonious models.

4.4.8. Bottleneck tests

Evidence of bottlenecks in each population was evaluated using three tests: heterozygote excess, allele frequency mode shift and *M*-ratio. For the first test, heterozygote excess, we used BOTTLENECK 1.2.02 (Cornuet & Luikart, 1996) and each population was tested for three different mutation models: infinite allele mutation (IAM), stepwise-mutation model (SMM) and two-phase mutational model (TPM). In TPM, we choose 70, 90, 95 and 99% SMM, and we assumed a 12% variance in multi-step mutations (Piry *et al.*, 1999). The significance of the test under all models was performed using one-tailed Wilcoxon sign-rank test with 1000 permutations. The second approach, the allele frequency mode shift, was also conducted in each population using BOTTLENECK. The principle being that, under recent bottlenecks, rare alleles may occurred at low frequencies leading to a mode-

shift distortion of the typical L-shaped allele frequency distribution (Luikart & Cornuet, 1998).

We also calculated the *M*-ratio, the mean ratio of the number of alleles (k) to the range in allele size (r), using M_P_VAL software (Garza & Williamson, 2001). This method assumes that rare alleles are lost faster during a bottleneck, reducing the number of observed allelic states (k) faster than the size range of those alleles (r) resulting in a reduced *M*-ratio ($M = k/r$). To determine the significance of a ratio we compared our observed value to critical values (M_c) that were established using the CRITICAL_M program. When the observed *M*-value was significantly ($P < 0.05$) below M_c we assumed that a population had experienced a significant reduction in size (Garza & Williamson, 2001). To calculate M_c and *P*-values we used three different θ values ($\theta = 4N_e\mu = 1$, 5 and 10; N_e, the effective population size; the mutation rate, μ) and the parameters were set as recommended by Garza & Williamson (2001) ($\mu = 5.0 \times 10^{-4}$ mutants/generation/locus; probability of changes greater than one step, $p_g = 0.10$; the size of non-one-step changes, $\Delta_g = 3.5$). Each set of simulations consisted of 10 000 iterations.

4.4.9. Isolation by distance

Isolation by distance was investigated using a Mantel test (1000 permutations; Pearson's correlation; using the *mantel* function in the VEGAN library from R) between the genetic [$F_{ST}/(1-F_{ST})$] or [$D_S/(1-D_S)$] and geographic distances (km). Pairwise F_{ST} and D_S (Nei, 1972) were calculated respectively using FSTAT and POPULATIONS 1.2.32 (Langella, 1999). Geographic distances were estimated using the *earth.dist* function in the FOSSIL library from R (Vavrek, 2012). We performed isolation by distance analysis for all populations, populations for each zone and each transect separately.

4.4.10. Genetic structure

Neighbor-joining trees were constructed based on D_S and using 1000 bootstraps over loci in POPULATIONS, one tree for all populations and one tree using cohort separate populations in two parts. The tree was visualized using TREEVIEW (Page, 1996).

We used the Bayesian clustering method implemented in STRUCTURE 2.3.4 (Pritchard *et al.*, 2000) to assess the number of populations (*K*), assign individuals to each *K* cluster, detect the population structure and show whether geographic populations are assigned in genetic populations. Our analyses were based on an admixture ancestral model with correlated allele frequencies and a priori sampling locations was used as prior information (LOCPRIOR setting). LOCPRIOR was used to detect any further structures unidentified by standard settings (Hubisz *et al.*, 2009). Twenty independent runs were performed for each value of *K* (1–26) with a burn-in of 100 000 following by 200 000 MCMC iterations. The most likely value of K was determined using the ΔK criterion (Evanno *et al.*, 2005). STRUCTURE HARVESTER version 0.6.93 was used to extract the results and created a graphic of the ΔK criterion (Earl & Vonholdt, 2012). The results were visualized for the best *K*, with DISTRUCT version 1.1. (Rosenberg, 2004).

Genetic variation was examined using the hierarchical analysis of molecular variance (AMOVA) based on Φ_{PT} statistic and conducted in GENALEX 6.5b3 (Peakall & Smouse, 2006). We examined the significant difference (9999 permutations) between transects (1, 2 and 3), between populations within transect and within populations, and between zones (C and D), between populations within zone and within populations for all populations and for each transect separately. We also examined the significant difference between groups, between populations within the group and within populations for grouping A and B. Grouping A included group 1 (1-D-A, 1-D-B, 2-D-A, 3-D-A), group 2 (1-D-D, 1-C-A, 1-C-B, 1-C-C, 1-C-D), group 3

(2-D-C, 2-D-D, 2-C-A, 2-C-B, 2-C-C, 2-C-D), group 4 (3-D-B, 3-D-C, 3-D-D, 3-C-A, 3-C-B, 3-C-C, 3-C-D) and group 5 (1-D-C). We took into account the four clusters identified by STRUCTURE to create the grouping A (see Results and Fig. 4.1). To simplify grouping A, grouping B was created with removing group 5 and we have included the population 1-D-C in group 2.

4.4.11. Gene flow and population sizes

We used the Bayesian approach implemented in MIGRATE-N version 3.6 (Beerli & Felsenstein, 2001; Beerli, 2006) to assess the direction and amount of gene flow among populations. We used this software to calculate the posterior probability distribution of the mutation-scaled effective population size ($\theta = 4N_e\mu$, where N_e = effective population size and μ = mutation rate per generation per locus) and the mutation-scaled past immigration rates ($M = m/\mu$, where m = migration rate) using a Metropolis–Hastings algorithm to explore all possible genealogies. The mutation-scaled population size (θ) for each population and the mutation-scaled immigration rates (M) between each pair of populations were estimated using the Brownian motion mutation model for microsatellites. A coalescent simulation explored the likelihood space for θ and M. To limit the number of parameters, the amount of gene flow was estimated between four populations: from the transect 1 (1-D-C, 1-D-D, 1-C-A, 1-C-B, 1-C-C, 1-C-D), 2 (2-D-C, 2-D-D, 2-C-A, 2-C-B, 2-C-C, 2-C-D), 3 (3-D-B, 3-D-C, 3-D-D, 3-C-A, 3-C-B, 3-C-C, 3-C-D) and the most northern populations (1-D-A, 1-D-B, 2-D-A, 3-D-A). The starting values of θ and M were generated from the F_{ST} estimates, as well as an exponential window prior set for both parameters (min = 0, mean = 5, max = 50 and $\Delta = 5$ for θ; min = 0, mean = 5, max = 50 and $\Delta = 5$ for M). We replicated two long chains of 10 000 000 genealogies recorded every 10 steps after a burn-in period of 10 000. The static heating scheme was set to 4 chains with temperatures of 100 000.0, 3.0, 1.5, and 1.0 and the swapping interval set at one. The program was run several times adding more sampling schemes and replications.

The starting parameters and the resulting estimates were compared until the results were congruent.

4.5. Results

4.5.1. Nuclear microsatellite diversity statistics

The total and mean number of alleles per locus ranged between 4 (SM60) and 31 (SM21A) and from 2.8 (SM60) to 14.8 (SM21A), respectively (Table A4.1). Significant departure from HWE was observed in 37 (9%) of the 414 possible population-locus combinations (Table A4.2). Four of the 18 loci (SM22, SM27, SM47 and SM56) failed to meet HWE in ≥ 6 (26%) populations. For those loci, deviations from HWE were due to heterozygote deficiencies ($F_{IS} \geq 0.227$; Table A4.1). Significant linkage disequilibrium between pairs of loci (within populations) was detected only in one out of 3519 tests after Bonferroni correction (SM14 × SM34 in population 3-C-A, Lac Paul). The loci were therefore all considered genetically independent. Markers that showed a departure from HWE, also had high frequencies of null alleles (≥ 0.10) in most populations (Table A4.3). Pairwise F_{ST} estimates obtained before and after corrections for null alleles were similar ($r = 0.98$, $P < 0.001$). In consequence, all loci (18) were retained in the analysis.

4.5.2. Genetic diversity and differentiation

Population 1-D-C (Rémigny) from the discontinuous zone of transect 1 had the lowest mean number of alleles per locus (A), mean allelic richness (A_R), mean expected heterozygosity (H_E) and inbreeding coefficient (F_{IS}) for all individuals and both cohorts (mature trees and saplings) (Table 4.1). This population had the highest pairwise and global population differentiation (F_{ST}) for saplings, mature trees and all individuals pooled (Table 4.1, A4.4). Pairwise F_{ST} were significant between 176, 73 and 51 pairs on 253 for the individuals pooled, saplings and matures trees, respectively after adjustment for multiple comparisons (Table A4.4).

Table 4.1 Genetic variability estimates of sugar maple (*Acer saccharum*) populations in Québec for mature trees, saplings or all individuals. IP, all individuals pooled; M, mature trees; Sa, saplings; N, sample size; A, mean number of alleles; A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient; F_{ST}, mean pairwise F_{ST}. Mean was determined using AI except for A_R^*.

Population	Cohort	N	A	A_R	A_R^*	H_O	H_E	F_{IS}	F_{ST}
1-D-A	IP	40	7.8	6.6	—	0.532	0.684	0.222	0.020
	M	20	6.2	5.1	4.9	0.566	0.668	0.152	0.019
	Sa	20	6.8	5.3	5.3	0.500	0.702	0.287	0.020
1-D-B	IP	40	8.1	7.0	—	0.590	0.693	0.149	0.015
	M	20	6.9	5.6	5.4	0.595	0.699	0.150	0.013
	Sa	20	6.9	5.4	5.4	0.587	0.690	0.150	0.016
1-D-C	IP	32	6.6	5.8	—	0.670	0.637	-0.051	0.041
	M	12	4.6	4.4	4.3	0.668	0.612	-0.090	0.051
	Sa	20	5.7	4.5	4.5	0.671	0.644	-0.042	0.039
1-D-D	IP	40	7.9	6.9	—	0.608	0.700	0.131	0.017
	M	20	6.8	5.4	5.2	0.591	0.700	0.156	0.020
	Sa	20	6.6	5.2	5.2	0.625	0.693	0.099	0.020
1-C-A	IP	40	8.7	7.5	—	0.620	0.704	0.120	0.011
	M	20	6.9	5.8	5.6	0.638	0.702	0.092	0.011
	Sa	20	7.3	5.5	5.5	0.604	0.709	0.147	0.009
1-C-B	IP	39	8.0	7.2	—	0.697	0.702	0.007	0.013
	M	19	6.8	5.8	5.6	0.705	0.689	-0.023	0.016
	Sa	20	7.1	5.5	5.5	0.687	0.707	0.029	0.012
1-C-C	IP	40	8.6	7.4	—	0.664	0.698	0.049	0.018
	M	20	7.2	5.7	5.5	0.648	0.679	0.045	0.022
	Sa	20	6.9	5.5	5.5	0.679	0.714	0.050	0.017
1-C-D	IP	40	8.5	7.3	—	0.546	0.696	0.216	0.011
	M	20	6.6	5.8	5.5	0.547	0.715	0.207	0.011
	Sa	20	7.2	5.4	5.4	0.535	0.686	0.220	0.009
2-D-A	IP	40	8.1	7.1	—	0.623	0.709	0.121	0.019
	M	20	6.8	5.5	5.3	0.617	0.700	0.119	0.025
	Sa	20	6.8	5.5	5.5	0.630	0.713	0.117	0.018
2-D-C	IP	40	8.5	7.4	—	0.548	0.715	0.234	0.014
	M	20	7.6	6.2	5.9	0.577	0.726	0.205	0.005
	Sa	20	6.4	5.3	5.3	0.520	0.706	0.264	0.022
2-D-D	IP	40	8.6	7.5	—	0.516	0.684	0.246	0.011
	M	20	7.0	5.8	5.6	0.493	0.683	0.279	0.008
	Sa	20	7.1	5.5	5.5	0.539	0.693	0.223	0.008
2-C-A	IP	40	8.2	7.1	—	0.596	0.684	0.129	0.012
	M	20	6.9	5.5	5.3	0.614	0.655	0.062	0.017
	Sa	20	6.8	5.3	5.3	0.579	0.705	0.180	0.010
2-C-B	IP	40	8.6	7.3	—	0.505	0.698	0.276	0.012
	M	20	6.9	5.7	5.4	0.495	0.692	0.284	0.009
	Sa	20	7.0	5.4	5.4	0.519	0.707	0.266	0.013
2-C-C	IP	42	8.6	7.2	—	0.589	0.691	0.147	0.010
	M	22	7.6	5.8	5.5	0.629	0.695	0.095	0.009
	Sa	20	6.7	5.2	5.2	0.544	0.688	0.209	0.012

Table 4.1 (*to continued*)

Population	Cohort	N	A	A_R	A_R^*	H_O	H_E	F_{IS}	F_{ST}
2-C-D	IP	40	8.6	7.2	—	0.569	0.687	0.172	0.009
	M	20	6.9	5.6	5.3	0.617	0.696	0.114	0.009
	Sa	20	6.9	5.4	5.4	0.520	0.676	0.230	0.011
3-D-A	IP	40	8.0	7.0	—	0.496	0.710	0.302	0.021
	M	20	7.0	5.8	5.6	0.478	0.718	0.335	0.022
	Sa	20	6.2	5.0	5.0	0.514	0.706	0.272	0.018
3-D-B	IP	40	7.8	7.0	—	0.681	0.687	0.008	0.017
	M	20	6.9	5.7	5.5	0.696	0.687	-0.012	0.015
	Sa	20	6.9	5.5	5.5	0.667	0.690	0.034	0.018
3-D-C	IP	40	7.4	6.3	—	0.639	0.661	0.033	0.026
	M	20	6.4	5.2	5.0	0.630	0.659	0.045	0.020
	Sa	20	6.2	5.0	5.0	0.649	0.667	0.027	0.027
3-D-D	IP	40	8.3	6.5	—	0.656	0.694	0.054	0.019
	M	20	6.5	5.5	5.3	0.681	0.705	0.035	0.017
	Sa	20	6.2	5.1	5.1	0.613	0.681	0.074	0.021
3-C-A	IP	40	8.4	7.1	—	0.548	0.699	0.215	0.019
	M	20	6.9	5.7	5.4	0.574	0.701	0.181	0.016
	Sa	20	6.6	5.2	5.2	0.524	0.701	0.252	0.017
3-C-B	IP	40	9.0	7.6	—	0.618	0.700	0.117	0.011
	M	20	7.6	6.0	5.8	0.651	0.715	0.090	0.011
	Sa	20	6.9	5.3	5.3	0.585	0.681	0.140	0.014
3-C-C	IP	40	8.0	6.9	—	0.499	0.691	0.278	0.012
	M	20	6.8	5.6	5.4	0.479	0.691	0.307	0.008
	Sa	20	6.4	5.1	5.1	0.515	0.694	0.258	0.014
3-C-D	IP	40	8.2	7.0	—	0.716	0.715	-0.000	0.012
	M	20	6.9	5.6	5.4	0.740	0.720	-0.027	0.011
	Sa	20	6.9	5.4	5.4	0.691	0.713	0.031	0.011
Mean		40	8.2	7.0	5.3	0.597	0.693	0.138	0.016

Mean A_R was significantly lower in populations from the discontinuous vs. the continuous zone (6.8 vs. 7.2; Table 4.2). This difference in mean A_R among zones was significant only in transect 1 (Table 4.2) for the individuals pooled (6.6 vs. 7.3), mature trees (5.1 vs. 5.8) and saplings (5.1 vs. 5.5). The mean F_{ST} was higher in populations from the discontinuous vs. the continuous zone (0.025 vs. 0.009) and in transect 1 (0.030 vs. 0.004) but not transects 2 and 3 (Table 4.2). Population differentiation (F_{ST}) was different both for mature trees (0.034 vs. 0.007) and saplings (0.029 vs. 0.003) in transect 1 (Table 4.2). No significant differences for A_R and F_{ST}, were found between transects (Table 4.2), between zones for transect 2 and 3 (Table

4.2) and between cohorts (matures trees and saplings; Table A4.5), or for all other genetic parameters.

4.5.3. Quantitative relationship

There were 10, 7, 19, 11 and 10 best models ($\Delta AIC_C \leq 4.0$; Table A4.6) for A_R, H_O, H_E, F_{IS} and F_{ST} respectively. Parameter estimates derived from multi-model inference showed no influence on H_E and F_{IS} for all variables tested (Table 4.3). A positive and negative relationship was found between the distance of each site to the northern limit (D_north), and A_R and F_{ST}, respectively. A positive relationship between mature sugar maple basal area and H_O was also observed (Table 4.3, Fig. 4.2).

4.5.4. Correlation with sample size

No significant correlations were found between sample size for each population and H_E (r = 0.03; P = 0.502) or F_{ST} (r = -0.38; P = 0.078). Significant correlations were observed between sample sizes for each population and H_O (r = -0.11; P = 0.021), and F_{IS} (r = 0.23; P = 0.000).

Table 4.2 Comparison of mean genetic variability estimates between populations of zones, transects and zones in each transect of sugar maple (*Acer saccharum*) in Québec for mature trees, saplings and all individuals.

Cohort	Genetic Indice	Zone			Transect				1 Zone			2 Zone			3 Zone		
		D	C	*P*-value	1	2	3	*P*-value	D	C	*P*-value	D	C	*P*-value	D	C	*P*-value
IP	A_R	6.840	7.246	**0.0080**	6.970	7.272	6.941	0.2450	6.601	7.339	**0.0100**	7.338	7.222	0.7380	6.707	7.176	0.0880
	H_O	0.600	0.600	0.9950	0.616	0.567	0.611	0.2610	0.597	0.634	0.4460	0.566	0.567	0.9870	0.623	0.599	0.5800
	H_E	0.689	0.698	0.2110	0.691	0.695	0.694	0.8610	0.680	0.701	0.0780	0.703	0.690	0.2630	0.687	0.701	0.1960
	F_{IS}	0.129	0.140	0.7730	0.108	0.184	0.120	0.2520	0.122	0.095	0.6760	0.194	0.178	0.8380	0.093	0.146	0.4230
	F_{ST}	0.025	0.009	**0.0010**	0.017	0.009	0.016	0.4630	0.030	0.004	**0.0050**	0.014	0.005	0.3910	0.022	0.011	0.2490
M	A_R	5.464	5.707	0.1000	5.458	5.708	5.621	0.4100	5.138	5.779	**0.0060**	5.816	5.626	0.4660	5.526	5.716	0.4430
	H_O	0.603	0.616	0.6670	0.620	0.583	0.622	0.4900	0.599	0.641	0.4030	0.568	0.593	0.6630	0.627	0.616	0.8430
	H_E	0.698	0.697	0.4020	0.687	0.693	0.699	0.4730	0.676	0.696	0.1990	0.703	0.686	0.3010	0.692	0.707	0.2940
	F_{IS}	0.126	0.116	0.8260	0.097	0.158	0.111	0.5220	0.114	0.079	0.6400	0.193	0.135	0.4870	0.094	0.129	0.6410
	F_{ST}	0.023	0.009	**0.0250**	0.021	0.007	0.013	0.2540	0.034	0.007	**0.0280**	0.013	0.003	0.4560	0.019	0.006	0.3290
Sa	A_R	5.200	5.343	0.1730	5.271	5.382	5.185	0.2730	5.078	5.464	**0.0200**	5.457	5.327	0.4790	5.130	5.240	0.5410
	H_O	0.598	0.585	0.6370	0.612	0.551	0.601	0.1610	0.596	0.627	0.5320	0.565	0.541	0.6510	0.620	0.582	0.4260
	H_E	0.689	0.698	0.1960	0.692	0.697	0.692	0.7790	0.682	0.703	0.0650	0.703	0.693	0.4270	0.685	0.698	0.2950
	F_{IS}	0.132	0.163	0.4690	0.116	0.210	0.131	0.1440	0.126	0.109	0.8110	0.197	0.219	0.7770	0.096	0.166	0.3310
	F_{ST}	0.027	0.009	**0.0010**	0.016	0.011	0.016	0.7640	0.029	0.003	**0.0220**	0.018	0.008	0.4340	0.022	0.010	0.2480

IP, all individuals pooled; M, mature trees; Sa, saplings; A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{ST}, mean pairwise F_{ST}; F_{IS}, inbreeding coefficient; D, discontinuous zone; C, continuous zone. Significant values ($\alpha = 0.05$) given in bold.

Table 4.3 Parameter estimates and unconditional confidence intervals from multi-model inference of sugar maple (*Acer saccharum*) A_R, H_O, H_E (√data), F_{IS} and F_{ST} in Québec. Asterisks identify parameters where confidence intervals excluded 0.

Explained variable	Explanatory variable	Model-averaged estimate	Unconditional SE	95% confidence interval	
				Lower	Upper
A_R	m_ers_BA	0.00605	0.00569	-0.0051	0.01721
	s_ers_BA	0.00155	0.0194	-0.03647	0.03957
	m_ers_d	0.0006	0.00048	-0.00034	0.00155
	s_ers_d	0.00002	0.00005	-0.00007	0.00011
	m_ers_PS	0	0	-0.00005	0
	s_ers_PS	0	0	0	0
	D_north*	0.00378	0.00119	0.00146	0.00611
H_O	m_ers_BA*	0.00154	0.00062	0.00031	0.00276
	s_ers_BA	-0.00438	0.0023	-0.00889	0.00013
	m_ers_d	0.00011	0.00006	0	0.00022
	m_ers_PS	0	0	0	0
	s_ers_PS	0	0	0	0
	D_north	0.00011	0.00019	-0.00027	0.00049
H_E	m_ers_BA	0.0002	0.0002	-0.0002	0.00059
	s_ers_BA	-0.00051	0.00076	-0.002	0.00097
	m_ers_d	0.00002	0.00002	-0.00002	0.00006
	s_ers_d	0	0	0	0
	m_ers_PS	0	0	0	0
	s_ers_PS	0	0	0	0
	D_north	0.00004	0.00004	-0.00004	0.00013
F_{IS}	m_ers_BA	-0.00171	0.00094	-0.00355	0.00012
	s_ers_BA	0.00566	0.00347	-0.00115	0.01247
	m_ers_d	-0.0001	0.00008	-0.00026	0.00006
	s_ers_d	0	0.00001	-0.00002	0.00001
	m_ers_PS	0	0	0	0
	s_ers_PS	0	0	0	0
	D_north	-0.00003	0.00022	-0.00046	0.00041
F_{ST}	m_ers_BA	-0.0002	0.00015	-0.00049	0.0001
	s_ers_BA	-0.00037	0.00052	-0.00139	0.00064
	m_ers_d	-0.00002	0.00001	-0.00004	0.00001
	s_ers_d	0	0	0	0
	m_ers_PS	0	0	0	0
	s_ers_PS	0	0	0	0
	D_north*	-0.00006	0.00003	-0.00011	-0.00001

Term abbreviations: m_ers_BA, mature sugar maple basal area (m^2 ha^{-1}); s_ers_BA, sugar maple sapling basal area (m^2 ha^{-1}); m_ers_d, mature sugar maple density (stems ha^{-1}); s_ers_d, sugar maple sapling density (stems ha^{-1}); m_ers_PS, mature sugar maple population size (stems); s_ers_PS, sugar maple sapling population size (stems); D_north, distance of each site to the northern limit (km); SE, standard error.

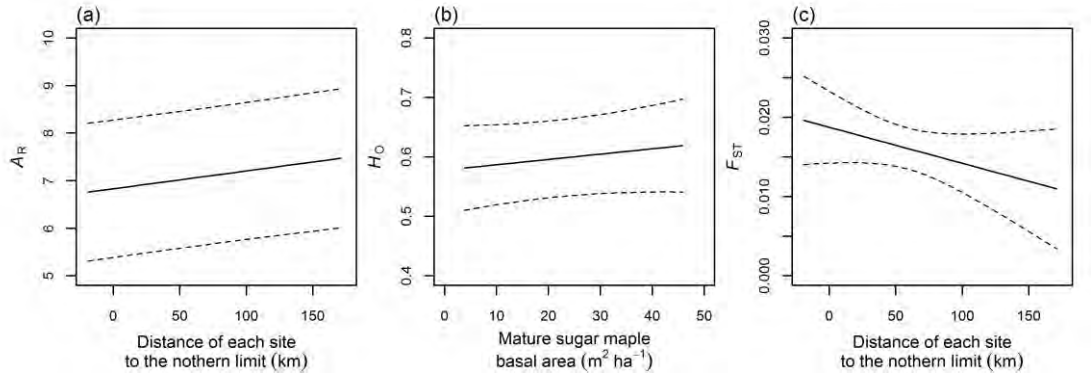

Figure 4.2 Predicted sugar maple (*Acer saccharum*) genetic indices (A_R, H_O and F_{ST}) in response to all influential explanatory variables in best supported models based on multi-model averaging of all candidate models (n = 414 for A_R and H_O, and n = 23 for F_{ST}) in Québec. Dashed lines indicate 95% confidence intervals. A_R, allelic richness; H_O, observed heterozygosity.

4.5.5. Proportions of rare alleles

Rare alleles were detected in all categories with the individuals pooled (Table A4.7). The same percentages were detected in all populations except for populations in the discontinuous zone of transect 1, where rare and private alleles (f < 0.02; RP2 category) were not detected (Table A4.7). However, a two-way ANOVA showed that this category differed among zones but not between transects (Table 4.4) with slightly fewer alleles in the discontinuous zone (mean: 0.25%; 95% confidence intervals (CI): -0.14, 0.65) than in the continuous zone (mean: 0.98%; 95% CI: 0.60, 1.36).

Rare alleles at f < 0.05 were detected in all categories for mature trees and saplings (Table A4.8). The same percentages were detected for both mature trees and saplings in all populations, except in the common and localized category ($f \geq 0.05$; CL5) where more alleles were present in saplings than in mature trees for transects 1 and 2 (Table A4.8). These differences were marginally significant (Table 4.4).

Table 4.4 Results of two-way ANOVA with interaction for percentage of allele frequency for the rare and private (frequency (f) < 0.02; RP2; n = 23) category and three-way ANOVA with interaction for the percentage of allele frequency in the common and localized ($f \geq 0.05$; CL5; n = 46) category prior to model simplification (model 1) and subsequent models (models 2 and 3).

Response variable	Model	Explanatory variable	Num. d.f.	Den. d.f.	F	P
RP2	1	zone	1	17	6.057	0.0248
		transect	2	17	1.255	0.3101
		zone × transect	2	17	0.117	0.8905
RP2	2	zone	1	21	6.279	0.0215
		transect	2	20	1.584	0.2312
RP2	3	zone	1	21	6.158	0.0216
CL5	1	zone	1	34	1.619	0.2119
		transect	2	34	0.181	0.8350
		cohort	1	34	3.807	0.0593
		zone × transect × cohort	7	34	0.800	0.5931
CL5	2	zone	1	42	1.884	0.1772
		cohort	1	42	4.192	0.0469
		zone × cohort	1	42	1.891	0.1763
CL5	3	cohort	1	45	4.029	0.0509

Num. d.f., numerator degrees of freedom; den. d.f., denominator degrees of freedom.

4.5.6. Bottlenecks

Inferences to be drawn from the heterozygosity excess tests were influenced by the mutational model. Under the IAM most of the populations were in excess of heterozygotes except for populations 1-C-D, 2-C-D and 2-D-D (Table 4.5). The mode shift model (SMM) showed no population in bottleneck.

For the *M*-ratio, no bottleneck was detected excepting three populations from the discontinuous zone (1-D-C, 1-D-D and 3-D-A) for $\theta = 1$ (Table 4.5). No significant bottlenecks were found for the other θ values (Table 4.5).

Table 4.5 Bottleneck results based on heterozygosity excess, Mode shift and *M*-ratio.

