Université de Montréal

Réhabilitation de forêts par la plantation sous couvert : écologie des arbres plantés dans le sud-ouest du Québec

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Faculté des études supérieures

Cette thèse intitulée :

Réhabilitation de forêts par la plantation sous couvert : écologie des arbres plantés dans le sud-ouest du Québec

présentée par :
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Résumé

La dégradation des écosystèmes forestiers a obligé le développement de nouvelles approches sylvicoles. Ces approches font appel à la plantation pour pallier à la régénération naturelle devenue insuffisante. Les connaissances relatives à l'écologie des arbres plantés et aux forêts aménagées par la plantation sont par ailleurs insuffisantes pour appuyer ces efforts. La présente thèse fait l'analyse de l'un de ces modes de réhabilitation. La plantation sous couvert vise l'enrichissement du peuplement à l'aide d'espèces désirables, tout en conservant une partie importante du couvert forestier et des structures et fonctions qui lui sont associées.

Une revue de littérature ainsi qu'une méta-analyse des essais réalisés à travers le monde ont été effectuées. Une coupe d'éclaircie légère s'est révélée suffisante dans une majorité de situation pour garantir des rendements optimums en croissance et survie pendant la phase d'établissement. Ce niveau maximise les effets de protection du couvert et minimise les effets de compétition, tout en permettant une plus grande conservation des structures et des fonctions forestières.

La méthode a été testée avec succès sur six ans dans de jeunes peuplements d'origine agricole. L'intérêt de cette étude a porté sur les effets d'un second dégagement appliqué deux ans après la mise en terre des plants, comparé à un témoin. La croissance du chêne rouge a été supérieure à celle du cerisier tardif et cette espèce a bien réagi au dégagement et ce, sans augmentation de la prédation par le cerf. Le cerisier tardif aurait probablement nécessité une plus grande ouverture pratiquée plus tôt pour voir sa croissance améliorée.

La plasticité morphologique des semis en fonction du climat lumineux en aménagement sous couvert a été analysée. Les résultats pour le cerisier tardif et l'érable à sucre sont opposés aux résultats attendus en fonction des modèles de tolérance à l'ombre. Ces résultats sont discutés en fonction des besoins de connaissances en régénération artificielle.

La lumière disponible en sous-bois a été un élément méthodologique important tout au long de ces travaux. Plusieurs techniques ont été comparées et une nouvelle méthode libre de contraintes quant au type de ciel a été développée.

Mots-clés

Reboisement en feuillus nobles; plantation d'enrichissement, peuplement pionnier; restauration; lumière disponible; densité du couvert; plasticité morphologique; tolérance à l'ombre et stade successoral; méta-analyse.

Organismes

Acer saccharum; Prunus serotina; Quercus rubra.

Abstract

Rehabilitation of forests through under-planting : the ecology of planted trees in southwestern Québec

The degradation of forest ecosystems has led to the development of new approaches to forest management, in which tree planting supplements natural regeneration. Not enough is known, however, about the ecology of planted trees or about the management of planted forests. This thesis is an analysis of the method of forest regeneration known as under-planting. The objective of under-planting is to enrich stands by using desirable species while conserving forest cover (shelterwood) and the structures and functions associated with it.

A literature review and a meta-analysis of under-planting trials throughout the world were carried out. Light thinning seems to be sufficient in the majority of situations to obtain maximum yields in growth and optimum survival rates during the establishment phase. This level of thinning maximizes the protective effects of forest cover and minimizes the effects of competition, while better conserving forest structures and functions.

Under-planting was tested over six years in young pioneer stands on abandoned agricultural land. Our study focused on the effects of a second thinning two years after planting. Red oak grew faster than black cherry, responding well to thinning while suffering no increase in deer predation. Black cherry probably would have needed earlier and heavier thinning to improve its growth.

The morphological plasticity of seedlings as a function of light climate under shelterwood management was studied. Results observed for both black cherry and sugar maple were the reverse of those predicted by shade tolerance models. These results are discussed in relation to present gaps in knowledge of the ecology and management of artificial regeneration.

The measurement of available light in the understory was an important methodological element of this study. Several methods were compared and a new technique free of the constraints of sky conditions was developed.

Keywords

Hardwood reforestation; enrichment planting; shelterwood; pioneer forests; restoration; available light; canopy cover; morphological plasticity; shade tolerance and successional status; meta-analysis.

Organisms

Acer saccharum; Prunus serotina; Quercus rubra.

Table des matières

Liste des tableaux

Liste des figures

À Lilou
À Marc-Antoine, Claudia, Félix, Maxime et Mathis
À Josalie et Monica
Aux enfants du Monde, ceux des villes et des campagnes, ceux des forêts
Qu'ils puissent avoir la chance de léguer à leurs enfants une forêt en santé
Capable de supporter la vie, incluant la leur
Pour qu'il y ait encore des arbres à couper pour en faire un cheval de bois

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Chapitre 1 : Introduction générale

Introduction

Des interruptions ou modifications importantes des processus de régénération forestière sont perçues dans plusieurs endroits du monde (Noble et Dirzo 1997, Vitousek *et al.* 1997, Kozlowski 2002). De nombreuses forêts présentent des problèmes de régénération, plusieurs décennies même après l'arrêt des opérations forestières ou l'abandon des activités agricoles. Ces problèmes vont de la simple insuffisance de la régénération à la modification de la composition vers des espèces moins intéressantes tant des points de vue écologique (*e.g.* espèces envahissantes, remplacement des espèces associées à la forêt primaire) qu'économique (*e.g.* espèces de moindre valeur, enrésinement, perte de qualité). En réponse à ces problèmes, de nouvelles techniques ont été mises de l'avant (*e.g.* aménagement écosystémique, coupe à rétention variable, coupe partielle), et d'anciennes pratiques sylvicoles ont été réhabilitées (*e.g.* plantation sous couvert, plantations mixtes, *continuous cover forestry*). Cette nouvelle foresterie est présentée comme une alternative valable aux pratiques passées qui n'ont pas toujours été en mesure d'assurer la pérennité de la ressource (Rowe 1992, Greene *et al.* 2002, Mitchell *et al.* 2004). Les nouvelles approches mises de l'avant comprennent maintenant des objectifs de conservation du couvert et de la structure forestière, avec les effets bénéfiques associés pour la régénération et la biodiversité. Ce sont des réponses concrètes aux situations, de plus en plus nombreuses, où les processus naturels de régénération ne sont plus suffisants ou trop aléatoires pour fournir les produits et services nécessaires au soutien de la croissance des populations humaines (Dobson *et al.* 1997, Tappeiner *et al.* 1997, Dekker-Robertson et Libby 1998, Kozlowski 2002).

La transformation des paysages par l'activité humaine a des impacts sérieux sur l'aménagement des ressources (Bouchard et Domon 1997, Kozlowski 2002, Hobbs *et al.* 2006), et la pression sur les forêts mondiales pour la livraison des services économiques, sociaux et environnementaux est aujourd'hui telle que la forêt naturelle seule ne peut subvenir aux besoins et commande la mise en place rapide de nouvelles approches (Noble et Dirzo 1997, Dekker-Robertson et Libby 1998, Harrington 1999, Burley 2004). Pour plusieurs régions, les quelques forêts naturelles restantes devront éventuellement être soustraites complètement à l'exploitation. Nous croyons que la sylviculture d'arbres plantés est une des méthodes permettant de réduire la pression sur les forêts naturelles, voire de reconstruire des milieux autrefois forestiers, au moins du point de vue de la production de services. Mais nous croyons aussi que la sylviculture intensive et la plantation peuvent se faire dans le