Transect	Zone	Site	Heterozygosity excess						Mode shift	*M*-ratio						
			IAM	TMM				SMM			$\theta = 1$		$\theta = 5$		$\theta = 10$	
				70%	90%	95%	99%				M_c	*P*-value	M_c	*P*-value	M_c	*P*-value
1	D	1DA	**0.03327**	0.81539	0.98288	0.99088	0.99671	0.99860	N	0.805	0.806	0.434	0.737	0.942	0.715	0.987
		1DB	**0.01041**	0.71008	0.94065	0.96316	0.99203	0.99552	N	0.792	0.806	0.342	0.737	0.345	0.715	0.577
		1DC	**0.01518**	0.56748	0.91632	0.95063	0.98658	0.99306	N	0.713	0.806	**0.033**	0.737	0.377	0.715	0.596
		1DD	**0.00032**	0.86774	0.99800	0.99987	0.99999	0.99999	N	0.717	0.806	**0.037**	0.737	0.345	0.715	0.517
	C	1CA	**0.02158**	0.95929	0.99615	0.99903	0.99979	0.99992	N	0.768	0.806	0.196	0.737	0.734	0.715	0.902
		1CB	**0.00200**	0.43252	0.85814	0.92924	0.97586	0.98482	N	0.761	0.806	0.210	0.737	0.531	0.715	0.811
		1CC	**0.01342**	0.89393	0.99088	0.99968	0.99997	0.99999	N	0.810	0.806	0.478	0.737	0.499	0.715	0.744
		1CD	0.14186	0.90927	0.97842	0.98959	0.99671	0.99800	N	0.768	0.806	0.203	0.737	0.797	0.715	0.927
2	D	2DA	**0.00021**	0.48306	0.68015	0.72456	0.86774	0.91632	N	0.778	0.806	0.251	0.737	0.828	0.715	0.936
		2DC	**0.00329**	0.75246	0.98816	0.99763	0.99979	0.99990	N	0.780	0.806	0.270	0.737	0.856	0.715	0.954
		2DD	0.18461	0.94065	0.99398	0.99615	0.99883	0.99961	N	0.792	0.806	0.350	0.737	0.921	0.715	0.820
	C	2CA	**0.01041**	0.92298	0.98959	0.99800	0.99860	0.99968	N	0.805	0.806	0.432	0.737	0.943	0.715	0.986
		2CB	**0.04488**	0.93513	0.99088	0.99615	0.99883	0.99961	N	0.798	0.806	0.394	0.737	0.930	0.715	0.983
		2CC	**0.04937**	0.95063	0.99480	0.99720	0.99961	0.99979	N	0.775	0.806	0.233	0.737	0.817	0.715	0.915
		2CD	0.10607	0.95063	0.99398	0.99860	0.99997	0.99998	N	0.776	0.806	0.239	0.737	0.627	0.715	0.932
3	D	3DA	**0.01184**	0.38301	0.56748	0.58414	0.79144	0.85814	N	0.811	0.806	0.484	0.737	0.961	0.715	0.994
		3DB	**0.00520**	0.35094	0.82673	0.94581	0.97586	0.97842	N	0.755	0.806	0.142	0.737	0.665	0.715	0.820
		3DC	**0.00010**	0.63314	0.96673	0.99398	0.99860	0.99903	N	0.756	0.806	0.148	0.737	0.675	0.715	0.834
		3DD	**0.00013**	0.26131	0.61699	0.76585	0.91632	0.91632	N	0.769	0.806	0.264	0.737	0.773	0.715	0.900
	C	3CA	**0.03327**	0.94065	0.99615	0.99860	0.99968	0.99974	N	0.719	0.806	**0.042**	0.737	0.363	0.715	0.539
		3CB	**0.02997**	0.90927	0.99306	0.99552	0.99832	0.99860	N	0.813	0.806	0.483	0.737	0.961	0.715	0.990
		3CC	**0.00385**	0.98288	0.99800	0.99979	0.99987	0.99994	N	0.737	0.806	0.084	0.737	0.521	0.715	0.705
		3CD	**0.00200**	0.53386	0.75246	0.86774	0.95063	0.96316	N	0.720	0.806	0.847	0.737	0.363	0.715	0.517

D, discontinuous zone; C, continuous zone. Significant values ($\alpha = 0.05$) given in bold for heterozygosity excess.

4.5.7. Isolation by distance

Isolation by distance was observed among populations (r = 0.36, P < 0.001) and zones (r = 0.35, P = 0.008 and r = 0.36, P = 0.002 respectively for continuous and discontinuous zones) using $F_{ST}/(1-F_{ST})$. Tests were not significant when each transect was tested separately (r = -0.06, P = 0.533; r = 0.33, P = 0.139; and r = 0.06, P = 0.390; respectively for transects 1, 2 and 3). Similar results were obtained using $D_S/(1-D_S)$ (Table 4.6).

Table 4.6 Isolation by distance analysis results performed separately for different geographic groups.

Group	Number of populations	$F_{ST}/(1-F_{ST})$		$D_S/(1-D_S)$	
		r	*P*	*r*	*P*
All populations	23	0.36	0.001	0.36	0.001
Zone					
Discontinuous	11	0.35	0.008	0.36	0.005
Continuous	12	0.36	0.002	0.36	0.002
Transect					
1	8	-0.06	0.533	-0.05	0.532
2	7	0.33	0.139	0.26	0.184
3	8	0.06	0.390	0.02	0.476

4.5.8. Genetic structure

The neighbor-joining tree separated the populations of the transect 1 (except for 1-D-C, Rémigny) from the populations of the two other transects (Fig. A4.1). However, bootstrap support (< 25%) was poor overall. The strongest link was found between populations 2-D-A and 3-D-A with 79% bootstrap support. When the populations were divided into two groups (mature trees and saplings), similar groupings occurred for 12 populations (bootstrap support range: 20–99) among which 7 had bootstrap support ≥ 50% (Fig. A4.1).

The STRUCTURE output produced the highest value of ΔK at K = 4 (Fig. A4.2). Many individuals membership were assigned in the four clusters indicating high levels of admixture (orange, blue, yellow and pink clusters; Fig. 4.1), however a

structure could still be drawn. Trees from the northern populations, 1-D-A, 1-D-B, 2-D-A and 3-D-A, were predominantly assigned to the orange cluster. The blue cluster was better represented in trees from populations of transect 3. High assignment probabilities to the blue and yellow clusters were found in the populations of transects 1 and 2. The pink cluster separated trees from population 1-D-C from all the others.

AMOVA analysis showed no genetic structure of the populations at the level of zone (0%) and transect (1%, $P = 0.000$) (Table A4.9). Most of the genetic variation was found within populations for all grouping (within 97%, $P = 0.000$; among 2–3%, $P = 0.000$; Table A4.9).

4.5.9. Gene flow and population sizes

The θ value showed that the largest sugar maple population was in the eastern area of Québec (transect 3; mean $\theta = 3.68$) and the smallest was in the centre (transect 2: mean $\theta = 1.22$; Table A4.10, Fig. 4.3). Northern populations also had a low mean scaled effective population size ($\theta = 1.43$). Remarkable levels of gene flow were observed among populations from the three transects with slightly more scaled immigration rate (M) from the east (transect 3) than the other two transects (Table A4.10, Fig. 4.3). Gene flow was asymmetrical with higher migration rates from the south (transects 2 and 3) toward the northern populations, while low and equal migration rates were observed between the west (transect 1) and northern populations (Table A4.10, Fig. 4.3).

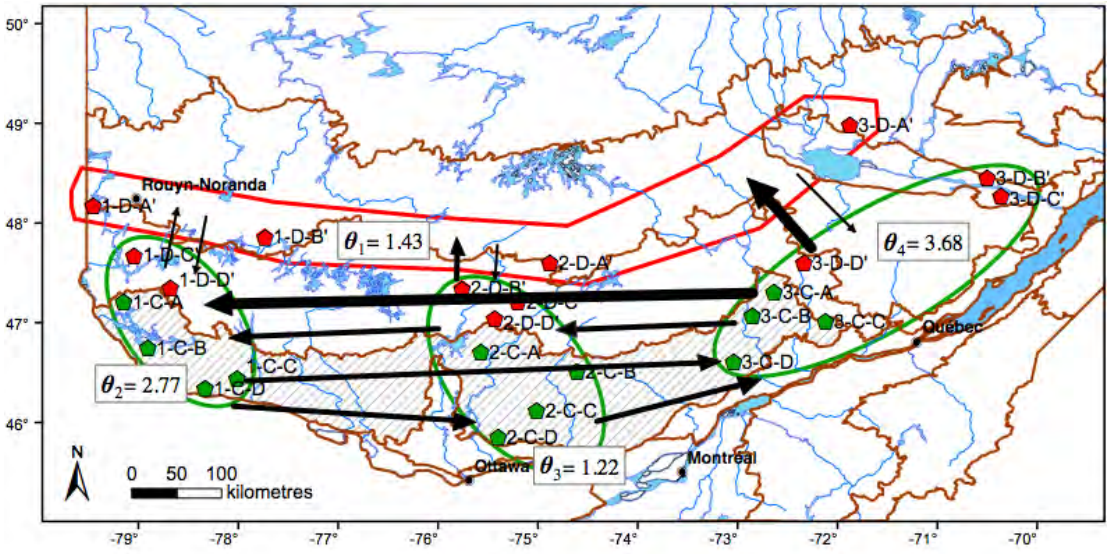

Figure 4.3 Migration pattern of four groups of Québec sugar maple (*Acer saccharum*) populations, using MIGRATE-N (Beerli, 2006). The groups (red lines for the northern group and green lines for other groups) are defined using the results of STRUCTURE. Mean mutation-scaled population sizes ($\theta = 4N_e\mu$, where N_e = effective population size and μ = mutation rate per generation per locus) are given for each group. Arrows represent direction of migration, and the thicknesses of the arrows are proportional to mean mutation-scaled immigration rate ($M = m/\mu$, where m = migration rate; small arrow, M = 6.6–8.5; medium arrow, M = 15.0–17.8; big arrow, M = 21–26). Locations of the 24 study sites (2-D-B was not included in genetics analysis) are given in red polygons for sites in discontinuous zone, and given in green polygons for sites in the continuous zone (see Graignic *et al.*, 2014 for more details). Sugar maple–yellow birch (*Betula alleghaniensis*) bioclimatic domains are in gray hatch and the boundary of all bioclimatic domains are given in thin brown lines (Saucier *et al.*, 2003).

4.6. Discussion

4.6.1. Genetic diversity levels and differentiation in sugar maple populations

Using eighteen microsatellite markers we recently developed, we detected a high level of genetic diversity in sugar maple populations (see Table 4.1). No other data was available for natural populations of sugar maple with microsatellite markers. When we compared our results to other tree species such as *Acer mono* (H_E = 0.80, range: 0.70–0.85) and two *Quercus* species (H_E = 0.82, range: 0.77–0.86), sugar maple did not have the highest genetic diversity (Table 4.7). The level of genetic diversity reported for sugar maple populations with allozymes (see Table 4.7) was relatively high (mean H_E = 0.122; range: 0.064–0.275) and quite similar to other *Acer*

species, except for *Acer pseudoplatanus* (H_E = 0.280, range: 0.254–0.319; Table 4.7). Overall H_E was lower for sugar maple than for other north-eastern American tree species (Table 4.7).

Large variations in the inbreeding coefficient estimates was observed for sugar maple populations in Québec (F_{IS} = 0.138, range: -0.051–0.302). Similar results were reported with microsatellites for *Acer takesimense* (F_{IS} = 0.28, range: 0.08–0.47) (Takayama *et al.*, 2013) and for *Populus tremuloides* (see Table 4.7).

We found a very low level of genetic differentiation between sugar maple populations (F_{ST} = 0.016, range: 0.009–0.041). Values were similar to those of *Quercus* (F_{ST} = 0.01–0.02; Table 4.7).

Table 4.7 Comparison of genetic diversity using allozyme and microsatellite markers for old-growth, undisturbed or natural populations of tree species in northeastern North America, and *Acer* species around the world.

Species	*A*	A_R	H_O	H_E	F_{IS}	F_{ST} / G_{ST}	Reference
Allozymes							
Angiosperm							
Acer platanoides	1.88 (1.50–2.17)	—	0.134 (0.085–0.179)	0.133 (0.090–0.172)	-0.014 (-0.379–0.185)	—	Rusanen et al. (2000)*
Acer platanoides	2.0 (1.6–2.4)	—	0.126 (0.038–0.195)	0.132 (0.053–0.191)	0.066 (-0.085–0.285)	0.099	Rusanen et al. (2003)
Acer pseudoplatanus	2.78 (2.56–3.00)	—	0.293 (0.237–0.327)	0.280 (0.254–0.319)	-0.032 (-0.159–0.085)	0.019 (0.003–0.035)	Belletti et al. (2007)
Acer macrophyllum	1.71 (1.5–2.2)	—	0.118 (0.102–0.160)	0.152 (0.102–0.189)	0.166 (-0.086–0.332)	0.054	Iddrisu and Ritland (2004)
Acer saccharum	1.95 (1.64–2.18)	—	—	0.110 (0.098–0.132)	—	0.033	Perry and Knowles (1989)
Acer saccharum	2.9	—	0.15	0.148	—	0.012	Foré et al. (1992a)
Acer saccharum	2.03	—	—	0.109	0.073	0.017	Young et al. (1993a)*
Acer saccharum	1.98 (1.78–2.41)	—	—	0.112 (0.088-0.138)	0.042 (-0.095–0.177)	0.033	Young et al. (1993b)
Acer saccharum	3.21 (2.50–3.75)	2.17 (1.66–2.98)	0.130 (0.072–0.294)	0.133 (0.064–0.275)	0.025 (-0.055–0.078)	0.060 (0.060–0.114)	Baucom et al. (2005)
Castanea dentata	1.69 (1.50–1.89)	—	0.184 (0.135–0.264)	0.151 (0.096–0.196)	-0.226	0.110	Huang et al. (1998)
Fagus grandifolia	2.9 (2.9–2.9)	—	0.387 (0.382–0.392)	0.395 (0.383–0.407)	0.024	0.063	Houston and Houston (1994)
Fagus grandifolia	3.0 (2.78–3.33)	—	0.163 (0.150–0.175)	0.165 (0.150–0.179)	0.009	0.030	Houston and Houston (2000)
Populus tremuloides	2.7 (2.1–2.9)	—	0.125 (0.101–0.160)	0.235 (0.207–0.270)	0.462 (0.295–0.568)	0.068	Hyun et al. (1987)
Populus tremuloides	2.6 (2.2–2.9)	—	0.217 (0.197–0.242)	0.220 (0.193–0.244)	0.017	0.003	Lund et al. (1992)
Quercus rubra	2.08 (1.8–2.3)	—	—	0.186 (0.145–0.245)	0.100	0.092	Sork et al. (1993)
Gymnosperm							
Picea glauca	3.03 (2.17–3.83)	2.14 (1.86–2.37)	0.342 (0.221–0.414)	0.344 (0.199–0.412)	0.002 (-0.092–0.087)	—	O'Connell et al. (2006)
Picea rubens	1.47 (1.25–1.64)	—	0.075 (0.059–0.092)	0.079 (0.061–0.104)	0.043 (-0.037–0.224)	0.007 (0.003-0.011)	Hawley and DeHayes (1994)
Pinus strobus	2.31 (2.24–2.37)	—	0.126 (0.125–0.126)	0.153 (0.149–0.157)	—	—	Buchert et al. (1997)*
Pinus strobus	2.35 (2.23–2.50)	—	0.215 (0.185–0.216)	0.195 (0.181–0.216)	-0.139 (-0.273–0.407)	0.061	Rajora et al. (1998)
Thuja occidentalis	1.6 (1.5–1.8)	—	0.116 (0.102–0.133)	0.129 (0.113–0.141)	0.106	0.073	Lamy et al. (1999)
Microsatellites							
Angiosperm							
Acer mono	12.63	—	—	0.802	-0.008	—	Kikuchi et al. (2009)
Acer mono	—	8.37 (7.38–9.65)	—	0.80 (0.70–0.85)	0.27 (0.20–0.32)	—	Takayama et al. (2012)
Acer okamotoanum	—	6.60 (6.11–7.41)	—	0.72 (0.66–0.76)	0.18 (0.03–0.24)	—	Takayama et al. (2012)
Acer pseudoplatanus	—	—	0.548 (0.543–0.553)	0.574 (0.573–0.574)	—	—	Pandey (2005)
Acer pseudosieboldianum	—	4.60 (3.79–5.25)	0.40 (0.32–0.46)	0.61 (0.53–0.68)	0.33 (0.21–0.43)	—	Takayama et al. (2013)
Acer saccharum	8.2 (6.6–9.0)	7.0 (5.8–7.6)	0.597 (0.496–0.716)	0.693 (0.637–0.715)	0.138 (-0.051–0.302)	0.016 (0.009–0.041)	Our study
Acer skutchii	2.1 (1.5–2.5)	—	—	0.129 (0.054–0.247)	0.174 (0.131–0.159)	0.075	Lara-Gomez et al. (2005)
Acer takesimense	—	3.82 (3.59–4.23)	0.38 (0.30–0.47)	0.53 (0.48–0.58)	0.28 (0.08–0.47)	—	Takayama et al. (2013)
Quercus ellipsoidallis	13	—	0.67 (0.62–0.72)	0.79 (0.77–0.81)	0.145 (0.10–0.19)	0.01	Lind and Gailing (2013)
Quercus rubra	14.5 (13–15)	—	0.73 (0.70–0.75)	0.84 (0.83–0.86)	0.12 (0.07–0.17)	0.02	Lind and Gailing (2013)
Populus tremuloides	8.83 (7.58–10.08)	—	0.465 (0.45–0.48)	0.67 (0.61–0.73)	0.30 (0.21–0.39)	—	Namroud et al. (2005)

Table 4.7 (*to continued*)

Species	*A*	A_R	H_O	H_E	F_{IS}	F_{ST} / G_{ST}	Reference
Populus tremuloides	—	5.99 (3.34–6.83)	—	0.758 (0.613–0.801)	0.019 (-0.12–0.19)	0.086	Callahan et al. (2013)
Populus tremuloides	7.44 (6.25–8.2)	—	0.556 (0.478–0.704)	0.725 (0.691–0.767)	0.201 (-0.054–0.325)	0.032	Wyman et al. (2003)
Gymnosperm							
Pinus strobus	9.43 (9.23–9.62)	—	0.522 (0.505–0.538)	0.607 (0.599–0.615)	—	—	Rajora et al. (2000)*
Pinus strobus	—	6.7	0.47	0.48	0.01	—	Marquardt and Epperson (2004)*
Thuja occidentalis	9.58 (7.83–11.17)	9.21 (7.66–10.68)	0.590 (0.505–0.640)	0.600 (0.519–0.662)	0.019 (-0.025–0.050)	—	Pandey and Rajora (2012a)
Thuja occidentalis	7.3 (5.67–9.33)	6.8 (5.16–8.51)	0.601 (0.492–0.662)	0.611 (0.490–0.678)	0.013 (-0.063–0.105)	0.078	Pandey and Rajora (2012b)
Thuja occidentalis	7.8 (5.0–10.0)	5.9 (4.6–6.9)	0.734 (0.463–0.883)	0.773 (0.712–0.840)	0.145	0.065	Xu et al. (2012)

* Study used logging or non-natural forest, we only reported populations from old-growth and natural forests. *A*, mean number of alleles per locus; A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient, F_{ST}, mean pairwise $F_{ST,}$ G_{ST}, mean pairwise G_{ST}. Range values are given in parentheses.

4.6.2. Genetic variation and the central–marginal hypothesis

Most of the genetic variation was found within sugar maple populations, a frequent pattern for long-lived perennials, outcrossing and wind dispersed seeds plants (Nybom, 2004). Despite this fact, a genetic structure was observed and isolation by distance was detected.

The central–marginal hypothesis (Eckert *et al.*, 2008) was tested by delineating bioclimatic domains that reflected sugar maple abundance (see Graignic *et al.*, 2014 for more details). As predicted by the central–marginal hypothesis, we found a lower allelic richness (A_R) and higher genetic differentiation (F_{ST}) between populations in the discontinuous zone that represents the periphery of the sugar maple range in Québec (Table 4.2). The relationship between the proximity to the northern limit and genetic diversity was negative whereas it was positive with genetic differentiation (Table A4.6, 4.3, Fig. 4.2a, c). When these relations were tested for each transect separately, the pattern (discontinuous/continuous) remained significant only for the western transect (transect 1). The central–marginal hypothesis predicted that a lower abundance could lead to lower genetic diversity (Eckert *et al.*, 2008). A lower level of sugar maple recruitment (lower seedlings density) in the discontinuous zone was only previously observed in transect 1 (Graignic *et al.*, 2014). The association between lower sexual reproductive capacity and lower genetic diversity in peripheral populations was also suggested for *Thuja occidentalis* (Xu *et al.*, 2012; Paul *et al.*, 2014) and *Cirsium acaule* (Jump *et al.*, 2003) at their northern ranges. The number of rare and private alleles ($f < 0.02$ and in one population) was more frequent in the continuous zone than in the discontinuous zone (Table 4.4). These results are similar to those obtained for *Thuja occidentalis* at its north-eastern range with lower A_R, higher F_{ST}, and a lower number of private alleles in peripheral populations than in core populations (Pandey & Rajora, 2012b).

No recent bottleneck was detected under the SMM while most populations were in bottleneck under the IAM (Table 4.5). The IAM is better at detecting subtle genetic bottlenecks, however is also known to occasionally identify heterozygosity excess in nonbottlenecked populations (Luikart & Cornuet, 1998). Luikart & Cornuet (1998) thought that the true model for most microsatellite loci was an intermediate between IAM and SMM. They recommended interpreting that a recent bottleneck had occurred when the IAM is significant and the SMM is close to significant ($0.10 \geq P > 0.05$). We found *P*-values above 0.86 for SMM when IAM was significant (Table 4.5). Therefore, we concluded that most of the sugar maple populations had not been through a recent bottleneck. The *M*-ratio analysis shown that three populations may have undergone an historical bottleneck when the mutation-scaled effective population size was estimated at $\theta = 1$, but no bottleneck was detected at $\theta = 5$ or higher (Table 4.5). Among these populations, only 3-D-A were assigned to a distinct cluster (defined by STRUCTURE) with a mutation-scaled estimate population size close to $\theta = 1$ (MIGRATE results), and had probably undergone a bottleneck in a distant past (Table A4.10 and Fig. 4.3). Xu *et al.* (2012) also reported the presence of bottlenecks in northern peripheral white cedar populations.

The results of other studies were not consistent with the central–marginal hypothesis (Rajora *et al.*, 1998; Gapare *et al.*, 2005; González-Martínez *et al.*, 2005; Hoban *et al.*, 2010; Jadwiszczak *et al.*, 2011). For example, Gapare *et al.* (2005) found higher inbreeding in peripheral (both marginal and continuous) populations of *Picea sitchensis* located at the northern and southern edges of the species range than core populations (both marginal and continuous). This pattern seems more consistent with the range–shift model that followed the LGM (Hampe & Petit, 2005). Hoban *et al.* (2010) tested both hypotheses and their results best supported the range shift model as the determinant of genetic structure for *Juglans cinerea*, rather than the ecological marginality in itself. In the present study, only the northern peripheral

populations (both discontinuous and continuous) were sampled in all sugar maple distribution and therefore we were not able to determine whether the range-shift or the central-marginal model was the best. The same problem was encountered in the works of González-Martínez *et al.* (2005) and Jadwiszczak *et al.* (2011) because only the eastern and south-western peripheral populations of *Pinus pinaster* and *Betula humilis* were sampled, respectively.

We found a genetic structure in our study area, it seems that core and peripheral populations were sampled. The most northern populations of each transect (1-D-A, 1-D-B, 2-D-A and 3-D-A), were assigned to the orange cluster (Fig. 4.1, 4.3). These populations were probably more representative of the northern peripheral zone than the discontinuous zone in itself.

4.6.3. Special case of 1-D-C, Rémigny

The population from Rémigny (1-D-C) was distinct compared to all the others. It had the lowest level of diversity (A, A_R, H_E and F_{IS}), the highest F_{ST} and a bottleneck was detected (M-ratio at $\theta = 1$). Both neighbor-joining trees and structure analysis clearly disjointed this population from the others. These differences were probably due to the recent establishment of sugar maple at this site. A study conducted by Pilon (2013) at a sugar maple stand nearby (approximately 7 km away) dated the sugar maple's arrival few years to 80-yr ago, after a fire which occurred 160–220-yr ago. The presence of sugar maple at Rémigny was sporadic or scarce during the last millennia (Pilon, 2013). Probably the presence of this species was too recent to reach level of diversity because Lesser *et al*. (2013) has shown that, more than 230-yr are needed to reach allele saturation after *Pinus ponderosa* establishment.

4.6.4. Mature tree and sapling cohorts

In many coniferous tree species, the level of heterozygosity increases with the age of the trees (seeds vs. adults, seeds vs. seedlings, different age classes), possibly

due to higher fitness of heterozygous individuals (Bush & Smouse, 1992; Nijensohn *et al.*, 2005). Ballal (1994) reported that sugar maple embryos had lower heterozygosity and higher F_{IS} than seedlings (1-yr to ≤ 1 cm basal area) and mature trees (≥ 30 cm dbh). Foré *et al.* (1992) found no difference between sugar maple embryos, 1-yr seedlings and three other cohorts (dbh ≤ 2 cm, 15–25 cm and ≥ 40 cm). We observed very small differences between the cohorts. First, F_{IS} was always higher for saplings than mature trees, however this difference was not significant. We also found a significant positive relationship between mature sugar maple basal area and H_O (Table A4.6, 4.3 and Fig. 4.2). This suggests that largest mature sugar maple trees were heterozygotic at a higher number of loci (Table A4.6, 4.3). However, no influence of mature sugar maple basal area on F_{IS} was detected and therefore did not support the hypothesis of higher heterozygosity in older cohort.

4.6.5. Genetic signature of migration routes

We found the largest population size in the eastern populations followed by the western and the central ones respectively (Table A4.8; Fig. 4.3), and a very different genetic structure between the eastern and the western transects (blue and yellow clusters in Fig. 4.1). That suggests two distinct migration routes, which separated a long time ago, or originated from different glacial refugia.

Earlier sugar maple migrations in Québec started approximately 9000-yr BP in south-eastern Québec (step 1 in Fig. 4; Lavoie & Richard, 2000) and near lake St-Jean (8500-yr BP; Richard & Grondin, 2009), and they could come from a north-westward or westward expansion (step 2 in Fig. 4.4). Sugar maple pollen was recorded 8,000-yr ago in southern Ontario, just south-west of Québec 6000-yr BP and south-west of Québec 5500-yr BP (steps 3, 4 and 5 in Fig. 4.4; Richard, 1980; Bennett, 1987). Therefore, the arrival of sugar maple in western Québec occurred around 3000-yr later than it did in the east and corroborating evidence of two distinct migration routes in Québec. Our hypothesis matches also Braun's hypothesis which

was based on pollen data analysis that suggests beech–maple associations moved northward via two routes following the ice retreat (Braun, 1950). The first movement was north-east, along the Appalachians and the second was directly northward from Louisiana to North Carolina. This second movement was delayed by a warm and dry post-glacial period in Ohio and Indiana. The northern lake states' beech-maple forests were derived from westward expansion of the first route and not from migrations directly from the south (Braun, 1950). Jackson *et al.* (2000) identified, from pollen and macrofossils data, two maple glacial refugia in the LGM (21 000-yr BP; Fig. 4.4). Interestingly, a genetic signature of these same refugia was identified for red maple (*Acer rubrum*) (McLachlan *et al.*, 2005) but no data was available for sugar maple across the US.

Southern populations in central Québec (transect 2) had a lower population size and were clustered with western and eastern populations (transect 1 and 3; Fig. 4.1). We hypothesized that these populations originated from an admixture of westward and eastward Québec migration (step 7 in Fig. 4.4). Similar routes for northern populations could also be drawn but with considerably more contribution from central-eastern populations (transects 2 and 3; step 7 in Fig. 4.4). We deduced that this is because very low contributions from the southwestern populations to the northernmost western populations were found (Table A4.10; Fig. 4.3). In addition, western populations arrived later than did the eastern populations in Québec (Richard, 1980). The population 3-D-A (Lac Patrick) was in bottleneck possibly because it represented a remnant of a larger northern sugar maple population. Some tree species were in decline in northern Québec 3000-yr BP because of the cool and dry climate (Carcaillet & Richard, 2000; Ali *et al.*, 2008). Therefore, population 3-D-A could be far older than other northern sugar maple populations and thus the withdrawal effect could have lasted longer.

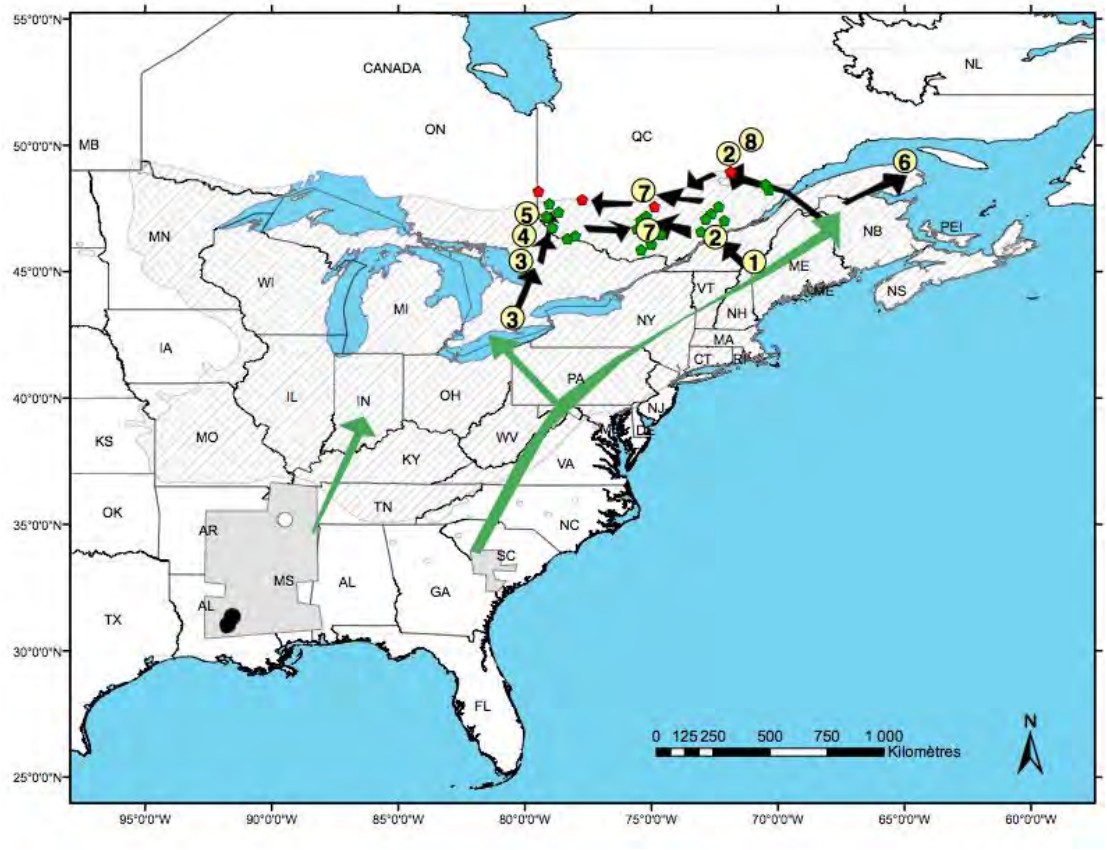

Figure 4.4 Map of sugar maple migration routes. Hatched zone, sugar maple modern distribution. Grey zones, isopoll map of maple pollen in Last Glacial Maximum; black circles, presence of maple macrofossils in Last Glacial Maximum; white circle, absence of maple macrofossils in Last Glacial Maximum (Jackson *et al*., 2000). Green arrows, hypothesized beech–maple association migration deduced from pollen (Braun, 1950); black arrows, sugar maple migration deduced from our microsatellite genomic DNA study and from pollen diagrams; numbers, hypothesized chronological steps of sugar maple migration (see Discussion for more details). Red polygons, northern populations group deduced from ours STRUCTURE results; green polygons, our studied southern populations. Standardized two-letter state and province abbreviations were used.

4.7. Conclusions

This is the first time that the genetic diversity and structure of sugar maple has been studied over a wide range at its northern range. Although there is evidence of some impact of marginality on its genetic structure, the question remains open of whether the "ecology marginality at the periphery" (central–marginal hypothesis; Eckert *et al.*, 2008) or "range shift following the last glacial maximum" (Hampe &

Petit, 2005) models, better describe the pattern of variation. We found a high level of genetic diversity in Québec and a lower diversity in northern populations. However, no clear conclusion could be drawn to validate the hypothesis that northern populations were remnants of a larger population that migrated further north of the species range after the retreat of ice sheet. It is possible that it only occurred in the north-eastern part of the Québec range with population 3-D-A (Lac Patrick), which showed a bottleneck, and that other northern populations came from long distance dispersion (Cain *et al.*, 2000). Northern populations could be more susceptible to climate change than core populations, especially the north-western populations (1-D-A and 1-D-B) that seem more isolated from the south-western populations and that appear to be on the leading edge of a westward migration (Fig. 4.3). Nuclear and cytoplasmic sequences could be useful in the future because they can be more reliably ordered into an evolutionary sequence than through the use of microsatellites (Ellegren, 2004). Additional palynological data would also be essential to accurately establish the arrival of the northernmost populations and their migration routes.

CHAPITRE V

GENETIC CONSEQUENCES OF SELECTION CUTTING ON SUGAR MAPLE (*ACER SACCHARUM* MARSHALL)

Noémie Graignic, Francine Tremblay & Yves Bergeron

5.1. Résumé

Les impacts de la déforestation et de la coupe sélective sur le niveau et la structure de la diversité génétique des arbres sont bien documentés. La coupe de jardinage consiste à prélever périodiquement des arbres choisis individuellement ou par petits groupes dans un peuplement mature à structure d'âge inéquienne. Le traitement crée de petites ouvertures du couvert forestier sur de grandes superficies et génère des structures forestières qui diffèrent souvent de celles des forêts anciennes. Dans cette étude, nos objectifs étaient d'évaluer si ce type de récolte avait un impact sur la diversité génétique de l'érable à sucre (*Acer saccharum* Marshall). Nous avons analysé la diversité génétique de semis, de jeunes arbres et d'arbres matures dans des peuplements coupés et des forêts anciennes au Québec, Canada. Nous avons observé un taux d'hétérozygotie observée (H_O) plus élevée et un coefficient de consanguinité (F_{IS}) plus bas pour les arbres matures comparativement aux cohortes plus jeunes, ceci dans les peuplements coupés et les vieilles forêts. Nous avons détecté la présence d'un goulot d'étranglement récent dans tous les peuplements jardinés. Toutefois, il ne s'est avéré significatif que pour le modèle du nombre infini d'allèles possibles (IAM). Les autres indices de diversité génétique (richesse allélique, hétérozygotie observée et attendue et allèles rares) étaient similaires entre les deux types de forêts. Nous en arrivons à la conclusion que la coupe de jardinage a peu ou pas d'effet sur la diversité génétique de l'érable à sucre. Nous n'avons détecté aucune présence d'érosion génétique au Québec après une récolte. Néanmoins, la présence d'un goulot d'étranglement dans les peuplements coupés indique que nous ne sommes pas en mesure de prédire avec précision l'effet cumulatif de plusieurs récoltes successives et c'est pour cette raison que nous recommandons un suivi à long terme.

5.2. Abstract

Selection cutting is a treatment for forests with uneven-aged structures. It emulates tree-by-tree replacement that creates small openings, which differ from old-growth forests structure. Because previous studies of others type of forest fragmentation showed no consistent influence on sugar maple (*Acer saccharum* Marshall) genetic diversity; in this study, our objectives were to evaluate, using new genetic markers, whether this type of harvesting has a perceptible impact on genetic diversity of this species. Genetic diversity among seedlings, saplings and mature trees was compared between logged and old-growth forest stands in Québec, Canada. We found higher observed heterozygosity (H_O) and lower inbreeding coefficient (F_{IS}) in mature trees than in younger regeneration cohorts in both forest types. We observed a recent bottleneck in all selection cuttings stands. However, this bottleneck was significant only for the infinite allele mutation (IAM) model and other genetic indices of diversity (allelic richness, observed and expected heterozygosity and rare alleles) were similar between forest types. We concluded that the effect of selection cutting on the genetic diversity of sugar maple was subtle, and no strong evidence of genetic erosion was detectable in Québec stands after one harvest. Nonetheless, we could not accurately predict the cumulative effect of multiple loggings and recommend long-term monitoring.

5.3. Introduction

Forest ecosystems are exposed to natural (i.e. fire, windstorms, pests, diseases) and human (i.e. urbanization, logging, agriculture) disturbances. The ongoing effects of climate change are superimposed on those disturbances in boreal (Bergeron *et al*., 2010), temperate (Fischer *et al*., 2013), and tropical (Brodie *et al*., 2012) forests. In north-eastern North America, long-term logging has led to changes in forest composition and structure (Boucher *et al*., 2009). Following logging, subsequent reductions in tree population size (tree density and forest cover) may increase genetic drift and bottlenecks and, ultimately, decrease genetic diversity (Finkeldey & Ziehe, 2004). Lost of diversity may decrease potential adaptation of population to cope with global changes (Hamrick, 2004). Decreased in genetic diversity have been observed in white spruce (*Picea glauca* [Moench] Voss; Rajora, 1999) and eastern white pine (*Pinus strobus* L.; Buchert *et al*., 1997; Rajora *et al*., 2000). These studies have reported reductions in the mean number of alleles, low frequency alleles and rare alleles, together with level of heterozygosity. In contrast, other studies have shown no negative effects of logging on tree genetic diversity for white spruce (Fageria & Rajora, 2013), black spruce (*Picea mariana* [Miller] BSP; Perry & Bousquet, 2001), and black walnut (*Juglans nigra* L.; Robichaud *et al*., 2010). These results suggest that high intra-population genetic diversity, greater longevity and efficient long-distance pollen dispersal, which are generally observed in trees, could counterbalance the losses and attenuate genetic losses following harvesting (Hamrick, 2004).

Sugar maple (*Acer saccharum* Marshall) is a long-lived deciduous tree that forms uneven-aged stands. In addition to the syrup that it produces, this species has major economic value as saw timber in north-eastern North America (Majcen *et al*., 1984; Godman *et al.*, 1990). It is insect- (bee) and wind-pollinated, and is shade-tolerant (Logan, 1965; Gabriel & Garrett, 1984). In Canada, its range extends from southern

Ontario and Québec, in the temperate deciduous forest, northwards into the boreal mixed-wood forest (Little, 1971; Saucier *et al.*, 2003).

The abundance of sugar maple has increase in North America over time following the colonization (Siccama, 1971; Nicholson *et al*., 1979). In Québec, forest clear-cutting and the deliberate setting of fires by settlers in the 20th century have favoured the expansion of sugar maple (Boucher *et al.*, 2006; Dupuis *et al.*, 2011). Since 1983, selection cutting, a type of partial cut, has become the most common harvesting treatment for sugar maple stands in Québec (Majcen, 1994). It consists of the removal of 25–35 % of the volume of trees having a d.b.h. (diameter at breast height, 1.3m) ≥ 10 cm (MRNFPQ, 2003). Cutting cycles occur at regular intervals of 15–25 years to sustain stand structure and maintain its quality. Stands that are harvested using single-tree selection have a smaller number of large and defective trees than do old-growth stands (Angers *et al.*, 2005). Ten years after selection cutting in a sugar maple stand, the diameter growth of sugar maple, American beech (*Fagus grandifolia* Ehrhart) and yellow birch (*Betula alleghaniensis* Britton) generally increased in comparison to pre-harvested stands (Forget *et al.*, 2007). Fifteen years after an experimental selection cut in sugar maple stands, basal area, radial growth, and the development of sugar maple, American beech and yellow birch saplings were found to be greater compared to control plots (Majcen *et al.*, 2005). However, a recent survey of hardwood forests that were treated with selection cuts in Québec showed that after 10 years, about 55 % of commercially harvested stands were less productive than experimental plots that had been treated with selection cutting (Guillemette *et al.*, 2013). This response is possibly due to the low initial (pre-harvest) quality of sugar maple stands or to higher intensity harvesting of good quality stems (Guillemette *et al.*, 2013).

Rainville (2007) noted that basic knowledge of hardwood tree species genetic diversity across Canada is lacking. Previous work on the genetic diversity of sugar

maple has focused on fragmentation effects that are incurred by agriculture and clear-cutting. Foré *et al.* (1992b) compared canopy tree (≥ 30 cm d.b.h.; pre-fragmentation cohort) and juvenile (≤ 1cm basal diameter; post-fragmentation cohort) distributions in isolated forest patches in an agricultural landscape; the patches had been isolated for at least 50 years (1935–1988). Genetic differentiation between patches with respect to canopy trees was greater than for juveniles. Foré *et al.* (1992b) concluded that the level of gene flow between forest patches was higher in this open landscape. In examining a subsample of seeds taken from the same forest patches (only those with a minimum distance of 30–40 m between two patches), Ballal (1994) showed that embryos had a lower genetic diversity than juveniles and canopy trees within patches; however, both Foré *et al.* (1992a) and Baucom *et al.* (2005) found no differences between cohorts within patches. In comparing the genetic diversity of 1-year-old seedlings between patches and continuous forest, Young *et al.* (1993a) and Young & Merriam (1994) found greater genetic diversity in the fragmented forest. Eighty years after one clear-cut, sugar maple seedlings had a lower percentage of polymorphic loci and allelic richness estimates compared to an old-growth forest (Baucom *et al.* 2005). These results show no consistent pattern of habitat fragmentation on sugar maple genetic diversity.

Selection cutting is a treatment that emulates tree-by-tree replacement in forests with uneven-aged structures. However, it creates small openings in large areas of canopy and often generates forest structures that differ markedly from old-growth forests. In this study, we evaluated whether this type of harvesting had an effect on sugar maple genetic diversity. Using new microsatellite, highly polymorphic markers (Graignic et al. 2013), we compared the genetic structure of mature and regenerating sugar maple cohorts in logged stands (selection cutting) to adjacent unlogged stands (old-growth). We hypothesized that: (1) the removal of around 30 % (by volume) of mature trees would reduce the level of diversity (mean number of alleles, rare alleles,

and the level of heterozygosity) of the mature sugar maple cohort compared to the old-growth mature sugar maple cohort; (2) sugar maple seedlings, which had established after logging, would have a lower level of genetic diversity due to reductions in the number of potential parent trees (mature trees); and (3) selection cutting may change levels of genetic structure among cohorts (adults–saplings–seedlings). The results are discussed with reference to the short-term consequences of logging on the genetic resources of sugar maple.

5.4. Materials and methods

5.4.1. Study area and sampling

The study took place in the continuous portion of the northern range of sugar maple, i.e., southern Québec, Canada (Fig. 5.1). The study area was located between 45°46' N and 46°8' N, and 75°53' W and 74°59' W, at elevations ranging between 305 and 410 m (Table A5.1). This zone lies within the sugar maple–yellow birch (*A. saccharum–B. alleghaniensis*) and sugar maple–basswood (*A. saccharum–Tilia americana* L.) bioclimatic domains, where sugar maple is abundant (Saucier *et al.*, 2003).

The stands that had been subjected to selection cutting (SC) were harvested once, during winter 1990 (at the end of 1990 and early 1991). Our sampling was conducted in 2008. The SC was a commercial harvest that consisted of the removal of 25–35 % of tree basal area every 15–25 years (MRNFPQ, 2003). The old-growth (OG) stands, which had not been logged, were classified as Exceptional Forest Ecosystems (EFE) by the *ministère des Ressources naturelles du Québec* (Québec Ministry of Natural Resources; MRNQ, 2013). The logged stands (SC) were paired with adjacent unlogged stands (OG). The two sites (OG1 and SC1) were located in the sugar maple–basswood bioclimatic domain, while the remaining ones were in the sugar maple–yellow birch bioclimatic domain (Fig. 5.1). All 6 sites, except for OG2, were

similar to those described by Angers *et al.* (2005), and OG2 and OG3 are similar to 2-C-D and 2-C-C, which were described by Graignic *et al.* (2014), respectively. The respective distances between logged and unlogged sites were 17.3 km (OG1-SC1), 7.8 km (OG2-SC2), and 1.6 km (OG3-SC3) (Table A5.1).

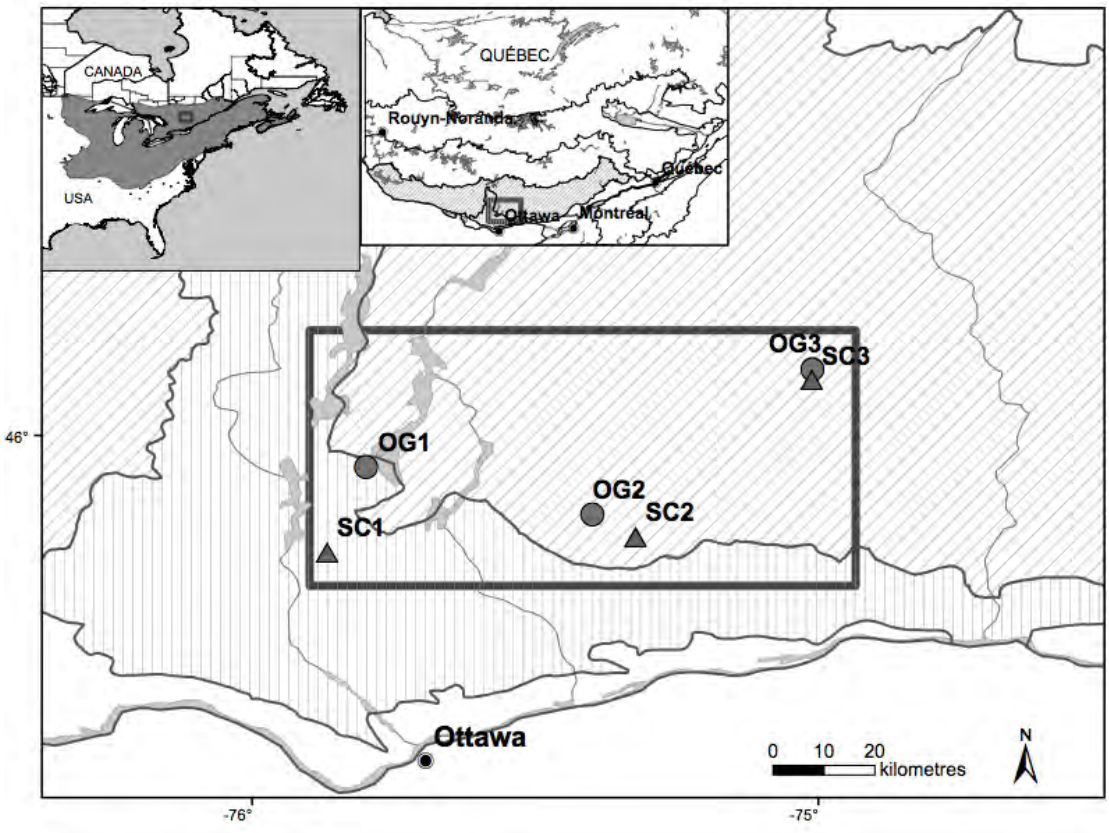

Figure 5.1 Map of the study area, which is situated at the northern continuous distributional limits of sugar maple (*Acer saccharum*) in Québec, showing the locations of the 6 study sites (circles, old-growth sites; triangles, selection cutting sites), sugar maple–yellow birch (*Betula alleghaniensis*) bioclimatic domain (slanted hatching), sugar maple–basswood (*Tilia americana*) bioclimatic domain (vertical hatching), and boundaries of all bioclimatic domain limits (thin lines) (Saucier *et al.*, 2003).

Tissue samples (usually leaves or bark) from 360 sugar maple individuals were collected in 2008 and 2009. Three cohorts were sampled per site: mature trees (M, ≥ 10 cm d.b.h., $N = 20–22$), saplings (Sa, 1 ≤ dbh < 10 cm, $N = 20$), and seedlings (S1, dbh < 1 cm, $N = 18–20$). Seedling age was determined as described by Graignic *et al.*

(2014), with seedlings corresponding to seed that had been produced between 1986 and 2006. The mast of oldest seedlings originated from 1996 (Graignic *et al.* 2014). Most seedlings had germinated after logging, while saplings and mature trees were present prior to logging. We included an additional class, i.e. post-harvested seedlings (S2, N = 11–17), which had only seedlings that originated from seeds produced between 1991 and 2006. Samples were dried over silica gel and maintained at room temperature until they were needed for genetic analyses.

5.4.2. Molecular methods

DNA was extracted using Extract-N-Amp™ Plant PCR Kits (Sigma-Aldrich, Oakville, ON, Canada). All samples were genotyped for 18 variable microsatellite loci using PCR and genotyping protocols as previously reported (Graignic *et al.*, 2013). The following modifications to the protocol were applied: (1) five different multiplex PCR sets were used (see Table A5.2); (2) 0.1 μM of each primer; and (3) 37 cycles in the PCR amplification procedure.

5.4.3. Marker genetic diversity

For each locus, the total number of alleles (A_T), mean number of alleles per locus (A), mean observed (H_O) and expected (H_E) heterozygosity, and the inbreeding coefficient (F_{IS}) were estimated using FSTAT 2.9.3.2 (Goudet, 2001). Departure from Hardy–Weinberg equilibrium (HWE) per locus in each population was tested, together with linkage equilibrium between all pairs of loci in each population, using exact tests that were conducted in GENEPOP 4.2.1 (Rousset, 2008). Markov chain parameters for HWE were 10 000 dememorizations, followed by 500 batches of 5000 iterations per batch. We corrected for multiple comparisons using a sequential Bonferroni adjustment of P-values to a predetermined experiment-wise error rate of 0.05 (Rice, 1989). Null allele frequencies were estimated using FREENA (10 000 replicates; Chapuis & Estoup, 2007). This program was selected because it uses the

algorithm of Dempster *et al.* (1977), which provided the most accurate estimate among the several algorithms that were tested by Chapuis & Estoup (2007). We performed a Mantel test (1000 permutations) between pairwise F_{ST} values with and without correction for null alleles that were calculated with FREENA. These tests were performed using the *mantel* function in the VEGAN library (Oksanen *et al*., 2011) within the R statistical environment (version 2.13.1, R Development Core Team, 2011).

5.4.4. Genetic diversity and differentiation between cohorts and forest types

For each stand, the mean number of alleles per locus (A), mean allelic richness (A_R), mean observed heterozygosity (H_O), mean expected heterozygosity (H_E), pairwise F_{ST}, mean pairwise F_{ST} and inbreeding coefficient (F_{IS}) were estimated using FSTAT. Tests for heterozygote deficiency were performed using GENEPOP (Markov chain parameters: 10 000 dememorizations, followed by 500 batches of 5000 iterations per batch; Fisher's exact tests). Tests were calculated for each stand using data for pooled individuals (PI), mature trees (M), saplings (Sa), and seedlings (S1 and S2) separately. Allelic richness was estimated for each cohort and sampled sites using a rarefaction method (El Mousadik & Petit, 1996).

To compare A_R, H_O, He and F_{IS} between forest types (OG and SC), pairs (1, 2 and 3), and cohorts (M, Sa and S1, or M, Sa and S2), we performed a linear mixed-model analysis (LMM, using the *lme* function in the NLME library of R; Pinheiro *et al.*, 2011). The fixed effects were forest type, pair and cohort and their two- and three-way interactions, and microsatellite marker was considered as a random effect. We used two data sets (M, Sa and S1; M, Sa and S2). Assumptions of normality and homoscedasticity were verified graphically. Models were simplified by stepwise backward elimination of non-significant fixed effects terms to produce the most parsimonious model. There was no significant difference between forest types for F_{ST}

and this index was subsequently not included in the analysis. To compare the same indices, we also performed the analysis using FSTAT (see Table A5.6).

5.4.5. Partitioning of molecular variation

The structure of the genetic variation was determined using the hierarchical analysis of molecular variance (AMOVA) that is implemented in GENALEX 6.5b3 (Peakall & Smouse, 2006). Genetic differentiation among populations was estimated by the Φ_{PT} statistic. We performed separate significance tests (9 999 permutations) between pairs (1, 2 and 3), between forest types (OG and SC) within pairs and within stands, and between pairs, between cohorts (M, Sa and S1) within pairs and within cohorts for OG and SC.

5.4.6. Allele frequencies

The effect of selection cutting on allele frequencies was tested using four classes: common ($f \geq 0.75$), intermediate ($0.75 > f \geq 0.25$), low ($0.25 > f \geq 0.01$) and rare ($f < 0.01$). We also added two classes, low ($0.25 > f \geq 0.05$) and rare ($f < 0.05$), using a level of 0.05, as suggested by Marshall and Brown (1975). Allele frequencies were estimated using FSTAT. The analyses were performed among forest types or cohorts (M, Sa, S1 and S2).

5.4.7. Bottlenecks

To test for recent reduction in effective population size following selection cutting, we used BOTTLENECK 1.2.02 (Cornuet & Luikart, 1996) for each population. Evidence of bottlenecks was tested using heterozygote excess and allele frequency mode shift tests. For the test of heterozygote excess, we used 3 different mutation models: infinite allele mutation (IAM), stepwise-mutation model (SMM), and two-phase mutational model (TPM). In TPM, we chose 70, 90, 95 and 99 % SMM, and 12 % variance of multi-step mutations was assumed (Piry *et al*., 1999). Significance tests used one-tailed Wilcoxon signed-rank tests. Population bottlenecks cause a mode-

shift distortion of the typical L-shaped allele frequency distribution (Luikart & Cornuet, 1998).

5.5. Results

5.5.1. Genetic variability of microsatellite markers

The total number of alleles per locus ranged from 3 to 28, while the mean number of alleles per locus ranged from 2.8 to 17.7 (Table A5.2). Five of the 18 loci (SM22, SM27, SM47, SM55 and SM56) failed to meet HWE in 3 populations (Table A5.3). These deviations from HWE were due to heterozygote deficiencies ($F_{IS} \geq 0.296$; Table A5.2). Four other markers also showed heterozygote deficiencies ($F_{IS} \geq 0.246$ for SM29, SM51, SM53 and SM60). These loci exhibited higher frequencies of null alleles (≥ 0.10) (Table A5.4). Their genetic structures (pairwise F_{ST}) were similar before and after correction for the presence of null alleles ($r = 0.90$, $P = 0.003$). All loci were considered independent because no significant linkage disequilibrium between pairs of loci within forest types was detected after Bonferroni correction. All loci (18) were used in further analyses.

5.5.2. Genetic diversity and differentiation between cohorts and forest types

The mean number of alleles per locus (A) ranged from 9.2 (SC3) to 9.5 (SC1, OG2, SC2 and OG3) between stands, and from 5.9 (S2 of SC3) to 7.6 (M of OG3) for cohorts (Table 5.1). No significant difference was detected between cohorts and forest types in terms of allelic richness (A_R) and expected heterozygosity (H_E), using both LMM (in R) and FSTAT (Table A5.6, A5.7).

Table 5.1 Genetic variability estimates of sugar maple (*Acer saccharum*) populations in Outaouais, Québec, for mature trees (M), saplings (Sa), seedlings (S1), pooled individuals (PI) and only seedlings that emerged after logging (S2), separately. To compare allelic richness between each cohort (M, Sa, S1 and S2), we calculated allelic richness using those cohorts in the same database (A_R*). Populations were old-growth (OG) forest or had received a single selection cutting (SC) in end of 1990–beginning of 1991.

Populations	Cohorts	N	A	A_R	A_R^*	H_O	H_E	F_{IS}	F_{ST}
OG1	M	20	7.1	6.5	5.4	0.583	0.692	0.158***	0.003
	Sa	20	6.6	6.0	5.1	0.440	0.676	0.348***	0.000
	S1	20	7.1	6.4	5.5	0.496	0.684	0.274***	0.004
	PI	60	9.4	9.0	—	0.507	0.686	0.260***	0.000
	S2	17	6.6	5.3	5.3	0.477	0.678	0.296***	0.004
SC1	M	20	7.2	6.6	5.5	0.583	0.706	0.174***	0.001
	Sa	20	6.9	6.2	5.3	0.480	0.697	0.312***	0.006
	S1	20	6.9	6.3	5.3	0.521	0.690	0.245***	0.003
	PI	60	9.5	9.1	—	0.529	0.699	0.243***	0.001
	S2	15	6.3	5.4	5.4	0.505	0.687	0.265***	0.004
OG2	M	20	6.9	6.4	5.3	0.617	0.696	0.114***	0.001
	Sa	20	6.9	6.3	5.4	0.520	0.676	0.230***	0.003
	S1	20	7.0	6.3	5.4	0.516	0.693	0.255***	0.002
	PI	60	9.5	9.0	—	0.552	0.688	0.198***	-0.001
	S2	17	6.7	5.3	5.3	0.510	0.678	0.248***	0.004
SC2	M	20	6.5	6.3	5.3	0.597	0.698	0.145***	0.005
	Sa	20	6.7	6.1	5.2	0.498	0.658	0.242***	0.003
	S1	20	7.0	6.4	5.4	0.539	0.712	0.243***	0.007
	PI	60	9.5	9.1	—	0.543	0.694	0.218***	0.000
	S2	15	6.1	5.2	5.2	0.528	0.703	0.249***	0.010
OG3	M	22	7.6	6.7	5.5	0.629	0.695	0.095**	0.002
	Sa	20	6.7	6.1	5.2	0.544	0.688	0.209***	0.005
	S1	18	6.8	6.3	5.4	0.548	0.687	0.202***	0.008
	PI	60	9.5	9.0	—	0.577	0.693	0.168***	0.002
	S2	11	6.0	5.6	5.6	0.555	0.699	0.206***	0.006
SC3	M	20	6.5	6.1	5.1	0.553	0.690	0.199***	0.001
	Sa	20	7.4	6.7	5.7	0.531	0.698	0.239***	0.003
	S1	20	6.8	6.1	5.2	0.452	0.683	0.337***	0.008
	PI	60	9.2	8.8	—	0.511	0.690	0.260***	0.001
	S2	15	5.9	5.1	5.1	0.460	0.673	0.317***	0.011
Means			9.4	9.0	5.5	0.536	0.692	0.225	0.000

N, number of individuals; A, mean number of alleles per locus; A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient; F_{ST}, mean pairwise F_{ST}; HD, P-values for heterozygote deficit; and HE, P-values for heterozygote excess. Means were determined using PI except for A_R^*. *** $P \leq 0.001$; ** $0.001 < P \leq 0.010$ for tests of heterozygote deficiency.

Observed heterozygosity (H_O) and the inbreeding coefficient (F_{IS}) ranged from 0.440 (saplings in OG1) to 0.629 (mature trees in OG3), and from 0.095 (mature trees in OG3) to 0.337 (seedlings in SC3), respectively (Table 5.1). All cohorts of all

populations had a significant heterozygote deficit (all $P < 0.0054$), suggesting a departure from random mating in both forest types (Table 5.1). We found a significant difference between cohorts for both forest types with higher mean H_O and lower mean F_{IS} for mature trees ($H_O = 0.562$; $F_{IS} = 0.144$) compared to saplings ($H_O = 0.470$; $F_{IS} = 0.269$), S1 ($H_O = 0.482$; $F_{IS} = 0.260$), and S2 ($H_O = 0.472$; $F_{IS} = 0.262$) (Table A5.7 and Fig. 5.2). There was also a significant forest type × pair interaction for H_O for S2 and a marginally significant difference for seedlings (Fig. 5.2). Similar results were obtained using FSTAT (Table A5.6).

Means populations F_{ST} were very low (-0.002–0.002; Table 5.1). Only 3 pairwise F_{ST} were significant (OG3-SC1, OG3-SC3, and SC1-SC3), but their values were very low (0.004, 0.004 and 0.002, respectively; Table A5.5).

5.5.3. Partitioning of molecular variation

AMOVA revealed that most of the variation (99–100 %, $P = 0.015$–0.176; Table 5.2) was attributable to genetic variation within populations (stands or cohorts). A slight effect of cohorts (1 %, $P = 0.034$; Table 5.2) was detected in the SC.

5.5.4. Allele frequencies

No difference for allele frequencies was detected between logged versus unlogged stands, and between cohorts (PI, M, Sa, S1 or S2) (Table A5.8; Table 5.3). We observed a lower number of alleles in the rare ($f < 0.01$) frequency class only for the S2 cohort. This reduction was around 10 % compared to other cohorts (Table 5.3). Reduction in the percentage of rare alleles could be due to lower sampling size of the S2 cohort; however, similar a number of alleles (total) was found in S2 and Sa (192 vs 198 - All), S2 and Sa (161 vs 165 - OG), and in S2 and M (162 vs 167 - SC) (Table 5.3).

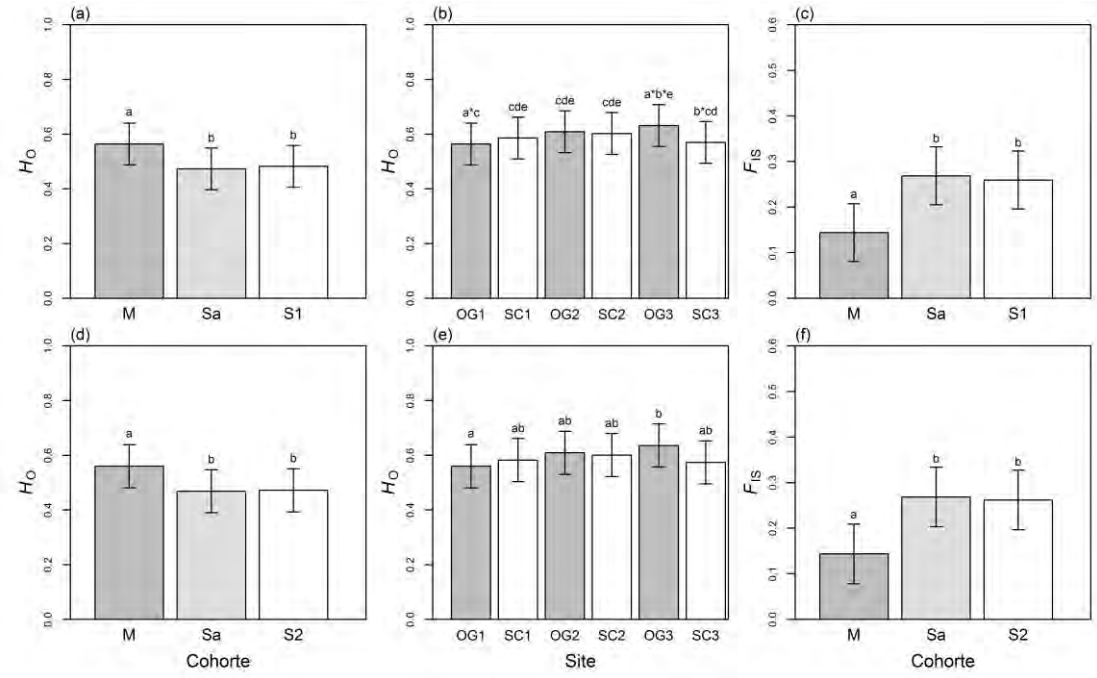

Figure 5.2 Predicted means (95% confidence intervals) of H_O for (a), (b), (d) and (e), F_{IS} for (c) and (f), cohorts (M: mature sugar maple, Sa: sugar maple sapling, and S1: sugar maple seedling and S2: post-harvest sugar maple seedling) for (a), (c), (d) and (f), forest types (OG: old-growth and SC: selection cutting) and pairs (1, 2, and 3) referred as sites names for (b) and (e), in Québec. (a), (b) and (c) used M, Sa and S1 data, and (d), (e) and (f) used M, Sa and S2 data. H_O, mean observed heterozygosity; F_{IS}, inbreeding coefficient. Means with the same letter do not differ at $\alpha = 0.05$, but differ (with an asterisk) at $\alpha = 0.10$.

Table 5.2 Results of analysis of molecular variance (AMOVA) showing the partitioning of genetic variance among pairs, forest types and cohorts.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variance	Phi (Φ) statistics	*P*-values
Between pairs	2	36.397	0.000	0	0.000	0.620
Between forest types within pairs	3	57.125	0.042	0	0.003	*0.070*
Within stands	354	5858.567	16.550	100	0.002	*0.062*
Total	359	5952.089	16.591	100		
OG						
Between pairs	2	34.050	0.000	0	0.000	0.476
Between cohorts within pairs	6	101.998	0.047	0	0.003	0.205
Within cohorts	171	2746.652	16.062	100	0.003	0.176
Total	179	2882.700	16.110	100		
SC						
Between pairs	2	39.261	0.006	0	0.000	0.416
Between cohorts within pairs	6	115.517	0.116	1	0.007	**0.034**
Within cohorts	171	2894.400	16.926	99	0.007	**0.015**
Total	179	3049.178	17.049	100		

d.f., degrees of freedom. Significant values at $\alpha = 0.05$ are in bold type and at $\alpha = 0.10$ in italics.

Table 5.3 Number of alleles per classes of frequency, per cohorts of the populations and grouping populations by forest types.

Populations	Cohorts	A_T	C	I	L0.01	R0.01	L0.05	R0.05
OG	M	179	0 (0%)	22 (12%)	116 (65%)	41 (23%)	55 (31%)	102 (57%)
	Sa	165	1 (1%)	21 (13%)	103 (62%)	40 (24%)	57 (35%)	86 (52%)
	S1	174	1 (1%)	20 (11%)	121 (70%)	32 (18%)	53 (30%)	100 (57%)
	PI	217	0 (0%)	21 (10%)	128 (59%)	68 (31%)	53 (24%)	143 (66%)
	S2	161	1 (1%)	20 (12%)	140 (87%)	0 (0%)	53 (33%)	87 (54%)
SC	M	167	0 (0%)	24 (14%)	110 (66%)	33 (20%)	53 (32%)	90 (54%)
	Sa	171	1 (1%)	18 (11%)	116 (68%)	36 (21%)	60 (35%)	92 (54%)
	S1	175	0 (0%)	20 (11%)	118 (67%)	37 (21%)	57 (33%)	98 (56%)
	PI	215	1 (0%)	18 (8%)	127 (59%)	69 (32%)	61 (28%)	135 (63%)
	S2	162	0 (0%)	20 (12%)	142 (88%)	0 (0%)	55 (34%)	87 (54%)
All	M	202	0 (0%)	21 (10%)	126 (62%)	55 (27%)	56 (28%)	125 (62%)
	Sa	198	1 (1%)	20 (10%)	121 (61%)	56 (28%)	55 (28%)	122 (62%)
	S1	207	0 (0%)	21 (10%)	125 (60%)	61 (29%)	52 (25%)	134 (65%)
	PI	243	0 (0%)	19 (8%)	57 (23%)	167 (69%)	129 (53%)	95 (39%)
	S2	192	1 (1%)	19 (10%)	138 (72%)	34 (18%)	55 (29%)	117 (61%)

A_T, total number of alleles; C, common $f \geq 0.75$; I, intermediate $0.75 > f \geq 0.25$; L0.01, low $0.25 > f \geq 0.01$; R0.01, rare $f < 0.01$; L0.05, low $0.25 > f \geq 0.05$; R0.05, rare $f < 0.05$; M, mature sugar maple; Sa, sugar maple sapling; S1, sugar maple seedling; PI, pooled individuals; S2, post-harvest sugar maple seedling.

5.5.5. Bottlenecks

Recent bottlenecks were detected in the three SC stands while none were apparent in the OG stands using IAM (Table 5.4). However, no bottleneck was detected in all stands using SMM, TMM, and mode-shift models.

Table 5.4 Bottlenecks results based on heterozygosity excess and mode shift.

Sites	Heterozygosity excess						Mode shift
	IAM	TMM				SMM	
		70%	90%	95%	99%		
OG1	0.08368	0.97003	0.99961	0.99994	1.00000	1.00000	Normal
SC1	**0.04488**	0.98075	0.99671	0.99883	0.99968	0.99974	Normal
OG2	0.06487	0.98658	0.99968	0.99992	0.99999	0.99999	Normal
SC2	**0.04071**	0.99552	0.99983	0.99995	0.99995	0.99997	Normal
OG3	0.05935	0.97842	0.99480	0.99832	0.99903	0.99961	Normal
SC3	**0.00140**	0.99800	0.99995	0.99999	1.00000	1.00000	Normal

Significant values ($\alpha = 0.05$) are in bold type.

5.6. Discussion

5.6.1. Genetic diversity in sugar maple populations

We observed a high level of genetic diversity in sugar maple. Previous studies (using allozymes) have also shown high levels of genetic diversity in this species (Table 5.5; A = 2.3, range: 1.10–5.00; H_E = 0.131, range: 0.015–0.275), which is typical of other *Acer* species and tree species in north-eastern North America (Table 5.5). Similar levels of diversity were reported for Norway maple (*Acer platanoides* L.), bigleaf maple (*A. macrophyllum* Pursh), American chestnut (*Castanea dentata* [Marsh.] Borkh.) and red oak (*Quercus rubra* L.), while lower levels have been observed in sycamore maple (*A. pseudoplatanus* L.) (Table 5.5). We previously found slightly lower values for A and A_R using the same 18 microsatellites (Table 5.5). In the present study, the number of individuals that were sampled per site was higher (N = 60 vs N= 40) and diversity was found principally within stands in both studies (Table 5.2; see Table A4.7 in Chapter IV). The values for A, A_R and H_E were

higher or similar to those reported for other *Acer* species and many other tree species in north-eastern North America (Table 5.5). However, A_R and H_E values were lower than those reported for mono maple (*A. mono* Maxim), northern pin oak (*Quercus ellipsoidallis* E.J.Hill) and red oak (Table 5.5).

We observed a positive and significant inbreeding coefficient (F_{IS} = 0.225, range: 0.168–0.260). The presence of heterozygote deficiency is common and has also been reported for *Acer* species and trembling aspen (*Populus tremuloides* Michaux) using microsatellite markers (Table 5.5). Heterozygote deficiency is often associated with inbreeding (high levels of consanguineous mating) or a Wahlund effect (mixing of differentiated gene pools). However, sugar maple is recognized for its low self-compatibility, which is related to dichogamy (Gabriel, 1968), and its frequent post-fertilization ovule abortion after self-pollination (Gabriel & Garrett, 1967). In the present study, sugar maple stands were localized compared to the species range and F_{IS} values could vary widely between populations. We previously reported, in Chapter IV, large variation in F_{IS} (-0.051–0.302; Table 5.5) for sugar maple populations that were sampled over a wide range in Québec. Namroud *et al.* (2005) also detected highly significant heterozygote deficiency in two trembling aspen populations in Québec, while Callahan *et al.* (2013) reported significant variation of F_{IS} (heterozygote excess to deficiency) in populations of this species across its natural geographic range (Table 5.5). In Korean maple (*Acer takesimense*), Takayama *et al.* (2013) observed high significant heterozygote deficiency in four populations, while others (3 populations) were at equilibrium. Hence, our F_{IS} values possibly reflected the level of genetic diversity for sugar maple in the study area.

Table 5.5 Comparison of genetic diversity using allozyme and microsatellite markers for populations of tree species in northeastern North America, and *Acer* species around the world.

Species	A	A_R	H_O	H_E	F_{IS}	Reference
Allozymes						
Angiosperm						
Acer platanoides	1.92 (1.50–2.50)	—	0.129 (0.066–0.238)	0.128 (0.063–0.207)	-0.012 (-0.373–0.189)	Rusanen *et al*. (2000)
Acer platanoides	2.0 (1.6–2.4)	—	0.126 (0.038–0.195)	0.132 (0.053–0.191)	0.066 (-0.085–0.285)	Rusanen *et al*. (2003)
Acer pseudoplatanus	2.78 (2.56–3.00)	—	0.293 (0.237–0.327)	0.238 (0.254–0.319)	-0.032 (-0.159–0.085)	Belletti *et al*. (2007)
Acer macrophyllum	1.71 (1.5–2.2)	—	0.118 (0.102–0.160)	0.152 (0.102–0.189)	0.166 (-0.086–0.332)	Iddrisu & Ritland (2004)
Acer saccharum	1.95 (1.64–2.18)	—	—	0.110 (0.098–0.132)	—	Perry & Knowles (1989)
Acer saccharum	2.2 (1.1–2.8)	—	0.169 (0.08–0.28)	0.171 (0.08–0.29)	—	Foré *et al*. (1992b)
Acer saccharum	2.9	—	0.15	0.148	—	Foré *et al*. (1992a)
Acer saccharum	2.07 (2.03–2.10)	—	—	0.115 (0.109–0.121)	0.062 (0.050–0.073)	Young *et al*. (1993a)
Acer saccharum	1.98 (1.78–2.41)	—	—	0.112 (0.088–0.138)	0.042 (-0.095–0.177)	Young *et al*. (1993b)
Acer saccharum	1.83	—	0.136	0.148	0.077	Simon *et al*. (1995)
Acer saccharum	3.46 (2.00–5.00)	1.99 (1.14–2.98)	0.113 (0.021–0.294)	0.116 (0.015–0.275)	0.025 (-0.108–0.073)	Baucom *et al*. (2005)
Castanea dentata	1.69 (1.50–1.89)	—	0.184 (0.135–0.264)	0.151 (0.096–0.196)	-0.226	Huang *et al*. (1998)
Fagus grandifolia	2.9 (2.9–2.9)	—	0.387 (0.382–0.392)	0.395 (0.383–0.407)	0.024	Houston & Houston (1994)
Fagus grandifolia	3.0 (2.78–3.33)	—	0.163 (0.150–0.175)	0.165 (0.150–0.179)	—	Houston & Houston (2000)
Populus tremuloides	2.7 (2.1–2.9)	—	0.125 (0.101–0.160)	0.235 (0.207–0.270)	0.462 (0.295–0.568)	Hyun *et al*. (1987)
Populus tremuloides	2.6 (2.2–2.9)	—	0.217 (0.197–0.242)	0.220 (0.193–0.244)	0.017	Lund *et al*. (1992)
Quercus rubra	2.08 (1.8–2.3)	—	—	0.186 (0.145–0.245)	0.100	Sork *et al*. (1993)
Gymnosperm						
Picea glauca	3.03 (2.17–3.83)	2.14 (1.86–2.37)	0.342 (0.221–0.414)	0.344 (0.199–0.412)	0.002 (-0.092–0.087)	O'Connell *et al*. (2006)
Picea rubens	1.47 (1.25–1.64)	—	0.075 (0.059–0.092)	0.079 (0.061-0.104)	0.043 (-0.037–0.224)	Hawley & DeHayes (1994)
Pinus strobus	2.02 (1.69–2.37)	—	0.129 (0.121–0.143)	0.152 (0.146–0.157)	—	Buchert *et al*. (1997)
Pinus strobus	2.35 (2.23–2.50)	—	0.215 (0.185–0.216)	0.195 (0.181–0.216)	-0.090 (-0.200–0.053)	Rajora *et al*. (1998)
Thuja occidentalis	1.6 (1.5–1.8)	—	0.116 (0.102–0.133)	0.129 (0.113–0.141)	0.106	Lamy *et al*. (1999)
Microsatellites						
Angiosperm						
Acer mono	12.63	—	—	0.802	-0.008	Kikuchi *et al*., (2009)
Acer mono	—	8.37 (7.38–9.65)	—	0.80 (0.70–0.85)	0.27 (0.20–0.32)	Takayama *et al*., (2012)
Acer okamotoanum	—	6.60 (6.11–7.41)	—	0.72 (0.66–0.76)	0.18 (0.03–0.24)	Takayama *et al*., (2012)
Acer pseudoplatanus	—		0.548 (0.543–0.553)	0.574 (0.573–0.574)		Pandey (2005)
Acer pseudosieboldianum	—	4.60 (3.79–5.25)	0.40 (0.32–0.46)	0.61 (0.53–0.68)	0.33 (0.21–0.43)	Takayama *et al*. (2013)

Table 5.5 (*to continued*)

Species	*A*	A_R	H_O	H_E	F_{IS}	Reference
Acer saccharum	9.4 (9.2–9.5)	9.0 (8.8–9.1)	0.536 (0.507–0.577)	0.692 (0.686–0.699)	0.225 (0.168–0.260)	Our study
Acer saccharum	8.2 (6.6–9.0)	7.0 (5.8–7.6)	0.597 (0.496–0.716)	0.693 (0.637–0.715)	0.138 (-0.051–0.302)	Chapter IV of this thesis
Acer skutchii	2.1 (1.5–2.5)	—	—	0.129 (0.054–0.247)	—	Lara-Gomez *et al*. (2005)
Acer takesimense	—	3.82 (3.59–4.23)	0.38 (0.30–0.47)	0.53 (0.48–0.58)	0.28 (0.08–0.47)	Takayama *et al*. (2013)
Quercus ellipsoidallis	13	—	0.67 (0.62–0.72)	0.79 (0.77–0.81)	0.145 (0.10–0.19)	Lind & Gailing (2013)
Quercus rubra	14.5 (13–15)	—	0.73 (0.70–0.75)	0.84 (0.83–0.86)	0.12 (0.07–0.17)	Lind & Gailing (2013)
Populus tremuloides	8.83 (7.58–10.08)	—	0.465 (0.45–0.48)	0.67 (0.61–0.73)	0.30 (0.21–0.39)	Namroud *et al*. (2005)
Populus tremuloides		5.99 (3.34–6.83)		0.758 (0.613–0.801)	0.019 (-0.12–0.19)	Callahan *et al*. (2013)
Populus tremuloides	7.44 (6.25–8.2()	—	0.556 (0.478–0.704)	0.725 (0.691–0.767)	0.201 (-0.054–0.325)	Wyman *et al*. (2003)
Gymnosperm						
Pinus strobus	8.21 (6.85–9.62)	—	0.516 (0.485–0.538)	0.597 (0.585–0.615)	—	Rajora *et al*. (2000)
Pinus strobus	7.7	7.0 (6.7–7.3)	0.465 (0.46–0.47)	0.485 (0.48–0.49)	0.03 (0.01–0.05)	Marquardt & Epperson (2004)
Thuja occidentalis	9.58 (7.83–11.17)	9.21 (7.66–10.68)	0.590 (0.505–0.640)	0.600 (0.519–0.662)	0.019 (-0.025–0.050)	Pandey & Rajora (2012a)
Thuja occidentalis	7.8 (5.0–10.0)	5.9 (4.6–6.9)	0.734 (0.463–0.883)	0.773 (0.712–0.840)	0.145	Xu *et al*. (2012)

A, mean number of alleles per locus; A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient. Range values were in parenthesis. "—" data not available.

5.6.2. Cohort differences

A lower observed heterozygosity (H_O) and higher F_{IS} was observed in the younger cohorts (Sa, S1 and S2) compared to mature sugar maple trees (Fig. 5.2). Contrary to our expectations, the level of genetic structure between cohorts was similar among forest types. The level of heterozygosity increased with age (here, in trees with d.b.h. ≥ 10 cm) in the SC and the OG stands, a result that is similar to other studies that have compared cohorts of different ages. This pattern has been reported in various coniferous tree species (Bush & Smouse, 1992; Nijensohn *et al.*, 2005). Wang *et al*. (2010) further demonstrated that the number of alleles (*A*) and H_E were higher in mature trees (> 300-years-old) than in seedlings (2- to 3-years-old) in an intact old-growth forest of dragon spruce (*Picea asperata* Mast.). Ballal (1994) reported lower heterozygosity and higher F_{IS} in sugar maple embryos than in seedlings and mature trees (≥ 30 cm d.b.h.). However, this pattern is not always observed. For example, Foré *et al.* (1992a) found no difference between embryos and older cohorts (1-year, d.b.h. ≤ 2 cm, 15–25 cm and ≥ 40 cm). Similarly, we found no difference between saplings (1–10 cm d.b.h.) and mature trees (≥ 10 cm d.b.h.) in sugar maple populations in Québec (see Chapter IV).

One explanation for the presence of higher level of heterozygosity in mature trees is selection against homozygotes that occurred during the self-thinning process. This may be explained either by higher/lower fitness of heterozygote/homozygote individuals, respectively (Charlesworth & Willis, 2009). Sugar maple typically forms uneven-aged stands and the mortality rate at the seedling stage is very high, particularly for younger seedlings (Graignic *et al.*, 2014). In theory, we could expect a decrease in the low-frequency allele class with age because during selection, rare deleterious alleles would be eliminated (Charlesworth & Willis, 2009). In fact, the percentage of rare alleles was similar among mature sugar maple, saplings and A5.1, and slightly lower in A5.2 (Table 5.3).

Another possibility is that mature sugar maple trees originated from overlapping generations, given that sugar maple can live from 300 to 400 years (Godman *et al.*, 1990). Seedlings (S2 cohort) originated from a maximum of four seed masts (Graignic *et al.*, 2014). The d.b.h. of mature sugar maple trees that were sampled ranged between 10 to 82 cm, which corresponds to ages between 35 and 285 years (Majcen *et al.*, 1984; Graignic *et al.*, 2014). Those generations could have been influenced by different random selection processes at their establishment and throughout their entire lifespans.

5.6.3. Selection cutting influences and implications

We detected a significant deviation from mutation-drift equilibrium under IAM in the three harvested stands, but not in the three old-growth stands (Table 5.4). However, IAM is very sensitive to violations of assumptions about mutation models and may not be the most appropriate model for microsatellite markers (Luikart & Cornuet, 1998). In addition, bottlenecks were not verified by the other models (Table 5.4).

Recent bottlenecks, which resulted from logging, are typically accompanied by a reduction in the mean number of alleles, the number of low frequency rare alleles, and allelic richness (Pautasso, 2009). In some cases, a reduction in the level of heterozygosity is observed (Rajora, 1999) because allelic diversity is reduced more rapidly than heterozygosity under bottlenecks (Nei *et al.*, 1975; Spencer *et al.*, 2000). We found no difference in A_R, H_E, H_O, and F_{IS} between OG and SC stands (Fig. 5.2). A very low level of differentiation between cohorts in SC stands was detected, while there was no differentiation in OG stands (Table 5.2). Thus, it appears that SC had a low negative effect on the genetic diversity of the remaining mature sugar maple trees.

The negative impact of SC on sugar maple stands was very weak and could be transient because we found (1) a high level of genetic diversity in sugar maple stands, (2) low genetic differentiation between stands ($F_{ST} \leq 0.004$) (Table 5.1 and Table A5.5), and (3) genetic diversity resided mostly within-population, as revealed by AMOVA (Table 5.2). Low F_{ST} values between stands that were separated by 80 km indicated high levels of gene flow. Long-distance effective wind-dispersal of pollen is reported for trees, e.g. up to 100 km for Scots pine (*Pinus sylvestris* L., Kremer *et al.*, 2012). Sugar maple is a wind-pollinated species (Gabriel & Garrett, 1984) and its seeds are dispersed to a maximum distance of 100 m (Johnson, 1988). Therefore, pollen gene flow is very important in sugar maple populations. Low levels of genetic differentiation have been reported for sugar maple stands in an adjacent region ($F_{ST} \leq 0.017$) and over a broader regional scale ($F_{ST} \leq 0.049$; Ontario to Nova Scotia, Canada; Young *et al.*, 1993a; Young *et al.*, 1993b).

5.7. Conclusions

In conclusion, our results indicated that the level of gene flow in OG and SC stands is sufficient to maintain the level of genetic diversity for future generations. However, we also found a small negative influence of SC on mature sugar maple diversity, which may create a genetic bottleneck. Harvesting on our sites had occurred 18 years before sampling and the next SC is planned in 15–25 years. A second harvesting in the same stands is thus possibly very soon. It could over-imposed several very weak lost of genetic diversity and possibly lead to erosion of maternal genetic diversity. After one SC harvest, we would suggest that this type of treatment, whereby forest stands are effectively managed as uneven-aged structures, was not detrimental in terms of its effects on genetic diversity. However, we could not accurately predict the effects of multiple logging. Therefore, we would recommend the monitoring of genetic diversity in sugar maple cohorts after multiple selection cutting.

5.8. Acknowledgements

We thank Elizabeth Turcotte who provided field assistance. We are grateful to William F. J. Parsons for careful language editing. This work was funded by an NSERC (Natural Sciences and Engineering Research Council of Canada) strategic grant (STPGP 336871) to Francine Tremblay.

CHAPITRE VI

CONCLUSION GÉNÉRALE

6.1. Effets des différents types de fragmentation

L'objectif de cette thèse était d'étudier la dynamique de régénération et la diversité génétique des populations nordiques, fragmentées d'érable à sucre. Il s'articule autour de l'hypothèse que ces populations pourraient être à l'origine de l'expansion vers le nord de l'érable à sucre dans un contexte de changements climatiques.

Nous avons montré que la reproduction sexuée était importante (Chapitre II), la diversité génétique était élevée (Chapitre IV) et la différenciation génétique était faible (Chapitre IV), chez les populations d'érable à sucre réparties sur l'ensemble du Québec. Le climat joue un rôle sur la reproduction de cette espèce, car des températures estivales chaudes et sèches coïncidaient avec de bonnes années semencières l'année suivante. Il joue aussi un rôle sur la survie des plantules d'érable à sucre, car un mois de juillet chaud et humide était lié à l'augmentation du nombre de plantules. Les changements climatiques anticipés devraient donc contribuer à l'augmentation du nombre de plantules d'érable à sucre au nord (Chapitre II). Tous ces éléments valident l'hypothèse selon laquelle les populations nordiques fragmentées d'érable à sucre seront en mesure de se régénérer, survivre et sont suffisamment diversifiées au niveau génétique pour être à l'origine de l'expansion vers le nord de cette espèce.

Par ailleurs, nous avons montré l'existence de différences, au niveau écologique et génétique, entre la zone de répartition discontinue fragmentée et la zone continue (Chapitre II et IV). Les différences observées permettent d'appuyer l'hypothèse d'un patron de variation génétique des populations centrales vers les populations marginales (Eckert *et al.*, 2008). Toutefois, comme nous n'avons échantillonné que des populations marginales situées au nord (et non est, ouest ou sud), nous ne sommes pas en mesure de privilégier cette hypothèse comparativement à celle d'un patron de variation génétique qui serait le résultat du déplacement de l'espèce vers le nord de son aire de répartition suite au dernier maximum glaciaire (Hampe & Petit, 2005).

Il faut toutefois noté que les différences observées n'étaient significatives que pour le transect ouest (région d'Abitibi-Témiscamingue). En effet, nous avons vu que l'érable à sucre se reproduisait moins bien au nord (zone discontinue) par rapport au sud (zone continue) en Abitibi-Témiscamingue (Chapitre II). Cette différence se situait tant au niveau du nombre de samares pleines (contenant une graine) pour la période se situant entre 2008–2011, qu'au niveau du nombre de plantules dénombrées en 2008–2009 (années semencières en 1996, 2002, 2006). Au niveau génétique (Chapitre IV), nous avons trouvé aussi une différence entre les populations du sud et du nord du gradient ouest avec une plus grande diversité génétique (richesse allélique, A_R) et une plus faible différenciation génétique (F_{ST}) au sud (A_R = 7.3; F_{ST} = 0.004) comparativement au nord (A_R = 6.6; F_{ST} = 0.030).

Les analyses génétiques ont mis en évidence que, pour l'érable à sucre, (1) les populations les plus nordiques (1-D-A, 1-D-B, 2-D-A et 3-D-A) étaient déterminantes pour révéler la différence entre la zone discontinue et continue, (2) la migration de l'érable à sucre au Québec aurait commencé à l'est, puis à l'ouest et (3) les populations nordiques de l'ouest sont probablement issues d'une migration d'est en ouest et non du sud vers le nord.

La coupe forestière quant à elle, n'a pas eu d'impact majeur au niveau génétique (Chapitre V). Toutefois, les populations qui ont subi des coupes de jardinage en 1990–1991, semblent toutes avoir subi un goulot d'étranglement (bottleneck) récent. Ce goulot d'étranglement nous semble intrigant, des investigations à plus longtemps terme (observations après plus de générations d'érable à sucre) nous paraissent indispensables.

6.2. Implications pour l'exploitation forestière et la conservation

6.2.1. Implications de nos travaux de recherches pour l'aménagement forestier

Nous n'avons observé aucune perte de diversité dans les érablières 18 ans après la coupe de jardinage, comparativement aux forêts anciennes. Les résultats ont révélé la présence d'un goulot d'étranglement, mais ils doivent être interprétés avec prudence puisque les seuils de significativité variaient suivant le modèle utilisé (effet significatif sous IAM et non significatif pour SMM; Luikart & Cornuet, 1998). C'est la raison pour laquelle l'exploitation de l'érable à sucre par la coupe de jardinage, telle que pratiquée actuellement, semble appropriée du point de vue de la préservation de la diversité génétique. Toutefois suivant le principe de précaution, des mesures de diversité et structure génétique devraient être faites après les coupes pratiquées sur la même zone, ceci afin de valider le peu d'effet à long terme de ce type de coupe sur la diversité génétique de l'érable à sucre.

L'exploitation par coupe de jardinage des érablières les plus nordiques serait à proscrire puisqu'elles sont moins diversifiées au niveau génétique et plus différenciées. Les populations au nord-ouest du Québec, en particulier, semblent ainsi encore plus à risques. Certaines populations nordiques, sont déjà protégées par le gouvernement du Québec, car elles sont des écosystèmes forestiers exceptionnels (EFE).

6.2.2. Intérêts pour les compagnies forestières

Les problèmes environnementaux et de gestion des ressources représentent un enjeu important et suscitent un intérêt de plus en plus important de la part des consommateurs. L'achat par le consommateur de bois issu d'une bonne gestion de la ressource est possible grâce à des certifications environnementales. La plus connue en Amérique du Nord est la certification FSC (Forest Stewardship Council), créée en 1993, elle est internationale et a connu un essor ces dernières années (https://ca.fsc.org). L'industrie forestière, consciente de cet intérêt, cherche à obtenir cette certification pour le bois qu'elle exploite. Au Québec, lors de l'entrée en vigueur du nouveau régime forestier, le 1er avril 2013, près de 51 % de la forêt du domaine de l'État avait été certifiée FSC par les compagnies forestières (https://www.mrn.gouv.qc.ca/forets/amenagement/amenagement-certification.jsp). Le 27 mars 2013, le MRNQ et le Conseil de l'industrie forestière du Québec ont convenu que les sociétés forestières demeureraient titulaires de ces certificats.

Deux des principes de la certification FSC sont en lien avec nos travaux. Le principe 6 du FSC souligne l'intérêt de maintenir et conserver les valeurs environnementales. Ces valeurs environnementales comprennent l'aspect de la fonction des écosystèmes incluant les processus évolutifs comme les flux génétiques. L'évaluation du maintien des valeurs environnementales pourraient donc passer par une évaluation avant et après coupes de la diversité et de la structure génétique de la zone coupée comme nous le suggérons pour les coupes de jardinage. La norme FSC exige de l'organisation que celle-ci identifie et protège des superficies représentatives des écosystèmes natifs (nommées « aires-échantillons »). Dans ce cadre, nous proposons que le gouvernement et les compagnies s'entendent pour couvrir l'aire de répartition d'une espèce avec des aires protégées de forêts anciennes comme c'est déjà le cas pour les EFE et en leur absence, des massifs forestiers les moins perturbés possibles. La certification FSC est internationale, une concertation serait donc

souhaitable entre les provinces canadiennes et entre le Canada et les USA afin d'améliorer la couverture de protection sur l'ensemble de l'aire de répartition d'une espèce. Le principe 9 de la certification FSC demande que l'organisation préserve et/ou augmente le nombre de massifs à Hautes Valeurs de Conservation (HVC) dans l'unité de gestion en appliquant le principe de précaution. Dans ce cadre, la protection des populations nordiques d'érable à sucre et les forêts anciennes plus au sud est fondamentale.

6.3. Perspectives de recherche

6.3.1. Élargir la zone d'étude & mariage à trois (écologie–génétique–palynologie)

Les données génétiques (Chapitre IV) et palynologiques tendent à démontrer que la migration de l'érable à sucre aurait débuté par l'est du Québec (Montréal–Québec–Saguenay–Lac-St-Jean) et une deuxième voie de migration serait arrivée par l'ouest du Québec (Témiscamingue). Les données palynologiques ont montré qu'une voie migratoire de l'érable à sucre en Amérique du Nord aurait suivi les Appalaches (Braun, 1950) pour atteindre le sud-est du Québec vers 9 000 ans AA (Lavoie & Richard, 2000), alors que la présence de l'érable à sucre est détectée 4 000 ans AA à la pointe de la Gaspésie (Richard & Grondin, 2009). Il serait intéressant d'échantillonner des populations en Gaspésie et de couvrir l'extrême sud-est du Québec afin de vérifier si une signature génétique confirme une migration plus tardive en Gaspésie. Faire une étude, en parallèle, approfondie au niveau écologique permettrait de mieux comprendre pour quelle raison la migration de l'érable à sucre a été retardée. Le sol n'était pas propice à l'établissement de l'érable à sucre? D'autres espèces étaient déjà établies et rentraient en compétition avec l'érable à sucre ?

Nous n'avons pas pu départager l'hypothèse de « centre-périphérie » (Eckert *et al.*, 2008) vs la « migration post-glaciaire » (Hampe & Petit, 2005), en relation avec la variation génétique retrouvée entre les populations d'érable à sucre nordiques

marginales et les populations de la zone continue (Chapitre IV). Cette question a un intérêt majeur est reste en suspens pour de nombreuses espèces (Guo, 2012). Afin de répondre à cette question, les recherches futures devront couvrir les niveaux écologiques (capacité des populations périphériques fragmentées à se reproduire) et génétiques (populations périphériques différenciées génétiquement) vers le sud, l'est et l'ouest de l'aire de répartition de l'érable à sucre.

Nous n'avons pas pu valider l'hypothèse du retrait de l'érable à sucre ou de « saut-de-puce » à l'origine des populations marginales nordiques d'érable à sucre. Afin d'arriver à répondre à cette question, une approche intéressante consisterait à prélever des carottes de sédiments lacustres dans les zones situées à proximité des populations très nordiques afin d'établir si l'abondance de l'espèce et la taille des populations ont varié dans le temps. L'analyse du pollen et des macrorestes nous indiquerait si, par le passé, l'érable à sucre était plus abondant dans la région par rapport à maintenant et à quel moment remonte son arrivée. Si une quantité suffisamente d'échantillon pouvait être récoltée, une analyse génétique sur l'ADN ancien d'érable à sucre pourrait aussi apporter des réponses à cette question.

6.3.2. Quels marqueurs utiliser ? Vers la révolution du séquençage à haut débit

De nouvelles études génétiques pourront êtres faites en utilisant nos marqueurs microsatellites nucléaires (Chapitre III et IV). Les marqueurs microsatellites ont un taux d'évolution rapide, une grande diversité dans les populations, et sont distribués abondamment et aléatoirement sur le génome (Ellegren, 2004). Ils font partie des marqueurs nucléaires d'un locus avec le plus de variabilité (Sunnucks, 2000). Moins de variabilité intra-spécifique est retrouvée pour les organelles que pour l'ADN du noyau (ADNn) (Wolfe *et al.*, 1987). Malgré cela, il nous a été difficile d'obtenir des marqueurs microsatellites nucléaires polymorphes pour cette espèce (Chapitre II). Dans ce cas, les marqueurs microsatellites nucléaires continuent à êtres utilisés pour

les études intra-spécifiques à large échelle pour plusieurs espèces comme, par exemple, pour le peuplier faux-tremble (Callahan *et al.*, 2013).

Cependant, pour avoir une signature de la migration postglaciaire plus pertinente, il est recommandé d'utiliser d'autres types de marqueurs nucléaires et des marqueurs génétiques provenant d'organelles (chloroplaste et mitonchondrie) pouvant être mieux ordonnés dans l'évolution que des marqueurs microsatellites (Ellegren, 2004). Chez certaines espèces, une concordance des structures de l'ADN du chloroplaste (ADNcp), de la mitonchondrie (ADNmt) et du noyau a été observée, tandis que chez d'autres espèces il y a divergence (Gamache *et al.*, 2003; Fontaine *et al.*, 2004; Petit *et al.*, 2005; Meng *et al.*, 2007; Bai *et al.*, 2010). L'ADN des organelles a un intérêt tout particulier puisqu'il est hérité d'un seul parent (contrairement à l'ADNn) et il est donc possible de séparer une dispersion par les graines et par le pollen (Ennos, 1994; Newton *et al.*, 1999). Le chloroplaste est d'origine maternelle pour les angiospermes et paternelle pour les gymnospermes. La mitochondrie est généralement d'origine maternelle sauf pour quelques gymnospermes. Chez l'érable à sucre, l'ADNcp et l'ADNmt sont donc d'origine maternelle et reflètent la dispersion par les graines. Les amorces cytoplasmiques utilisées avec succès pour l'érable rouge et l'érable argenté (Mclachlan *et al.*, 2005; Saeki *et al.*, 2011), pour des pruniers, appartenant à la même classe que l'érable à sucre (Shaw & Small, 2005) et des amorces universelles (Taberlet *et al.*, 1991; Demesure *et al.*, 1995) pourront être testées pour amplifier l'ADN des organelles de l'érable à sucre.

Toutefois, comme ce type de marqueurs est moins variable, le séquençage à haut débit représenterait une alternative intéressante (Emerson *et al.*, 2010; Peñalba *et al.*, 2014). Cette technique a beaucoup évolué ces dernières années et elle est devenue beaucoup moins coûteuse. Nous l'avons utilisé dans le développement de nouveaux marqueurs microsatellites pour l'érable à sucre et découvrir d'autres types de marqueur est possible (Chapitre II) (Davey *et al.*, 2011). Nous proposons d'utiliser

cette technique pour séquencer tout l'ADN chloroplastique de nos 23 populations d'érable à sucre (Mariac *et al.*, 2014).

6.3.3. Le séquençage à haut débit au service de la détection de gènes adaptatifs

La technique du séquençage à haut débit est très performante et facilite la détection des gènes adaptatifs (Stapley *et al.*, 2010). Par exemple, elle permet de détecter un très grand nombre de marqueurs polymorphiques pour un seul nucléotide (SNPs, single nucleotide polymorphisms; Emerson *et al.,* 2010). Ce type de marqueur est parfois situé au niveau d'un gène (loci non neutre), ce qui le rend utile pour tester une signature d'adaptation locale. Ce type de marqueur est intéressant pour l'érable à sucre, car cette espèce montre des variations clinales, signe d'adaptation aux conditions locales (Kriebel, 1957). L'érable à sucre étant un organisme non-modèle, très peu de séquences ont été obtenues jusqu'à maintenant et aucun SNP développé, ce qui en fait un candidat intéressant pour la découverte de SNPs par séquençage à haut débit (Seeb *et al.*, 2011). L'identification de SNPs associé au *fitness* de l'espèce, offrirait un bon indicateur du niveau de variation adaptative au sein des populations (Van Tienderen *et al.*, 2002; Namroud *et al.*, 2008; Keller *et al.*, 2012).

Le séquençage de nouvelle génération peut aussi être utilisé pour cribler des gènes candidats de traits phénologiques en utilisant la différence d'expression des gènes (ARN), le séquençage aléatoire global du transcrit (whole-transcriptome shotgun sequencing; Ueno *et al.*, 2013).

Les recherches qui associent les gènes et les traits sont importantes dans un contexte de changements climatiques, car il sera possible d'identifier des populations menacées (Buckley & Kingsolver, 2012). Il serait recommandé d'utiliser ces nouvelles techniques sur des populations couvrant l'ensemble de l'aire de répartition de l'érable à sucre, ou tout au moins sur les populations marginales situées au nord et au sud (Alberto *et al.*, 2013). Les populations au sud de l'aire de répartition sont-elles

adaptées à la sécheresse et celles au nord au froid (Namroud *et al.*, 2008; Eckert *et al.*, 2009; Holliday *et al.*, 2010; Keller *et al.*, 2012) ? Les nouvelles techniques nous permettraient d'avoir une vue d'ensemble rapide et peu coûteuse sur les variations génétiques de ces populations. Pour répondre à ces questions, il est important d'observer les traits de ces populations, et il est nécessaire de faire des nouveaux tests de provenances localisés en dehors de l'aire de répartition de l'espèce d'intérêt (Alberto *et al.*, 2013).

ANNEXE A2

SUPPORTING INFORMATION FOR CHAPTER II

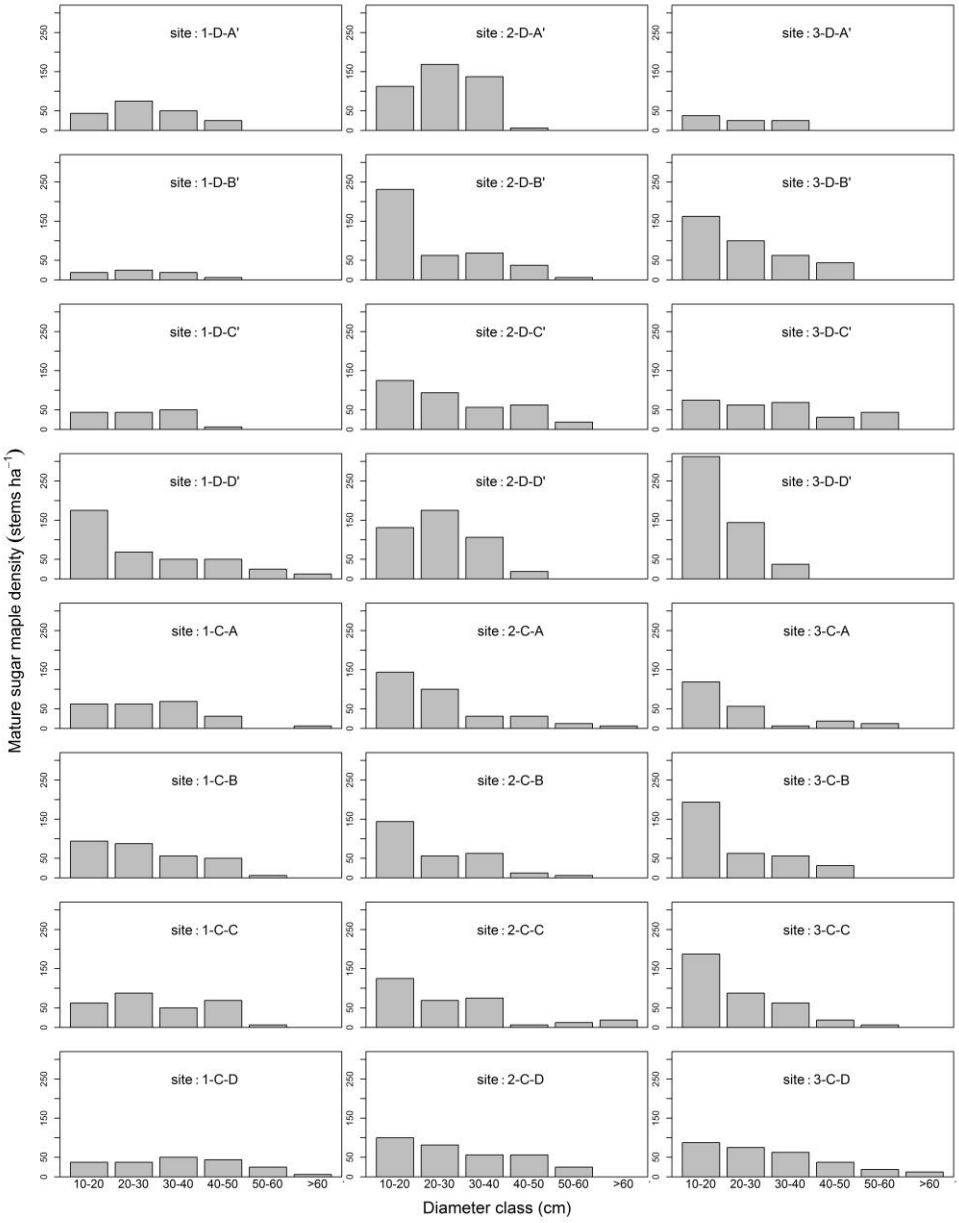

Figure A2.1 Diameter at breast height (1.30 m) structure of mature sugar maple trees in all 24 sites (*n* = 1133) in Québec.

Table A2.1 Summary of sample site coordinates, protection types, and site and stand characteristics. EFE, 'écosystèmes forestiers exceptionnels'; D, discontinuous; C, continuous; 1AY, undifferentiated till 50–100 cm thick; 1A, undifferentiated till; 1AM, undifferentiated till 25–50 cm thick; R1A, undifferentiated till < 50 cm thick. Data age class ecotone: VIN, old uneven-aged, more than three age classes and > 80-years-old; 70, 61–80 years old; 30, 21–40 years old.

Study ID	Study name	Protection type	Zone	Latitude	Longitude	Elevation (m)
		Transect 1				
1-D-A	Lac Labelle	EFE	D	48° 10′ 41.42″ N	79° 27′ 21.54″ W	379
1-D-B	Lac Okiwakamik	EFE	D	47° 51′ 46.18″ N	77° 44′ 6.85″ W	349
1-D-C	Rémigny		D	47° 40′ 52.23″ N	79° 2′ 18.82″ W	332
1-D-D	Lac de la Tour		D	47° 21′ 30.12″ N	78° 40′ 48.27″ W	351
1-C-A	Lac St Amand		C	47° 13′ 2.04″ N	79° 8′ 38.83″ W	318
1-C-B	Kipawa		C	46° 45′ 0.40″ N	78° 54′ 20.16″ W	345
1-C-C	Lac Six Milles		C	46° 26′ 43.69″ N	78° 0′ 44.32″ W	348
1-C-D	Lac Percival	EFE	C	46° 20′ 57.3″ N	78° 19′ 44.36″ W	330
		Transect 2				
2-D-A	Lac Pénobscot	EFE	D	47° 35′ 55.79″ N	74° 52′ 43.39″ W	493
2-D-B	Lac aux Cèdres		D	47° 20′ 47.83″ N	75° 45′ 15.95″ W	441
2-D-C	Réservoir Mitchinamécus		D	47° 12′ 52.70″ N	75° 11′ 59.32″ W	439
2-D-D	Lac des Polonais		D	47° 2′ 22.49″ N	75° 25′ 49.44″ W	343
2-C-A	Montagne du Diable	EFE	C	46° 42′ 41.36″ N	75° 34′ 7.03″ W	401
2-C-B	Lac Ecuyer		C	46° 30′ 46.30″ N	74° 36′ 21.02″ W	455
2-C-C	Lac Marie-Lefranc	EFE	C	46° 7′ 5.34″ N	75° 0′ 36.47″ W	410
2-C-D	Lac de l'Ecluse	EFE	C	45° 51′ 35.64″ N	75° 23′ 55.75″ W	388
		Transect 3				
3-D-A	Lac Patrick		D	48° 59′ 8.66″ N	71° 52′ 20.89″ W	268
3-D-B	Fjord du Saguenay	Réserve écologique G.Oscar-Villeneuve; EFE	D	48° 27′ 46.76″ N	70° 29′ 54.38″ W	362
3-D-C	Baie Eternité	Parc du Saguenay; EFE	D	48° 16′ 39.68″ N	70° 21′ 51.55″ W	157
3-D-D	Lac Edouard	Réserve écologique Judith-de-Brésole; EFE	D	47° 36′ 18.18″ N	72° 20′ 9.56″ W	450
3-C-A	Lac Paul		C	47° 18′ 39.89″ N	72° 37′ 57.65″ W	338
3-C-B	Lac Dickey		C	47° 4′ 29.06″ N	72° 51′ 12.02″ W	374
3-C-C	Lac Grandbois	EFE	C	47° 1′ 13.98″ N	72° 7′ 9.16″ W	342
3-C-D	Lac Larose		C	46° 36′ 34.34″ N	73° 2′ 27.67″ W	330

Table A2.1 (*to continued*)

Study ID	Study name	Aspect	Slope inclination	Deposit type	Drainage	data age class SIFORT	Age* (years)	d.b.h*. (cm)
				Transect 1				
1-D-A	Lac Labelle	south	18%	1AY	moderate	VIN	123	33.8
1-D-B	Lac Okiwakamik	north	2%	1A	good	30	148	34.7
1-D-C	Rémigny	south	12%	1AM	moderate	VIN	162	45.6
1-D-D	Lac de la Tour	north	18%	1AY	moderate	VIN	182	56.2
1-C-A	Lac St Amand	east	14%	1AM	moderate	VIN	120	49.1
1-C-B	Kipawa	east	16%	1AY	good	VIN	156	47.5
1-C-C	Lac Six Milles	north	7%	1A	moderate	VIN	114	32.5
1-C-D	Lac Percival	north	23%	1AM	good	VIN	147	54.5
				Transect 2				
2-D-A	Lac Pénobscot	south	18%	1AM	good	VIN	153	38.6
2-D-B	Lac aux Cèdres	north	14%	1AM	good	VIN	140	46.2
2-D-C	Réservoir Mitchinamécus	west	19%	1AM	moderate	VIN	167	50.4
2-D-D	Lac des Polonais	west	19%	1AM	moderate	VIN	173	40.8
2-C-A	Montagne du Diable	north	32%	1AY	good	VIN	161	49.7
2-C-B	Lac Ecuyer	south	12%	1AY	good	VIN	136	43.5
2-C-C	Lac Marie-Lefranc	south	5%	1AY	moderate	VIN	207	61.3
2-C-D	Lac de l'Ecluse	south	9%	1AM	good	VIN	155	51.5
				Transect 3				
3-D-A	Lac Patrick	south	9%	1AY	good	70	96	30.4
3-D-B	Fjord du Saguenay	south	47%	R1A	moderate	VIN	132	46.0
3-D-C	Baie Eternité	south	23%	1AY	moderate	VIN	222	55.9
3-D-D	Lac Edouard	total	0%	1AY	moderate	VIN	71	33.9
3-C-A	Lac Paul	north	11%	1AY	moderate	VIN	110	50.3
3-C-B	Lac Dickey	east	9%	1AM	good	VIN	139	44.5
3-C-C	Lac Grandbois	west	51%	1AM	good	VIN	99	42.0
3-C-D	Lac Larose	east	18%	1A	good	VIN	185	59.2

*Age or d.b.h., mean estimated of five largest trees

Table A2.2 Climatic data for the study area in the D (discontinuous) and C (continuous) zones along the three transects located in Québec, Canada.

Transect	1		2		3	
Zone	D	C	D	C	D	C
Mean annual temperature (°C)	1.6	4.1	2.2	3.3	1.4	3.1
Growing degree days above 5 °C	1405	1702	1445	1575	1341	1555
Mean temperature of coldest month (January, °C)	−16.9	−13.2	−14.9	−14.2	−17.0	−14.7
Mean temperature of warmest month (July, °C)	17.3	19.2	16.9	18.3	16.8	18.3
Total annual precipitation (mm)	927	929	1139	1062	1079	1029
Snow fall	28%	25%	31%	24%	32%	22%

Table A2.3 Difference in Akaike information criterion (ΔAIC_c) and weights (ω) of age structure models (negative exponential and power function) for sugar maple seedling 5-year age-class frequency distributions in all sites (n = 2880) located in Québec.

			Negative exponential		Power function	
Transect	Zone	Site	ΔAIC_c	ω	ΔAIC_c	ω
1	discontinuous	1-D-A′	0.0	1.00	20.6	0.00
		1-D-B′	27.9	0.00	0.0	1.00
		1-D-C′	49.6	0.00	0.0	1.00
		1-D-D′	48.8	0.00	0.0	1.00
	continuous	1-C-A	2.7	0.21	0.0	0.79
		1-C-B	17.0	0.00	0.0	1.00
		1-C-C	16.2	0.00	0.0	1.00
		1-C-D	1.1	0.37	0.0	0.63
2	discontinuous	2-D-A′	46.1	0.00	0.0	1.00
		2-D-B′	35.0	0.00	0.0	1.00
		2-D-C′	6.5	0.04	0.0	0.96
		2-D-D′	14.2	0.00	0.0	1.00
	continuous	2-C-A	43.6	0.00	0.0	1.00
		2-C-B	66.8	0.00	0.0	1.00
		2-C-C	31.0	0.00	0.0	1.00
		2-C-D	41.5	0.00	0.0	1.00
3	discontinuous	3-D-A′	9.7	0.01	0.0	0.99
		3-D-B′	24.2	0.00	0.0	1.00
		3-D-C′	102.7	0.00	0.0	1.00
		3-D-D′	23.2	0.00	0.0	1.00
	continuous	3-C-A	0.0	0.99	13.4	0.00
		3-C-B	0.0	0.81	2.9	0.19
		3-C-C	0.0	0.63	1.1	0.37
		3-C-D	0.0	0.98	8.1	0.02

Table A2.4 Results of two-way ANOVA with interaction for mature trees (n = 24) and linear mixed-effects models for saplings (n = 111) in Québec, prior to model simplification. Num. d.f., numerator degrees of freedom; den. d.f., denominator degrees of freedom.

Response variable	Explanatory variables	Num. d.f.	Den. d.f.	F	P
Total mature tree density	zone	1	18	8.9691	0.0078
	transect	2	18	1.4972	0.2503
	zone × transect	2	18	0.9381	0.4097
Mature sugar maple density	zone	1	18	0.1714	0.6837
	transect	2	18	3.9380	0.0381
	zone × transect	2	18	1.2546	0.3090
Total sapling density	zone	1	6	0.3446	0.5786
	transect	2	99	5.8395	0.0040
	zone × transect	2	99	1.4791	0.2328
Sugar maple sapling density	zone	1	6	0.4230	0.5395
	transect	2	99	4.9508	0.0089
	zone × transect	2	99	3.1813	0.0458
Total mature tree basal area	zone	1	18	0.0440	0.8363
	transect	2	18	1.1911	0.3267
	zone × transect	2	18	0.3520	0.7080
Mature sugar maple basal area	zone	1	18	2.3250	0.1447
	transect	2	18	1.3391	0.2870
	zone × transect	2	18	0.9355	0.4106
Total sapling basal area	zone	1	6	0.0026	0.9609
	transect	2	99	2.9039	0.0595
	zone × transect	2	99	0.2113	0.8099
Sugar maple sapling basal area	zone	1	6	0.3875	0.5565
	transect	2	99	1.1968	0.3067
	zone × transect	2	99	0.2708	0.7633

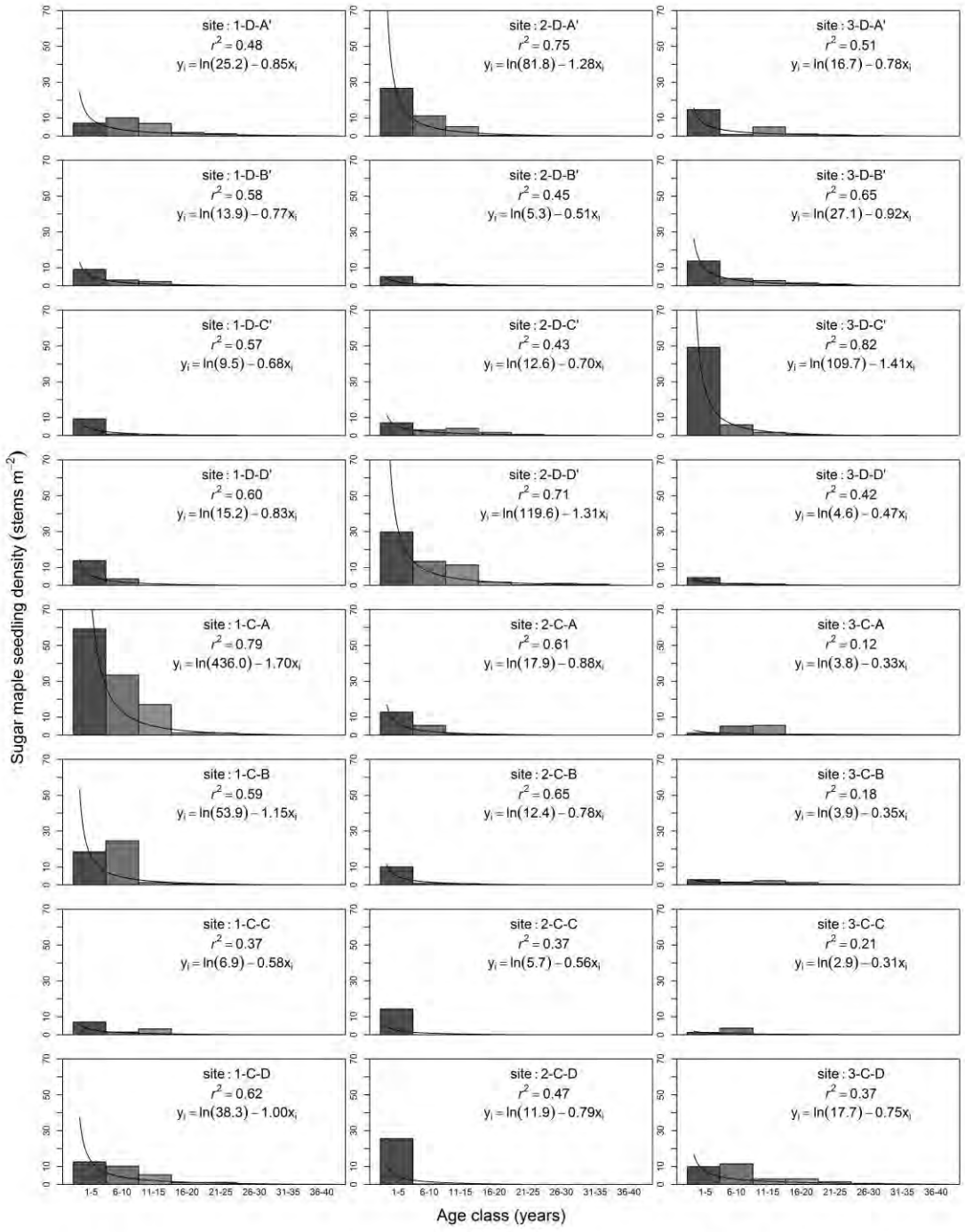

Figure A2.2 Sugar maple age structures of all 24 sites (n = 2880) in Québec. For each population, the linearized form of the power function is included, together with its coefficient of determination (r^2). $y_i = r - M \times x_i$, where y_i is ln(stems m^{-2} + 1), r is intercept of the curve [ln(R), where R is initial recruitment], M is slope of the curve (mortality rate), and x_i is ln(age).

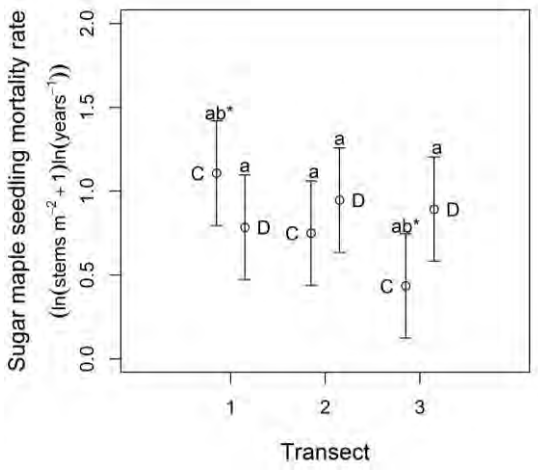

Figure A2.3 Predicted means (± 95% confidence intervals) of sugar maple seedling mortality rate (n = 24) in Québec. Means with the same letter do not differ at $\alpha = 0.05$, but differ (with an asterisk) at $\alpha = 0.10$. C, continuous zone; D, discontinuous zone.

Table A2.5 Difference in Akaike information criterion (ΔAIC_c), weights (ω) and number of estimated parameters (K) for model comparisons of the relative importance of stand characteristics and climate conditions as predictors of sugar maple seedling density (n = 353) in Québec. For brevity, only models with a cumulative $\omega \leq 0.95$ were shown.

Model	K	ΔAIC_c	ω
m_BA + m_ers_BA + s_BA + s_ers_BA + July_T + July_P	9	0.00	0.79
m_d + m_ers_d + s_ers_d + July_T + July_P	8	5.66	0.05
m_BA + m_ers_BA + s_BA + s_ers_BA + Oct_T + Oct_P	9	6.40	0.03
m_BA + m_ers_BA + s_BA + s_ers_BA + May_T + May_P	9	6.65	0.03
m_BA + m_ers_BA + s_BA + s_ers_BA + April_T + April_P	9	7.19	0.02
m_BA + m_ers_BA + s_BA + s_ers_BA	7	7.53	0.02

Explanatory variable abbreviations: m_BA, mature tree basal area; m_ers_BA, mature sugar maple basal area; s_BA, sapling basal area; s_ers_BA, sugar maple sapling basal area; m_d, mature tree density; m_ers_d, mature sugar maple basal area; s_ers_d, sugar maple sapling basal area; July_T, July mean temperature; July_P, July mean precipitation; Oct_T, October mean temperature; Oct_P, October mean precipitation; May_T, May mean temperature; May_P, May mean precipitation; April_T, April mean temperature; April_P, April mean precipitation.

ANNEXE A4

SUPPORTING INFORMATION FOR CHAPTER IV

Table A4.1 Genetic variability estimates of microsatellite markers used in the study of sugar maple (*Acer saccharum* Marsh.) in Québec.

Locus	GenBank access no.	M	Size range (bp)	A_T	A	H_O	H_E	F_{IS}	References
SM11	KC731552	3	178–200	13	6.3	0.575	0.629	0.083	(Graignic *et al*., 2013)
SM14	KC751436	4	70–120	22	14.3	0.773	0.888	0.130	(Graignic *et al*., 2013)
SM21A	KC751437	4	173–243	31	14.8	0.780	0.866	0.096	(Graignic *et al*., 2013)
SM22	KC751438	2	293–325	19	12.6	0.658	0.890	0.248	(Graignic *et al*., 2013)
SM27	KC751440	4	242–260	9	6.4	0.548	0.722	0.227	(Graignic *et al*., 2013)
SM29	KC751441	4	272–307	12	6.4	0.598	0.724	0.164	(Graignic *et al*., 2013)
SM34	KC751442	3	118–171	26	13.7	0.819	0.854	0.041	(Graignic *et al*., 2013)
SM36	KC751443	5	146–196	21	11.3	0.795	0.844	0.057	(Graignic *et al*., 2013)
SM37	KC751444	2	174–200	14	7.9	0.633	0.669	0.061	(Graignic *et al*., 2013)
SM42	KC751445	1	90–135	20	7.9	0.726	0.789	0.080	(Graignic *et al*., 2013)
SM47	KC751446	2	201–225	11	6.2	0.428	0.634	0.328	(Graignic *et al*., 2013)
SM51	KC751447	1	269–290	9	4.5	0.395	0.482	0.172	(Graignic *et al*., 2013)
SM53	KC751448	5	287–310	10	3.1	0.435	0.520	0.156	(Graignic *et al*., 2013)
SM55	KC751449	2	246–276	14	9.1	0.567	0.678	0.166	(Graignic *et al*., 2013)
SM56	KC751450	3	287–299	6	4.7	0.433	0.618	0.278	(Graignic *et al*., 2013)
SM60	KC751452	3	231–243	4	2.8	0.393	0.457	0.137	(Graignic *et al*., 2013)
Aop943	EF531298	1	143–158	6	4.6	0.529	0.527	-0.005	(Segarra-Moragues *et al*., 2008) (Graignic *et al*., 2013)
Am116	AB303350	1	230–273	21	10.3	0.659	0.682	0.031	(Kikuchi and Shibata 2008) (Graignic *et al*., 2013)

M, multiplexing arrangement; A_T, total number of alleles; A, mean number of alleles; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient.

Table A4.2 Summary of *P*-values for the Hardy–Weinberg equilibrium using GENEPOP (Marchov chain parameters: 10,000 dememorizations, followed by 500 batches of 5,000 iterations per batch).

	1DA	1DB	1DC	1DD	1CA	1CB	1CC	1CD	2DA	2DB	2DC	2DD	2CA	2CB	2CC	2CD	3DA	3DB	3DC	3DD	3CA	3CB	3CC	3CD
SM11	0.0084	0.4624	0.5799	0.0734	0.0534	0.0360	0.3199	0.0337	0.2573	X	0.0423	0.0453	0.0395	0.0793	0.2054	0.5682	0.0083	0.9193	0.3279	0.5603	0.0012	0.3101	0.2052	0.5629
SM14	0.1373	0.2148	0.0197	0.0768	0.0162	0.1430	0.0700	0.0014	0.2848	X	0.0018	0.6783	0.2159	0.2097	0.1402	0.3979	0.0040	0.0028	0.2548	0.5538	0.2092	0.2191	0.2174	0.3110
SM21A	0.0501	0.0786	0.3479	0.4064	0.0142	0.4691	0.7796	0.0002	0.0143	X	0.0373	0.3263	0.0331	0.7113	0.7279	0.0666	0.0342	0.5222	0.9107	0.5043	**0.0000**	0.1551	0.0316	0.0098
SM22*	**0.0000**	0.0173	0.2494	0.0024	0.0591	0.0362	**0.0001**	**0.0000**	0.0240	X	0.0010	**0.0000**	0.0003	**0.0000**	0.0002	**0.0000**	**0.0000**	0.2187	0.1322	0.5501	0.0062	0.0426	**0.0000**	0.5493
SM27*	0.0041	0.0061	0.1534	0.0186	0.0552	0.7882	0.7882	**0.0000**	**0.0001**	X	**0.0000**	0.0007	0.0193	**0.0001**	0.2009	0.0003	**0.0000**	0.1258	0.9890	0.7288	0.6601	0.6601	**0.0000**	0.7657
SM29	0.3152	0.1248	0.5151	0.1278	0.4147	0.8772	0.2453	0.0099	0.0099	X	0.0011	**0.0000**	0.1115	0.0002	0.0209	0.0078	**0.0001**	0.2102	0.5353	0.0892	0.1776	0.3961	**0.0000**	0.5572
SM34	0.3955	0.4077	0.5409	0.5499	0.1266	0.6818	0.6818	0.4333	0.0772	X	0.4617	0.0957	0.7941	0.1372	0.1517	0.3600	0.5645	0.4699	0.0625	0.2237	0.0851	0.0851	0.4614	0.2222
SM36	0.6068	0.0593	0.2524	0.3244	0.1953	0.2661	0.7693	0.0374	0.8950	X	0.8950	0.4894	0.8393	0.7280	0.2362	0.6907	0.0096	0.1099	0.1302	0.7423	0.1329	0.0420	0.0420	0.9558
SM37	0.3314	0.1111	**0.0000**	0.9321	0.8434	0.5688	0.1369	0.9524	0.0240	X	0.3770	0.1183	0.7735	0.2469	0.5934	0.0214	0.0024	0.5528	0.4821	0.5336	0.4371	0.4371	0.1365	0.9537
SM42	0.0116	0.1733	0.1762	0.0175	0.5883	0.3816	0.3063	0.5406	0.3180	X	0.1948	0.6008	0.2435	0.9011	0.1066	0.0187	0.6354	0.3495	0.2544	0.0680	0.0680	0.3038	0.1323	0.1042
SM47*	**0.0001**	**0.0001**	0.0034	**0.0000**	**0.0000**	0.0148	0.0109	0.0109	0.0436	X	0.0344	0.0049	0.0005	**0.0000**	0.0005	0.0139	**0.0000**	0.8770	0.0748	0.0723	**0.0001**	0.0002	**0.0000**	0.0129
SM51	0.4826	0.0358	1.0000	0.4594	0.2546	0.7119	0.9345	0.0168	0.8109	X	0.0084	0.1212	0.0879	**0.0000**	0.4727	0.0964	**0.0000**	1.0000	0.1210	0.9500	0.0009	1.0000	0.0013	0.6977
SM53	0.0404	0.1050	0.4928	0.0198	0.2152	0.5037	0.0127	0.3701	0.5096	X	0.0001	0.0563	0.5266	0.0079	0.0002	0.1633	0.0793	0.4904	0.7101	0.5299	0.0407	0.1953	0.0050	0.3397
SM55	0.3359	0.3359	1.0000	0.0649	0.7161	0.2880	0.4801	0.7785	0.4721	X	**0.0001**	0.0024	0.1680	**0.0000**	0.0046	0.0013	0.1252	0.5268	0.0038	0.2160	0.1743	0.0520	0.0017	0.1076
SM56*	0.0048	0.1476	0.2541	0.2859	0.1478	0.0094	0.9618	0.0232	0.1542	X	**0.0000**	0.0091	0.0056	**0.0000**	0.0014	**0.0001**	**0.0000**	0.2096	0.4728	0.4354	**0.0001**	0.2286	**0.0000**	0.5389
SM60	0.5242	0.2293	0.6131	0.6162	0.4016	0.3282	1.0000	0.0186	0.0058	X	0.0018	0.0591	0.6880	0.0431	0.0199	0.6393	0.0005	0.8042	0.0092	0.1839	0.2218	0.1332	0.0012	0.4719
Aop943	0.1550	0.1506	0.2770	0.2268	0.1954	0.9360	0.2570	0.4430	0.7489	X	0.4999	0.0912	0.1071	0.7181	0.7937	0.3839	0.8410	1.0000	1.0000	0.3578	0.0059	0.2053	0.5332	0.9946
Am116	0.4107	0.1192	0.8810	0.1784	0.1821	0.2278	0.9833	0.1946	0.8047	X	0.1805	0.0236	0.4223	0.1911	0.6536	0.8772	0.6798	0.0297	0.4957	0.2049	0.1392	0.7788	0.4427	0.5740

Significant *P*-values after Bonferroni correction are in bold type. *indicates locus at which most populations show signs of deviance from HWE.

Table A4.3 Summary of null allele frequencies for each pair of loci and populations using FREENA.

	1DA	1DB	1DC	1DD	1CA	1CB	1CC	1CD	2DA	2DB	2DC	2DD	2CA	2CB	2CC	2CD	3DA	3DB	3DC	3DD	3CA	3C-B	3CC	3CD
SM11	**0.102**	0.000	0.013	0.000	0.062	0.020	0.000	0.079	0.021	X	**0.101**	0.058	0.054	0.066	0.031	0.038	0.052	0.000	0.038	0.000	**0.101**	0.036	0.000	0.003
SM14	0.037	0.017	0.069	0.034	0.064	0.000	0.051	0.092	0.025	X	0.099	0.024	0.031	0.045	0.043	0.030	**0.123**	**0.112**	0.045	0.036	0.080	0.063	0.069	0.059
SM21A	0.093	0.051	0.029	0.022	0.071	0.000	0.013	0.098	0.000	X	0.097	0.067	0.063	0.000	0.000	0.094	**0.107**	0.000	0.000	0.000	**0.144**	0.000	0.048	0.009
SM22*	**0.165**	0.080	0.000	**0.131**	0.039	0.014	**0.149**	**0.205**	**0.105**	X	**0.138**	**0.286**	0.094	**0.242**	**0.146**	**0.161**	**0.212**	0.006	0.063	0.005	0.07	0.075	**0.254**	0.015
SM27*	**0.156**	**0.147**	0.026	**0.110**	0.046	0.041	0.023	**0.213**	**0.172**	X	**0.230**	**0.156**	**0.111**	**0.204**	0.084	**0.142**	**0.192**	0.000	0.000	0.000	0.094	0.031	**0.232**	0.000
SM29	0.029	0.039	0.000	0.057	0.017	0.000	0.035	0.032	**0.127**	X	**0.177**	**0.212**	0.059	**0.178**	0.049	**0.139**	**0.202**	0.000	0.000	0.066	0.099	0.041	**0.149**	0.000
SM34	0.003	0.000	0.000	0.000	0.039	0.000	0.000	0.065	0.000	X	0.000	0.034	0.000	0.018	0.000	0.000	0.026	0.017	0.031	0.015	0.085	0.044	0.000	0.000
SM36	0.074	0.034	0.005	0.064	0.056	0.000	0.000	0.094	0.000	X	0.000	0.000	0.000	0.022	0.027	0.000	0.056	0.008	0.000	0.000	0.064	0.058	0.065	0.000
SM37	0.077	0.078	0.000	0.000	0.009	0.000	0.000	0.000	0.022	X	0.000	0.076	0.000	0.046	0.000	0.071	**0.127**	0.005	0.034	0.000	0.000	0.036	0.096	0.000
SM42	**0.109**	0.011	0.037	0.056	0.009	0.030	0.000	0.061	0.021	X	0.018	0.000	0.000	0.000	0.070	0.048	0.034	0.000	0.002	0.088	0.000	0.025	0.009	0.019
SM47*	**0.157**	**0.176**	0.000	**0.218**	**0.178**	0.085	**0.156**	0.093	0.042	X	**0.113**	**0.160**	**0.143**	**0.179**	0.095	**0.137**	**0.173**	0.009	0.096	0.085	**0.161**	**0.162**	**0.231**	0.090
SM51	0.034	0.081	0.000	0.000	0.035	0.000	0.000	**0.104**	0.014	X	**0.131**	**0.107**	0.064	**0.237**	0.059	**0.105**	**0.206**	0.000	0.000	0.000	**0.165**	0.000	**0.160**	0.000
SM53	0.084	0.058	0.041	0.000	0.000	0.000	0.021	0.046	0.038	X	**0.161**	**0.112**	0.035	**0.172**	**0.187**	0.076	**0.105**	0.040	0.000	0.000	**0.113**	0.079	**0.167**	0.000
SM55	0.019	0.054	0.000	0.070	0.000	0.010	0.010	0.031	0.036	X	**0.146**	**0.155**	0.063	**0.214**	0.074	0.054	0.084	0.000	**0.116**	0.069	0.012	0.076	**0.129**	0.057
SM56*	**0.125**	0.083	0.000	0.080	0.082	**0.116**	0.010	**0.135**	0.081	X	**0.212**	**0.152**	**0.150**	**0.226**	**0.155**	**0.145**	**0.313**	0.000	0.000	0.000	**0.191**	0.076	**0.257**	0.000
SM60	0.037	0.075	0.000	0.012	0.047	0.000	0.000	**0.125**	**0.132**	X	**0.130**	**0.106**	0.000	**0.112**	**0.127**	0.033	**0.179**	0.000	0.000	0.076	0.030	0.068	**0.158**	0.000
Aop943	0.020	0.000	0.000	0.000	0.049	0.000	0.000	0.064	0.000	X	0.058	0.000	0.099	0.002	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
Am116	0.051	0.080	0.000	0.046	0.025	0.000	0.000	0.000	0.000	X	0.034	0.000	0.000	0.033	0.000	0.000	0.000	0.035	0.000	0.000	0.048	0.000	0.002	0.000

High (≥ 10 %) frequency of null alleles are in bold type. *indicates locus at which most populations show signs of null allele.

Table A4.4 Pairwise population F_{ST} of (a) all individuals pooled, (b) mature trees and (c) saplings of sugar maple (*Acer saccharum*) for all 23 sites in Québec below the diagonal. *P*-values are found above the diagonal. Significant values after adjusted nominal level ($\alpha = 0.05$) for multiple comparisons are given in bold.

(a)	1DA	1DB	1DC	1DD	1CA	1CB	1CC	1CD	2DA	2DC	2DD	2CA	2CB	2CC	2CD	3DA	3DB	3DC	3DD	3CA	3CB	3CC	3CD
1DA	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0057	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1DB	0.0163	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0172	**0.0002**	**0.0002**	0.2727	**0.0002**	**0.0002**	**0.0002**	0.0103	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0012	**0.0002**
1DC	0.0457	0.0376	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1DD	0.0210	0.0149	0.0546	—	0.0012	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**	0.0006	**0.0002**	0.0004	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1CA	0.0122	0.0072	0.0356	0.0060	—	**0.0002**	**0.0002**	0.0858	**0.0002**	0.0004	0.1654	**0.0002**	**0.0002**	**0.0002**	0.0006	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0295	**0.0002**
1CB	0.0198	0.0112	0.0335	0.0136	0.0044	—	0.0010	0.0061	**0.0002**	0.0004	0.0016	**0.0002**	**0.0002**	**0.0002**	0.0055	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**
1CC	0.0209	0.0131	0.0408	0.0147	0.0047	0.0079	—	0.0544	**0.0002**	**0.0002**	0.0638	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1CD	0.0140	0.0033	0.0303	0.0130	0.0012	0.0000	0.0029	—	**0.0002**	0.0008	0.1132	0.0053	0.0101	0.0332	0.0103	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	0.0190	**0.0002**
2DA	0.0271	0.0168	0.0505	0.0197	0.0139	0.019	0.0211	0.0167	—	**0.0002**	0.0022	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
2DC	0.0144	0.0150	0.0344	0.0128	0.0127	0.0108	0.0175	0.0101	0.0214	—	0.0708	0.0008	0.0091	**0.0002**	0.0334	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**
2DD	0.0174	0.0079	0.0329	0.0112	0.0051	0.0093	0.0132	0.0073	0.0103	0.0089	—	0.1192	0.6575	0.1441	0.6166	0.0018	0.0028	**0.0002**	0.0006	0.0077	0.0935	0.3455	0.1191
2CA	0.0141	0.0137	0.0362	0.0146	0.0096	0.0094	0.0147	0.0078	0.0236	0.0051	0.0038	—	0.0065	0.0595	0.0014	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	0.0063	0.0004
2CB	0.0208	0.0113	0.0427	0.0082	0.0086	0.0136	0.0242	0.0120	0.0148	0.0039	0.0009	0.0075	—	0.0059	0.0293	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0129	0.0316	0.0004
2CC	0.0179	0.0109	0.0455	0.0119	0.0078	0.0089	0.0168	0.0061	0.0161	0.0112	0.0051	0.0022	0.0054	—	0.1777	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0020	0.2374	**0.0002**
2CD	0.0138	0.0098	0.0327	0.0103	0.0047	0.0021	0.0130	0.0050	0.0156	0.0045	0.0052	0.0077	0.0060	-0.0003	—	0.0006	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0067	0.1186	0.0006
3DA	0.029	0.0202	0.0519	0.0316	0.0211	0.0207	0.0267	0.0150	0.0107	0.0244	0.0223	0.0307	0.018	0.0150	0.0097	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	**0.0002**
3DB	0.0191	0.0251	0.0574	0.0181	0.0158	0.0188	0.0278	0.0186	0.0179	0.0170	0.0116	0.0115	0.0125	0.0075	0.0120	0.0205	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3DC	0.0380	0.0332	0.0613	0.0320	0.0223	0.0217	0.0379	0.0265	0.0334	0.0316	0.0258	0.0163	0.0198	0.0121	0.0230	0.0335	0.0185	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3DD	0.0266	0.029	0.038	0.0310	0.0172	0.0143	0.0225	0.0184	0.0254	0.0131	0.0138	0.0144	0.0197	0.0133	0.0074	0.0187	0.0196	0.0238	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3CA	0.0298	0.0205	0.0578	0.0146	0.0153	0.0213	0.0197	0.0140	0.0227	0.0200	0.0093	0.0125	0.0072	0.0118	0.0189	0.0242	0.0112	0.0224	0.0297	—	**0.0002**	**0.0002**	**0.0002**
3CB	0.0175	0.0133	0.0448	0.0112	0.0095	0.0125	0.0166	0.0110	0.0097	0.0089	0.0075	0.0076	0.0055	0.0034	0.0018	0.0150	0.0100	0.0180	0.0126	0.0130	—	0.2328	**0.0002**
3CC	0.0193	0.0098	0.0415	0.0164	0.0041	0.0079	0.0167	0.0086	0.0157	0.0174	0.0037	0.0073	0.0086	0.0007	0.0033	0.0193	0.0154	0.0195	0.0170	0.0158	0.0042	—	0.0055
3CD	0.0165	0.0163	0.0397	0.0180	0.0062	0.0085	0.0135	0.0084	0.0192	0.0108	0.0141	0.0079	0.0112	0.005	0.0045	0.0137	0.0118	0.0181	0.0096	0.0173	0.0068	0.0090	—

Table A4.4 (*to continued*)

(b)	1DA	1DB	1DC	1DD	1CA	1CB	1CC	1CD	2DA	2DC	2DD	2CA	2CB	2CC	2CD	3DA	3DB	3DC	3DD	3CA	3CB	3CC	3CD
1DA	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0057	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1DB	0.0163	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0172	**0.0002**	**0.0002**	0.2727	**0.0002**	**0.0002**	**0.0002**	0.0103	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0012	**0.0002**
1DC	0.0457	0.0376	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1DD	0.0210	0.0149	0.0546	—	0.0012	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**	0.0006	**0.0002**	0.0004	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1CA	0.0122	0.0072	0.0356	0.0060	—	**0.0002**	**0.0002**	0.0858	**0.0002**	0.0004	0.1654	**0.0002**	**0.0002**	**0.0002**	0.0006	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0295	**0.0002**
1CB	0.0198	0.0112	0.0335	0.0136	0.0044	—	0.0010	0.0061	**0.0002**	0.0004	0.0016	**0.0002**	**0.0002**	**0.0002**	0.0055	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**
1CC	0.0209	0.0131	0.0408	0.0147	0.0047	0.0079	—	0.0544	**0.0002**	**0.0002**	0.0638	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1CD	0.0140	0.0033	0.0303	0.0130	0.0012	0.0000	0.0029	—	**0.0002**	0.0008	0.1132	0.0053	0.0101	0.0332	0.0103	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	0.0190	**0.0002**
2DA	0.0271	0.0168	0.0505	0.0197	0.0139	0.019	0.0211	0.0167	—	**0.0002**	0.0022	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
2DC	0.0144	0.0150	0.0344	0.0128	0.0127	0.0108	0.0175	0.0101	0.0214	—	0.0708	0.0008	0.0091	**0.0002**	0.0334	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0008	**0.0002**
2DD	0.0174	0.0079	0.0329	0.0112	0.0051	0.0093	0.0132	0.0073	0.0103	0.0089	—	0.1192	0.6575	0.1441	0.6166	0.0018	0.0028	**0.0002**	0.0006	0.0077	0.0935	0.3455	0.1191
2CA	0.0141	0.0137	0.0362	0.0146	0.0096	0.0094	0.0147	0.0078	0.0236	0.0051	0.0038	—	0.0065	0.0595	0.0014	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	0.0063	0.0004
2CB	0.0208	0.0113	0.0427	0.0082	0.0086	0.0136	0.0242	0.0120	0.0148	0.0039	0.0009	0.0075	—	0.0059	0.0293	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0129	0.0316	0.0004
2CC	0.0179	0.0109	0.0455	0.0119	0.0078	0.0089	0.0168	0.0061	0.0161	0.0112	0.0051	0.0022	0.0054	—	0.1777	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0020	0.2374	**0.0002**
2CD	0.0138	0.0098	0.0327	0.0103	0.0047	0.0021	0.0130	0.0050	0.0156	0.0045	0.0052	0.0077	0.0060	-0.0003	—	0.0006	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0067	0.1186	0.0006
3DA	0.029	0.0202	0.0519	0.0316	0.0211	0.0207	0.0267	0.0150	0.0107	0.0244	0.0223	0.0307	0.018	0.0150	0.0097	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	**0.0002**
3DB	0.0191	0.0251	0.0574	0.0181	0.0158	0.0188	0.0278	0.0186	0.0179	0.0170	0.0116	0.0115	0.0125	0.0075	0.0120	0.0205	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3DC	0.0380	0.0332	0.0613	0.0320	0.0223	0.0217	0.0379	0.0265	0.0334	0.0316	0.0258	0.0163	0.0198	0.0121	0.0230	0.0335	0.0185	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3DD	0.0266	0.029	0.038	0.0310	0.0172	0.0143	0.0225	0.0184	0.0254	0.0131	0.0138	0.0144	0.0197	0.0133	0.0074	0.0187	0.0196	0.0238	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**
3CA	0.0298	0.0205	0.0578	0.0146	0.0153	0.0213	0.0197	0.0140	0.0227	0.0200	0.0093	0.0125	0.0072	0.0118	0.0189	0.0242	0.0112	0.0224	0.0297	—	**0.0002**	**0.0002**	**0.0002**
3CB	0.0175	0.0133	0.0448	0.0112	0.0095	0.0125	0.0166	0.0110	0.0097	0.0089	0.0075	0.0076	0.0055	0.0034	0.0018	0.0150	0.0100	0.0180	0.0126	0.0130	—	0.2328	**0.0002**
3CC	0.0193	0.0098	0.0415	0.0164	0.0041	0.0079	0.0167	0.0086	0.0157	0.0174	0.0037	0.0073	0.0086	0.0007	0.0033	0.0193	0.0154	0.0195	0.0170	0.0158	0.0042	—	0.0055
3CD	0.0165	0.0163	0.0397	0.0180	0.0062	0.0085	0.0135	0.0084	0.0192	0.0108	0.0141	0.0079	0.0112	0.005	0.0045	0.0137	0.0118	0.0181	0.0096	0.0173	0.0068	0.0090	—

Table A4.4 (*to continued*).

	1DA	1DB	1DC	1DD	1CA	1CB	1CC	1CD	2DA	2DC	2DD	2CA	2CB	2CC	2CD	3DA	3DB	3DC	3DD	3CA	3CB	3CC	3CD
1DA	—	0.0038	**0.0002**	**0.0002**	0.1348	0.0014	**0.0002**	0.0376	**0.0002**	0.0004	0.0629	0.0047	0.0144	0.0014	0.0032	0.0004	0.0004	**0.0002**	**0.0002**	0.0004	0.0004	**0.0002**	**0.0002**
1DB	0.0188	—	**0.0002**	0.0480	0.1887	0.0360	0.2668	0.6065	0.0008	0.0018	0.4737	**0.0002**	0.1935	0.1170	0.2332	0.0004	**0.0002**	**0.0002**	**0.0002**	0.0061	**0.0002**	0.0215	0.0008
1DC	0.0438	0.0297	—	**0.0002**	**0.0002**	**0.0002**	**0.0002**	0.0004	**0.0002**	**0.0002**	0.0006	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**	**0.0002**
1DD	0.0238	0.0061	0.0529	—	0.0063	0.0004	0.0613	0.0190	**0.0002**	0.0024	0.0125	0.0004	0.0295	0.0004	0.0061	0.0010	**0.0002**	**0.0002**	**0.0002**	0.0034	**0.0002**	0.0004	**0.0002**
1CA	0.0018	0.0049	0.0270	0.0109	—	0.0381	0.0077	0.8992	0.0004	0.0051	0.2298	0.0682	0.0340	0.0658	0.3595	0.0016	0.0006	0.0008	**0.0002**	0.0044	0.0217	0.1710	0.0075
1CB	0.0149	0.0062	0.0345	0.0198	0.0031	—	0.1872	0.9055	0.0012	0.0014	0.1316	0.0253	0.0059	0.1233	0.1490	0.0010	**0.0002**	**0.0002**	**0.0002**	0.0210	0.0010	0.1283	0.0069
1CC	0.0217	0.0119	0.0392	0.0095	0.0081	0.0073	—	0.4842	0.0012	0.0050	0.0743	**0.0002**	0.0040	0.0097	0.0354	0.0059	**0.0002**	**0.0002**	**0.0002**	0.0030	0.0012	0.0028	0.0014
1CD	0.0162	0.0018	0.0242	0.0101	-0.0030	-0.0014	0.0010	—	0.0047	0.0166	0.8344	0.2150	0.3719	0.7710	0.5812	0.0370	0.0049	0.0030	0.0004	0.2372	0.2937	0.3504	0.0461
2DA	0.0233	0.0132	0.0440	0.0245	0.0067	0.0132	0.0147	0.0133	—	**0.0002**	0.0407	**0.0002**	0.0457	**0.0002**	0.0012	0.0223	**0.0002**	0.0004	**0.0002**	**0.0002**	**0.0002**	0.0075	**0.0002**
2DC	0.0176	0.0267	0.0345	0.0239	0.0154	0.0220	0.0169	0.0225	0.0255	—	0.0617	0.0006	0.0251	0.0223	0.0712	0.0008	**0.0002**	**0.0002**	**0.0002**	0.0004	0.0060	0.0065	0.0006
2DD	0.0190	0.0038	0.0269	0.0097	0.0041	0.0058	0.0119	-0.0030	0.0054	0.0219	—	0.0551	0.5314	0.2913	0.9476	0.1168	0.0026	0.0004	0.0573	0.0453	0.4700	0.1012	0.3822
2CA	0.0092	0.0225	0.0330	0.0223	0.0033	0.0056	0.0164	0.0052	0.0159	0.0109	0.0019	—	0.0779	0.4449	0.0646	**0.0002**	0.0004	**0.0002**	0.0004	0.0636	0.0032	0.0217	0.0320
2CB	0.0246	0.0105	0.0333	0.0121	0.0061	0.0126	0.0193	0.0086	0.0045	0.0107	0.0002	0.0076	—	0.4210	0.3441	0.0310	0.0036	0.0111	**0.0002**	0.0192	0.0431	0.0073	0.0057
2CC	0.0236	0.0111	0.0471	0.0157	0.0117	0.0126	0.0151	0.0024	0.0184	0.0215	0.0013	0.0019	0.0069	—	0.3609	0.0085	0.0304	0.0154	**0.0002**	0.1636	0.2259	0.2127	0.1658
2CD	0.0159	0.0122	0.0242	0.0198	-0.0003	0.0098	0.0159	0.0010	0.0192	0.0145	-0.0021	0.0073	0.0099	0.0132	—	0.0178	0.0014	**0.0002**	0.0449	0.0004	0.5028	0.3763	0.0385
3DA	0.0223	0.0223	0.0391	0.0313	0.0159	0.0217	0.0185	0.0137	0.0141	0.0239	0.0066	0.0235	0.0086	0.008	0.0116	—	0.0018	0.0006	**0.0002**	0.0018	0.0004	0.0200	0.0030
3DB	0.0153	0.0249	0.0566	0.0241	0.0151	0.0218	0.0330	0.0160	0.0188	0.0299	0.0107	0.0089	0.0151	0.0104	0.0169	0.0162	—	**0.0002**	**0.0002**	0.0285	0.0010	**0.0002**	0.0113
3DC	0.0371	0.0447	0.0688	0.0413	0.0227	0.0175	0.0322	0.0267	0.0327	0.0413	0.0257	0.0117	0.0268	0.0136	0.0342	0.0284	0.0224	—	**0.0002**	0.0079	**0.0002**	**0.0002**	**0.0002**
3DD	0.0253	0.0342	0.0391	0.0334	0.0121	0.0178	0.0243	0.0182	0.0277	0.0238	0.0093	0.0105	0.0266	0.0218	0.0040	0.0218	0.0225	0.0259	—	**0.0002**	**0.0002**	0.0006	**0.0002**
3CA	0.027	0.0192	0.0590	0.0181	0.0161	0.0139	0.0189	0.0102	0.0200	0.0313	0.0081	0.0057	0.0106	0.0069	0.0220	0.0174	0.0083	0.0135	0.0376	—	0.0872	0.0312	0.0105
3CB	0.0200	0.0185	0.0497	0.0145	0.0090	0.0161	0.0242	0.0092	0.0123	0.0230	0.0081	0.0112	0.0146	0.0050	-0.0004	0.0155	0.0064	0.0248	0.0171	0.0092	—	0.5057	0.0014
3CC	0.0249	0.0080	0.0450	0.0238	0.0058	0.0028	0.0252	0.0065	0.0181	0.0277	0.0054	0.0051	0.0129	0.0025	0.0052	0.0162	0.0165	0.0273	0.0251	0.0093	0.0017	—	0.0061
3CD	0.0086	0.0199	0.0384	0.0221	0.0018	0.0044	0.0089	0.0086	0.0174	0.019	0.0067	0.0016	0.0138	0.0055	0.0038	0.0102	0.0114	0.0104	0.0095	0.0134	0.0111	0.0155	—

Table A4.5 Comparison of mean genetic variability estimates between cohorts and cohorts in zones, transects and zones in each transect of sugar maple (*Acer saccharum*) in Québec.

Genetic Indices	Cohorts			Zones						Transects								
	M	Sa	*P*-value	D			C			1			2			3		
				M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value
A_R	5.378	5.275	0.2620	5.262	5.200	0.6480	5.484	5.343	0.2320	5.251	5.271	0.8840	5.482	5.382	0.4810	5.414	5.185	0.1340
H_O	0.610	0.591	0.3670	0.603	0.598	0.8740	0.616	0.585	0.2500	0.620	0.612	0.8020	0.583	0.551	0.423	0.622	0.601	0.1340
H_E	0.693	0.694	0.8990	0.689	0.689	0.9790	0.697	0.698	0.8560	0.687	0.692	0.5440	0.693	0.697	0.6260	0.699	0.692	0.5450
F_{IS}	0.121	0.148	0.3690	0.126	0.132	0.8780	0.116	0.163	0.2460	0.097	0.097	0.6830	0.158	0.210	0.3890	0.111	0.131	0.7050
F_{ST}	0.015	0.017	0.6650	0.023	0.027	0.6390	0.009	0.009	0.9730	0.021	0.021	0.5470	0.007	0.011	0.6120	0.013	0.016	0.6880

	Transects & Zones																	
	D									C								
	1			2			3			1			2			3		
	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value	M	Sa	*P*-value
A_R	4.951	5.078	0.5040	5.591	5.457	0.5360	5.326	5.130	0.2970	5.552	5.464	0.6810	5.400	5.327	0.6900	5.501	5.240	0.1950
H_O	0.599	0.596	0.9700	0.568	0.565	0.9670	0.627	0.620	0.8750	0.641	0.627	0.7750	0.593	0.541	0.3120	0.616	0.582	0.4900
H_E	0.676	0.682	0.6350	0.703	0.703	0.9970	0.692	0.685	0.6360	0.696	0.703	0.6140	0.686	0.693	0.5420	0.707	0.698	0.4860
F_{IS}	0.114	0.126	0.8730	0.193	0.197	0.9610	0.094	0.096	0.9810	0.079	0.109	0.6770	0.135	0.219	0.2560	0.129	0.166	0.6150
F_{ST}	0.034	0.029	0.6610	0.013	0.018	0.7160	0.019	0.022	0.7590	0.007	0.003	0.6900	0.003	0.008	0.6430	0.006	0.010	0.7690

A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{ST}, mean pairwise F_{ST}; F_{IS}, inbreeding coefficient; D, discontinuous zone; C, continuous zone; M, mature trees; Sa, saplings. Significant values ($\alpha = 0.05$) given in bold.

Table A4.6 Difference in Akaike information criterion (ΔAIC_C), weights (ω) and number of estimated parameters (K) for model comparisons of the relative importance of stand characteristics and distance from northern limit as predictors of A_R, H_O, H_E and F_{IS} (n = 414), and F_{ST} (n = 23) in Québec. For brevity, only models with a $\Delta AIC_C \leq 4.0$ and the next model were shown.

Explained variables	Model	K	ΔAIC_C	ω
A_R	m_ers_PS + D_north	5	0.00	0.19
	s_ers_PS + D_north	5	0.27	0.16
	m_ers_PS + s_ers_PS + D_north	6	0.39	0.15
	D_north	4	0.70	0.13
	m_ers_d + D_north	5	1.24	0.10
	m_ers_BA + D_north	5	1.67	0.08
	s_ers_BA +D_north	5	2.68	0.05
	s_ers_d + D_north	5	2.68	0.05
	m_ers_d + s_ers_d + D_north	6	2.99	0.04
	m_ers_BA + s_ers_BA + D_north	6	3.71	0.03
	m_ers_BA	4	7.37	1.00
H_O	m_ers_BA + s_ers_BA	5	0.00	0.30
	m_ers_BA + s_ers_BA + D_north	6	1.75	0.12
	m_ers_BA	4	1.86	0.12
	m_ers_PS + D_north	5	2.50	0.09
	m_ers_PS + s_ers_PS + D_north	6	2.99	0.07
	m_ers_d	4	3.19	0.06
	m_ers_BA + D_north	5	3.90	0.04
	m_ers_d + D_north	5	4.51	0.03
H_E	m_ers_d	4	0.00	0.09
	m_ers_PS + D_north	5	0.07	0.09
	m_ers_BA	4	0.09	0.09
	D_north	4	0.35	0.08
	s_ers_PS	4	0.40	0.07
	m_ers_PS	4	0.52	0.07
	s_ers_PS + D_north	5	0.70	0.06
	s_ers_BA	4	0.79	0.06
	m_ers_PS + s_ers_PS + D_north	6	1.05	0.05
	s_ers_d	4	1.08	0.05
	m_ers_BA + s_ers_BA	5	1.29	0.05
	m_ers_d + D_north	5	1.41	0.04
	m_ers_BA	5	1.95	0.03
	m_ers_d + s_ers_d	5	1.96	0.03
	s_ers_BA + D_north	5	2.12	0.03
	m_ers_PS + s_ers_PS	5	2.22	0.03
	s_ers_d + D_north	5	2.38	0.03

Table A4.6 (*to continued*)

Explained variables	Model	*K*	ΔAIC_C	ω
	m_ers_BA + s_ers_BA + D_north	6	3.29	0.02
	m_ers_d + s_ers_d + D_north	6	3.46	0.02
F_{IS}	m_ers_BA + s_ers_BA	5	0.00	0.22
	m_ers_BA	4	1.23	0.12
	m_ers_BA + s_ers_BA + D_north	6	1.49	0.10
	m_ers_d	4	2.29	0.07
	s_ers_BA	4	2.31	0.07
	m_ers_PS	4	2.70	0.06
	m_ers_PS + D_north	5	3.16	0.04
	m_ers_BA + D_north	5	3.16	0.04
	s_ers_PS	4	3.27	0.04
	D_north	4	3.53	0.04
	s_ers_d	4	3.65	0.03
	m_ers_d + s_ers_d	5	4.02	0.03
F_{ST}	D_north	3	0.00	0.22
	m_ers_d + D_north	4	0.41	0.18
	m_ers_BA + D_north	4	1.71	0.09
	s_ers_BA + D_north	4	1.98	0.08
	m_ers_BA	3	1.99	0.08
	s_ers_PS + D_north	4	2.83	0.05
	s_ers_d + D_north	4	2.93	0.05
	m_ers_PS + D_north	4	2.96	0.05
	m_ers_d + s_ers_d + D_north	5	3.68	0.03
	m_ers_d	3	3.83	0.03
	m_ers_PS	3	4.26	0.03

Explanatory variable abbreviations: m_ers_BA, mature sugar maple basal area (m^2 ha^{-1}); s_ers_BA, sugar maple sapling basal area (m^2 ha^{-T}); m_ers_d, mature sugar maple density (stems ha^{-1}); s_ers_d, sugar maple sapling density (stems ha^{-1}); m_ers_PS, mature sugar maple population size (stems); s_ers_PS, sugar maple sapling population size (stems); D_north, distance of each site to the northern limit (km).

Table A4.7 Raw data (%) of allele classification based on the frequency and geographic distribution of all individuals from 23 Québec sugar maple (*Acer saccharum*) sites.

Transects	Zones	Sites	CW5	CL5	CP5	RW5	RL5	RP5	CW2	CL2	CP2	RW2	RL2	RP2
1	Discontinuous	1DA	53	1	0	41	5	1	73	2	1	21	4	0
		1DB	57	0	0	39	5	0	77	3	0	18	2	0
		1DC	54	0	0	42	4	0	68	0	0	28	4	0
		1DD	55	1	0	37	8	1	78	3	1	13	6	0
	Continuous	1CA	52	0	0	39	9	1	71	4	0	20	4	1
		1CB	58	1	0	36	5	0	81	2	0	14	3	0
		1CC	54	1	1	41	5	2	77	2	1	17	3	2
		1CD	50	1	0	43	6	0	66	3	0	27	3	0
2	Discontinuous	2DA	60	0	0	38	3	0	79	1	0	18	2	0
		2DC	56	0	0	37	7	1	76	2	1	16	5	0
		2DD	49	1	0	43	8	1	75	3	0	16	6	1
	Continuous	2CA	51	0	0	41	7	1	78	3	0	15	5	1
		2CB	54	0	0	38	8	2	70	4	0	22	4	2
		2CC	52	0	0	43	6	0	74	2	0	20	4	0
		2CD	51	0	0	42	7	1	75	1	0	18	6	1
3	Discontinuous	3DA	56	0	0	36	8	1	78	4	0	13	4	1
		3DB	63	1	0	33	4	0	84	3	0	12	1	0
		3DC	58	2	1	34	6	0	74	4	1	18	5	0
		3DD	68	1	0	27	4	1	82	1	0	13	4	1
	Continuous	3CA	56	0	0	37	7	1	72	1	0	21	6	1
		3CB	50	1	0	44	5	2	76	2	1	18	4	1
		3CC	55	0	0	40	5	0	78	1	0	17	3	0
		3CD	59	0	0	32	9	2	77	0	0	14	9	2

CW5, common (allele frequency (f) $\geq$ 0.05) and widespread; CL5, common and localized; CP5, common and private; RW5, rare (f < 0.05) and widespread; RL5, rare and localized; RP5, rare and private; CW2, common ($f \geq$ 0.02) and widespread; CL2, common and localized; CP2, common and private; RW2, rare (f < 0.02) and widespread; RL2, rare and localized; RP2, rare and private.

Table A4.8 Raw data (%) of allele classification based on the frequency and geographic distribution of each cohort for all 23 sugar maple (*Acer saccharum*) sites in Québec.

Transects	Zone	Sites	Mature trees						Saplings					
			CW5	CL5	CP5	RW5	RL5	RP5	CW5	CL5	CP5	RW5	RL5	RP5
1	Discontinuous	1DA	68	1	0	27	4	2	66	4	0	25	6	1
		1DB	72	2	0	19	6	1	69	2	0	26	3	1
		1DC	71	0	0	24	5	0	67	2	0	28	3	1
		1DD	63	2	0	27	7	1	73	2	1	20	5	0
	Continuous	1CA	65	3	0	26	6	2	62	5	1	29	4	0
		1CB	76	1	0	18	6	0	69	2	0	23	7	0
		1CC	70	3	1	22	5	1	73	0	0	21	6	2
		1CD	64	2	0	26	8	1	59	2	0	32	7	1
2	Discontinuous	2DA	69	1	0	25	6	0	76	4	1	18	2	0
		2DC	68	1	1	22	9	1	73	4	1	16	6	1
		2DD	68	1	0	25	6	1	61	4	0	28	8	1
	Continuous	2CA	62	2	0	29	7	2	68	2	0	23	7	2
		2CB	67	2	2	26	5	1	63	3	0	27	7	2
		2CC	50	1	0	40	9	1	68	1	0	26	6	2
		2CD	68	1	0	26	6	2	71	1	0	18	10	2
3	Discontinuous	3DA	70	6	0	19	6	1	73	2	0	20	5	2
		3DB	77	1	0	20	2	0	73	4	0	18	5	0
		3DC	70	3	1	22	6	1	73	3	1	20	5	1
		3DD	79	1	0	17	3	0	78	1	0	20	2	1
	Continuous	3CA	67	2	0	20	10	2	69	1	0	24	6	1
		3CB	69	2	0	22	7	1	68	2	1	26	5	1
		3CC	71	0	0	21	7	0	70	2	0	24	3	0
		3CD	75	1	0	18	6	2	70	2	0	21	7	2
		mean	68.6	1.7	0.2	23.5	6.3	0.8	69.1	2.3	0.2	23.1	5.4	0.9
		(SD)	5.8	1.3	0.4	4.9	1.8	0.6	4.7	1.4	0.4	4.1	1.9	0.7

CW5, common (allele frequency (f) $\geq$ 0.05) and widespread; CL5, common and localized; CP5, common and private; RW5, rare (f < 0.05) and widespread; RL5, rare and localized; RP5, and rare and private; SD, standard deviation.

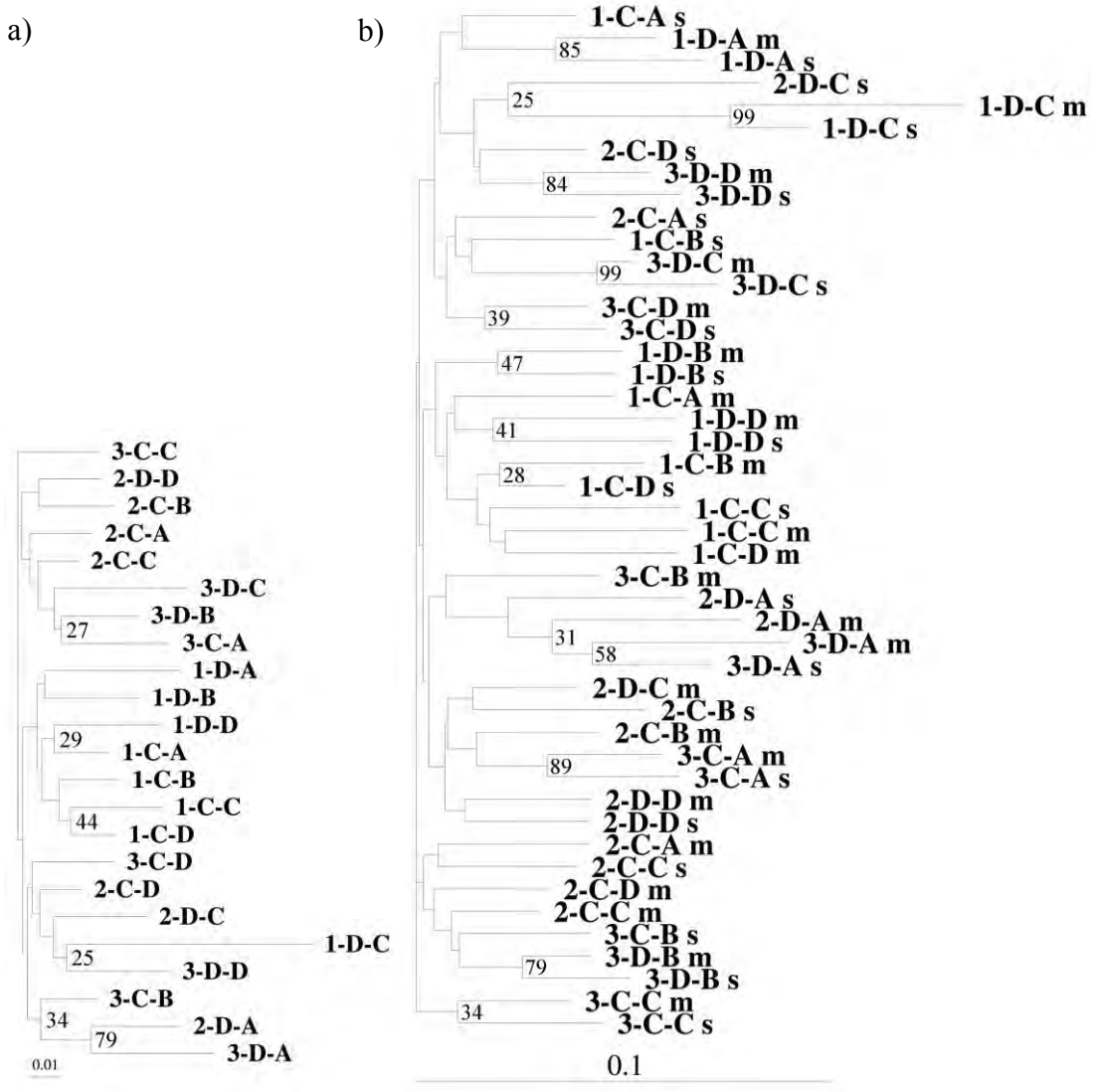

Figure A4.1 Neighbour-joining tree based on 18 microsatellite loci (a) for the 23 sugar maple (*Acer saccharum*) sites in Québec and (b) separated into two cohorts. Genetic distances (D_S) were based on Nei's (1972) genetic distance. Numbers given in nodes indicate the support value (%) of the respective group based on 1000 bootstrapped trees. Results are shown only for branches with ≥ 25% support. Abbreviations given after site name: m, mature sugar maple and s: sugar maple sapling.

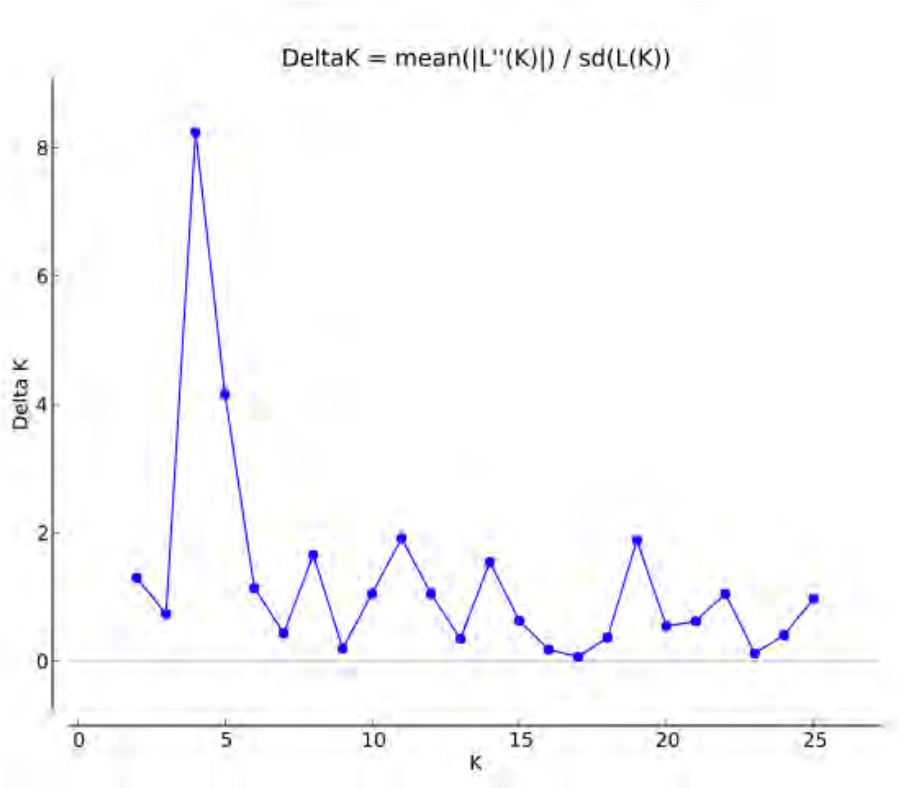

Figure A4.2 Detection of the number of clusters, Δ*K* plot showing greatest support at *K* = 4, using STRUCTURE for 23 sugar maple (*Acer saccharum*) sites according to Evanno *et al*. (2005).

Table A4.9 Results of analysis of molecular variance (AMOVA) showing the partitioning of genetic variance among transects and zones.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variance	Phi (Φ) statistics	*P*-values
Original grouping: transect						
Between transect	2	132.851	0.108	1	0.007	**0.000**
Between populations within transect	20	672.927	0.454	3	0.028	**0.000**
Within populations	890	13906.340	15.625	97	0.035	**0.000**
Total	912	14712.118	16.187	100		
Original grouping: zone						
Between zone	1	29.170	0.000	0	-0.001	1.000
Between populations within zone	21	776.608	0.538	3	0.033	**0.000**
Within populations	890	13906.340	15.625	97	0.032	**0.000**
Total	912	14712.118	16.163	100		
Original grouping: zone in transect 1						
Between zone	1	42.443	0.057	0	0.004	**0.012**
Between populations within zone	6	201.280	0.465	3	0.029	**0.000**
Within populations	303	4693.708	15.491	97	0.033	**0.000**
Total	310	4937.431	16.013	100		
Original grouping: zone in transect 2						
Between zone	1	34.716	0.034	0	0.002	*0.092*
Between populations within zone	5	150.366	0.335	2	0.020	**0.000**
Within populations	275	4558.382	16.576	98	0.022	**0.000**
Total	281	4743.465	16.945	100		
Original grouping: zone in transect 3						
Between zone	1	30.866	0.000	0	-0.002	0.960
Between populations within zone	6	213.256	0.516	3	0.033	**0.000**
Within populations	312	4654.250	14.917	97	0.032	**0.000**
Total	319	4898.372	15.433	100		
STRUCTURE grouping A						
Between groups	4	249.711	0.187	1	0.012	**0.000**
Between populations within group	18	556.067	0.381	2	0.024	**0.000**
Within populations	890	13906.340	15.625	96	0.035	**0.000**
Total	912	14712.118	16.193	100		
STRUCTURE grouping B						
Between groups	3	182.386	0.124	1	0.008	**0.000**
Between populations within group	19	623.392	0.433	3	0.027	**0.000**
Within populations	890	13906.340	15.625	97	0.034	**0.000**
Total	912	14712.118	16.182	100		

d.f., degree of freedom. Significant values at $\alpha = 0.05$ given in bold and at $\alpha = 0.10$ given in italics.

Table A4.10 Mean mutation-scaled population size ($\theta = 4N_e\mu$, where N_e = effective population size and μ = mutation rate per generation per locus) and mean mutation-scaled immigration rate ($M = m/\mu$, where m = migration rate) between pairs of sugar maple (*Acer saccharum*) populations. Both parameters are estimated using MIGRATE-N (Beerli, 2006).

	θ	NP	Transect 1	Transect 2	Transect 3
NP→i	*1.43 (0.57–2.27)*	_	7.8 (6.7–8.8)	8.5 (6.7–9.9)	7.6 (5.8–9.8)
Transect 1→i	*2.77 (1.7–3.80)*	6.6 (4.6–7.5)	_	15.5 (14.6–16.4)	15.6 (14.5–16.9)
Transect 2→i	*1.22 (0.03–2.37)*	16.7 (15.5–17.9)	17.8 (16.7–18.8)	_	15.0 (13.9–16.1)
Transect 3→i	*3.68 (2.33–5.30)*	25.7 (24.8–26.7)	20.8 (19.1–22.5)	16.9 (15.6–18.8)	_

95% confidence intervals are shown in parentheses. Source groups are presented in the first column and sink groups are presented in the first row. NP, northern popualtions (1-D-A, 1-D-B, 2-D-A, 3-D-A). Here Transect 1 représents 1-D-C, 1-D-D, 1-C-A, 1-C-B, 1-C-C, 1-C-D; Transect 2, 2-D-C, 2-D-D, 2-C-A, 2-C-B, 2-C-C, 2-C-D; and Transect 3,3-D-B, 3-D-C, 3-D-D, 3-C-A, 3-C-B, 3-C-C, 3-C-D.

ANNEXE A5

SUPPORTING INFORMATION FOR CHAPTER V

Table A5.1 Summary of sample site coordinates and protection types.

Study ID	Study name	Protection type	Latitude	Longitude	Elevation (m)	Distance to paired OG
OG1	Lac Tucker	EFE	45° 56′ 36.6″ N	75° 47′ 53.5″ W	386	
SC1	Lac St Charles		45° 47′ 37.3″ N	75° 52′ 3.7″ W	305	17.3
OG2	Lac de l'Ecluse	EFE	45° 51′ 35.6″ N	75° 23′ 55.8″ W	388	
SC2	Lac Faucon		45° 49′ 15.5″ N	75° 19′ 18.8″ W	288	7.8
OG3	Lac Marie-Lefranc	EFE	46° 70′ 5.34″ N	75° 00′ 36.5″ W	410	
SC3	Lac Marie-Lefranc		46° 50′ 52.8″ N	75° 00′ 40.3″ W	386	1.6

OG, old-growth stand; SC, selection cutting stand; EFE, *écosystèmes forestiers exceptionnels*. For more details on stand characteristics (except for OG2), see Angers *et al*. (2005), and for OG2 and OG3 (same as 2-C-D and 2-C-C, respectively), see Graignic *et al*. (2014).

Table A5.2 Genetic variability estimates of microsatellite markers used in the Québec study of sugar maple (*Acer saccharum*).

Locus	GenBank access no.	M	Size range (bp)	A_T	A	H_O	H_E	F_{IS}	References
SM11	KC731552	3	178–199	12	8.2	0.586	0.629	0.070	Graignic *et al*. (2013)
SM14	KC751436	4	70–120	21	16.2	0.742	0.894	0.170	Graignic *et al*. (2013)
SM21A	KC751437	4	179–237	28	17.7	0.755	0.867	0.129	Graignic *et al*. (2013)
SM22	KC751438	2	293–323	17	13.7	0.526	0.896	0.414	Graignic *et al*. (2013)
SM27	KC751440	4	242–260	9	7.0	0.403	0.673	0.405	Graignic *et al*. (2013)
SM29	KC751441	4	278–307	10	7.5	0.527	0.724	0.274	Graignic *et al*. (2013)
SM34	KC751442	3	118–167	23	15.8	0.772	0.843	0.084	Graignic *et al*. (2013)
SM36	KC751443	5	146–182	18	13.3	0.714	0.828	0.137	Graignic *et al*. (2013)
SM37	KC751444	2	174–196	12	9.0	0.564	0.667	0.153	Graignic *et al*. (2013)
SM42	KC751445	1	90–133	17	9.5	0.678	0.804	0.157	Graignic *et al*. (2013)
SM47	KC751446	2	201–225	12	8.2	0.390	0.667	0.415	Graignic *et al*. (2013)
SM51	KC751447	1	269–290	7	5.5	0.344	0.464	0.258	Graignic *et al*. (2013)
SM53	KC751448	5	287–310	7	3.0	0.352	0.517	0.317	Graignic *et al*. (2013)
SM55	KC751449	2	248–276	15	10.3	0.480	0.686	0.296	Graignic *et al*. (2013)
SM56	KC751450	3	287–299	6	5.0	0.364	0.611	0.400	Graignic *et al*. (2013)
SM60	KC751452	3	231–237	3	2.8	0.305	0.410	0.246	Graignic *et al*. (2013)
Aop943	EF531298	1	143–160	8	5.7	0.565	0.567	0.002	Segarra-Moragues *et al*. (2008) Graignic *et al*. (2013)
Am116	AB303350	1	230–267	18	11.5	0.589	0.701	0.160	Kikuchi & Shibata (2008) Graignic *et al*. (2013)

M, multiplexing arrangement; A_T, total number of alleles; A, mean number of alleles per locus; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{IS}, inbreeding coefficient.

Table A5.3 Summary of *P*-values for Hardy–Weinberg equilibrium using GENEPOP (Markov chain parameters: 10,000 dememorizations, followed by 500 batches of 5,000 iterations per batch).

	OG1	SC1	OG2	SC2	OG3	SC3
SM11	0.1903	0.1722	0.5947	0.0212	0.1487	0.0110
SM14	0.0011	0.0026	0.0102	0.0027	0.0035	**0.0000**
SM21A	0.0384	0.1047	0.0140	0.0066	0.8285	0.0370
SM22*	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**
SM27*	**0.0002**	**0.0000**	**0.0000**	0.0017	0.0028	**0.0000**
SM29	**0.0004**	0.0024	0.0072	0.0052	0.0735	0.0077
SM34	0.0163	0.1669	0.1153	0.3337	0.3417	0.2668
SM36	0.1236	0.0788	0.5338	0.1049	0.2210	**0.0000**
SM37	0.7559	0.0632	0.0316	0.0175	0.3030	0.0013
SM42	0.2747	0.0067	**0.0000**	0.3748	0.0674	0.0007
SM47*	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0000**	**0.0001**
SM51	0.0328	0.1688	0.0963	0.0050	0.2176	0.0583
SM53	**0.0000**	0.5993	0.0048	0.4135	0.0008	0.0007
SM55*	**0.0000**	0.0541	0.0027	**0.0000**	0.0023	**0.0001**
SM56*	0.0039	**0.0000**	**0.0000**	**0.0001**	**0.0000**	0.2673
SM60	0.5995	**0.0000**	0.0519	0.0959	0.0025	0.2962
Aop943	0.0979	0.8544	0.0638	0.7918	0.7999	0.0339
Am116	**0.0000**	0.0189	0.5458	**0.0000**	0.5295	0.1456

P-values significant after Bonferroni correction are in bold type. *indicates locus at which most populations show signs of deviance from HWE.

Table A5.4 Summary of null allele frequencies for each pair of loci and populations using FREENA.

	OG1	SC1	OG2	SC2	OG3	SC3
SM11	0.068	0.043	0.022	0.076	0.036	0.005
SM14	0.061	0.088	0.058	0.066	0.067	**0.110**
SM21A	0.066	0.073	0.086	0.080	0.000	0.041
SM22*	**0.248**	**0.212**	**0.182**	**0.185**	**0.151**	**0.165**
SM27*	**0.141**	**0.197**	**0.186**	**0.111**	**0.127**	**0.220**
SM29*	**0.142**	**0.121**	**0.112**	**0.128**	0.071	**0.116**
SM34	0.092	0.010	0.005	0.022	0.000	0.036
SM36	0.047	0.039	0.013	0.032	0.040	**0.147**
SM37	0.000	0.058	0.074	0.037	0.000	**0.132**
SM42	0.031	0.034	0.070	0.035	0.063	**0.104**
SM47*	**0.158**	**0.145**	**0.202**	**0.203**	**0.104**	**0.164**
SM51	0.075	0.082	0.092	**0.106**	0.065	0.096
SM53*	**0.184**	0.023	**0.125**	0.038	**0.139**	**0.128**
SM55*	**0.168**	**0.108**	0.034	**0.153**	**0.105**	**0.138**
SM56*	**0.133**	**0.185**	**0.185**	**0.170**	**0.205**	0.067
SM60	0.013	**0.150**	0.065	0.075	**0.134**	0.045
Aop943	0.061	0.006	0.000	0.000	0.000	0.061
Am116	**0.155**	0.087	0.000	**0.164**	0.000	0.083

High (≥ 10 %) frequencies of null alleles are in bold type. *indicates locus at which most populations show signs of null alleles.

Table A5.5 Pairwise population F_{ST} (below the diagonal) of pooled individuals, mature trees, saplings, seedlings and post-harvest seedlings of sugar maple (*Acer saccharum*) for the 6 sites, in Québec.

	OG1	SC1	OG2	SC2	OG3	SC3
Pooled individuals						
OG1	—	0.58000	0.57667	0.22333	0.45667	0.11000
SC1	-0.0001	—	0.89333	0.57667	**0.00333**	**0.00333**
OG2	-0.0014	-0.0016	—	0.31667	0.10000	0.04333
SC2	0.0015	-0.0005	-0.0010	—	0.03000	0.02333
OG3	0.0014	**0.0039**	-0.0002	0.0008	—	**0.00333**
SC3	-0.0020	**0.0021**	0.0000	0.0009	**0.0044**	—
Mature trees						
OG1	—	0.07667	0.01667	0.02667	0.03333	0.56000
SC1	0.0041	—	0.27333	0.14667	0.05333	0.16333
OG2	0.0078	0.0005	—	0.01667	0.51333	0.05000
SC2	0.0077	-0.0003	0.0061	—	0.02000	0.14000
OG3	0.0040	0.0022	-0.0056	0.0069	—	0.02000
SC3	-00053	-0.0009	-0.0002	0.0084	0.0031	—
Saplings						
OG1	—	0.06000	0.16667	0.28333	0.49333	0.18667
SC1	0.0065	—	0.21333	0.14667	0.18667	0.17333
OG2	-0.0022	0.0059	—	0.28000	0.32667	0.50000
SC2	-0.0044	0.0113	-0.0013	—	0.08333	0.04000
OG3	-0.0007	0.0071	0.0132	0.0051	—	0.27000
SC3	-0.0019	0.0059	-0.0006	0.0065	0.0073	—
Seedlings						
OG1	—	0.19667	0.21667	0.20000	0.17000	0.07667
SC1	0.0019	—	0.89333	0.75000	0.01667	0.19333
OG2	-0.0035	-0.0053	—	0.03333	0.06667	0.37333
SC2	0.0155	0.0034	0.0118	—	0.15000	0.18333
OG3	0.0051	0.0063	0.0051	0.0079	—	0.01000
SC3	0.0071	0.0135	0.0013	0.0063	0.0209	—
Post-harvest seedlings						
OG1	—	0.29667	0.39667	0.16333	0.32667	0.11667
SC1	0.0037	—	0.81667	0.53667	0.24000	0.06667
OG2	-0.0044	-0.0051	—	0.03000	0.30667	0.29333
SC2	0.0179	0.0026	0.0200	—	0.12333	0.05333
OG3	0.0021	0.0018	0.0049	0.0074	—	0.02667
SC3	0.0031	0.0228	0.0074	*0.0138*	0.0218	—

P-values are above the diagonal. Significant values after adjusted nominal level ($\alpha = 0.05$) for multiple comparisons are in bold type.

Table A5.6 Comparison of mean genetic variability estimates (A_R, H_O, H_E, F_{ST} and F_{IS}) between old-growth (OG) and selection cutting stands (SC) of sugar maple (*Acer saccharum*) in Québec for mature trees (M), saplings (Sa), seedlings (S1), post-harvest seedlings (S2) and pooled individuals (PI) separately, between cohorts (M, Sa and S1, and M, Sa and S2) for PI, OG and SC separately, and between OG and SC for each pair of stands. Analyses were performed using FSTAT and tested for significance using 1,000 permutations.

Genetic Indices		OG	SC	*P*-value		M	Sa	S1	*P*-value	M	Sa	S2	*P*-value
A_R	PI	9.011	8.983	0.9880	PI	6.288	6.227	6.299	0.8370	5.369	5.318	5.323	0.8700
H_O		0.546	0.528	0.5030		0.594	0.503	0.512	**0.0040**	0.594	0.503	0.504	**0.0010**
H_E		0.689	0.694	0.1960		0.696	0.682	0.691	0.1050	0.696	0.682	0.686	0.1270
F_{IS}		0.208	0.240	0.4040		0.146	0.262	0.260	**0.0030**	0.146	0.262	0.266	**0.0010**
F_{ST}		-0.000	0.001	0.7340		0.002	0.004	0.006	0.5360	0.002	0.004	0.008	0.2890
A_R	M	6.557	6.310	0.2900	OG	6.401	6.131	6.352	0.2260	5.432	5.236	5.438	0.3150
H_O		0.610	0.577	0.1780		0.610	0.502	0.519	**0.0150**	0.610	0.502	0.509	**0.0160**
H_E		0.694	0.698	0.6100		0.694	0.679	0.688	0.3500	0.694	0.679	0.683	0.3840
F_{IS}		0.121	0.173	0.1780		0.121	0.261	0.245	**0.0190**	0.121	0.261	0.255	**0.0180**
F_{ST}		0.002	0.002	0.9260		0.002	0.004	0.002	0.9550	0.002	0.004	0.000	0.8570
A_R	Sa	6.131	6.323	0.5330	SC	6.175	6.323	6.245	0.7090	5.305	5.399	5.208	0.4570
H_O		0.502	0.503	1.0000		0.577	0.503	0.504	0.1750	0.577	0.503	0.498	0.1570
H_E		0.679	0.684	0.8140		0.698	0.684	0.695	0.3890	0.698	0.684	0.688	0.4260
F_{IS}		0.261	0.264	0.8320		0.173	0.264	0.275	0.1780	0.173	0.264	0.277	0.1920
F_{ST}		0.004	0.008	0.3640		0.002	0.008	0.008	0.5810	0.002	0.008	0.013	0.1840
A_R	S1	6.352	6.245	0.4170									
H_O		0.519	0.504	0.7200									
H_E		0.688	0.695	0.7080									
F_{IS}		0.245	0.275	0.6200									
F_{ST}		0.002	0.008	0.4370		OG1	SC1	*P*-value	OG2	SC2	*P*-value	OG3	SC3	*P*-value
A_R	S2	5.438	5.208	0.2460	PI	6.250	6.317	0.7170	6.281	6.193	0.6300	6.344	6.233	0.5120
H_O		0.509	0.498	0.7100		0.507	0.529	0.6480	0.569	0.543	0.5960	0.577	0.511	0.1240
H_E		0.683	0.688	0.7170		0.684	0.698	0.1730	0.686	0.689	0.8120	0.690	0.690	0.9840
F_{IS}		0.255	0.277	0.5100		0.259	0.242	0.7930	0.171	0.212	0.5400	0.164	0.260	0.1000
F_{ST}		0.000	0.013	0.1470		0.003	0.002	0.8250	0.002	0.011	0.2000	0.006	0.000	0.3020

A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{ST}, mean pairwise F_{ST}; F_{IS}, inbreeding coefficient. Significant values ($\alpha = 0.05$) are in bold type.

Table A5.7 Results of linear mixed-effects models for genetic variability estimates (n = 432) in Québec, prior to model simplification.

Data used	Response variable	Explanatory variables	Num. d.f.	Den. d.f.	F	P
M, Sa and S1	A_R	forest type	1	289	0.177	0.6739
		pair	2	289	0.073	0.9294
		cohort	2	289	0.164	0.8492
		forest type × pair	2	289	0.262	0.7694
		forest type × cohort	2	289	1.252	0.2874
		pair × cohort	4	289	0.717	0.5812
		forest type × pair × cohort	4	289	1.461	0.2141
	H_O	forest type	1	289	1.447	0.2299
		pair	2	289	2.155	0.1178
		cohort	2	289	19.962	**<0.001**
		forest type × pair	2	289	3.590	**0.0288**
		forest type × cohort	2	289	0.550	0.5778
		pair × cohort	4	289	1.416	0.2288
		forest type × pair × cohort	4	289	0.671	0.6128
	H_E	forest type	1	289	0.430	0.5127
		pair	2	289	0.021	0.9792
		cohort	2	289	1.228	0.2945
		forest type × pair	2	289	0.342	0.7109
		forest type × cohort	2	289	0.023	0.9770
		pair × cohort	4	289	1.100	0.3570
		forest type × pair × cohort	4	289	0.443	0.7775
	F_{IS}	forest type	1	289	1.890	0.1703
		pair	2	289	1.365	0.2570
		cohort	2	289	17.347	**<0.0001**
		forest type × pair	2	289	1.879	0.1545
		forest type × cohort	2	289	0.660	0.5177
		pair × cohort	4	289	1.239	0.2945
		forest type × pair × cohort	4	289	0.361	0.8366
M, Sa and S2	A_R	forest type	1	289	0.516	0.4730
		pair	2	289	0.374	0.6882
		cohort	2	289	0.129	0.8787
		forest type × pair	2	289	0.876	0.4176
		forest type × cohort	2	289	1.718	0.1813
		pair × cohort	4	289	0.471	0.7568
		forest type × pair × cohort	4	289	1.498	0.2028

Table A5.7 (*to continued*)

Data used	Response variable	Explanatory variables	Num. d.f.	Den. d.f.	*F*	*P*
M, Sa and S2	H_O	forest type	1	289	1.385	0.2402
		pair	2	289	2.778	0.0638
		cohort	2	289	19.528	**<0.0001**
		forest type × pair	2	289	3.314	**0.0378**
		forest type × cohort	2	289	0.506	0.6036
		pair × cohort	4	289	0.901	0.4636
		forest type × pair × cohort	4	289	0.567	0.6868
	H_E	forest type	1	289	0.173	0.6781
		pair	2	289	0.177	0.8379
		cohort	2	289	1.108	0.3317
		forest type × pair	2	289	0.621	0.5381
		forest type × cohort	2	289	0.004	0.9963
		pair × cohort	4	289	0.622	0.6474
		forest type × pair × cohort	4	289	0.685	0.6032
	F_{IS}	forest type	1	289	1.790	0.1819
		pair	2	289	1.802	0.1668
		cohort	2	289	16.291	**<0.0001**
		forest type × pair	2	289	1.379	0.2536
		forest type × cohort	2	289	0.610	0.5440
		pair × cohort	4	289	0.791	0.5320
		forest type × pair × cohort	4	289	0.195	0.9409

Num. d.f., numerator degrees of freedom; den. d.f., denominator degrees of freedom; M, mature sugar maple; Sa, sugar maple sapling; S1, sugar maple seedling; S2, post-harvest sugar maple seedling. A_R, mean allelic richness; H_O, mean observed heterozygosity; H_E, mean expected heterozygosity; F_{ST}, mean pairwise F_{ST}; F_{IS}, inbreeding coefficient. Significant values at $\alpha = 0.05$ are in bold type and at $\alpha = 0.10$ in italics.

Table A5.8 Number of alleles per classes of frequency, per cohorts of the populations and grouping populations by pairs and forest types.

Populations	Cohorts	A_T	C	I	L0.01	R0.01	L0.05	R0.05
OG1	M	128	2 (2%)	20 (16%)	106 (83%)	0 (0%)	64 (50%)	42 (33%)
	Sa	119	1 (1%)	26 (22%)	92 (77%)	0 (0%)	54 (45%)	38 (32%)
	S1	128	1 (1%)	22 (17%)	105 (82%)	0 (0%)	67 (52%)	38 (30%)
	PI	169	1 (1%)	18 (11%)	122 (72%)	28 (17%)	58 (34%)	92 (54%)
	S2	118	2 (2%)	20 (17%)	96 (81%)	0 (0%)	62 (53%)	34 (29%)
SC1	M	129	0 (0%)	24 (19%)	105 (81%)	0 (0%)	66 (51%)	39 (30%)
	Sa	124	1 (1%)	23 (19%)	100 (81%)	0 (0%)	59 (48%)	41 (33%)
	S1	124	1 (1%)	20 (16%)	103 (83%)	0 (0%)	64 (52%)	39 (31%)
	PI	171	0 (0%)	22 (13%)	116 (68%)	33 (19%)	58 (34%)	91 (53%)
	S2	114	2 (2%)	23 (20%)	89 (78%)	0 (0%)	48 (42%)	41 (36%)
OG2	M	125	0 (0%)	22 (18%)	103 (82%)	0 (0%)	64 (51%)	39 (31%)
	Sa	125	1 (1%)	23 (18%)	101 (81%)	0 (0%)	66 (53%)	35 (28%)
	S1	126	0 (0%)	22 (17%)	104 (83%)	0 (0%)	62 (49%)	42 (33%)
	PI	171	0 (0%)	23 (13%)	114 (67%)	34 (20%)	55 (32%)	93 (54%)
	S2	120	2 (2%)	21 (18%)	97 (81%)	0 (0%)	53 (44%)	44 (37%)
SC2	M	117	1 (1%)	25 (21%)	91 (78%)	0 (0%)	63 (54%)	28 (24%)
	Sa	120	2 (2%)	20 (17%)	98 (82%)	0 (0%)	58 (48%)	40 (33%)
	S1	126	0 (0%)	23 (18%)	103 (82%)	0 (0%)	64 (51%)	39 (31%)
	PI	171	0 (0%)	22 (13%)	113 (66%)	36 (21%)	51 (30%)	98 (57%)
	S2	109	0 (0%)	27 (25%)	82 (75%)	0 (0%)	47 (43%)	35 (32%)
OG3	M	137	1 (1%)	21 (15%)	115 (84%)	0 (0%)	48 (35%)	67 (49%)
	Sa	121	1 (1%)	24 (20%)	96 (79%)	0 (0%)	58 (48%)	38 (31%)
	S1	123	1 (1%)	21 (17%)	101 (82%)	0 (0%)	60 (49%)	41 (33%)
	PI	171	0 (0%)	22 (13%)	113 (66%)	36 (21%)	52 (30%)	97 (57%)
	S2	108	1 (1%)	19 (18%)	88 (81%)	0 (0%)	58 (54%)	30 (28%)
SC3	M	117	1 (1%)	21 (18%)	95 (81%)	0 (0%)	58 (50%)	37 (32%)
	Sa	134	2 (1%)	18 (13%)	114 (85%)	0 (0%)	73 (54%)	41 (31%)
	S1	122	1 (1%)	24 (20%)	97 (80%)	0 (0%)	57 (47%)	40 (33%)
	PI	166	1 (1%)	18 (11%)	115 (69%)	32 (19%)	59 (36%)	88 (53%)
	S2	106	2 (2%)	21 (20%)	83 (78%)	0 (0%)	52 (49%)	31 (29%)

A_T, total number of alleles; C, common $f \geq 0.75$; I, intermediate $0.75 > f \geq 0.25$; L0.01, low $0.25 > f \geq 0.01$; R0.01, rare $f < 0.01$; L0.05, low $0.25 > f \geq 0.05$; R0.05, rare $f < 0.05$; M, mature sugar maple; Sa, sugar maple sapling; S1, sugar maple seedling; PI, pooled individuals; S2, post-harvest sugar maple seedling.

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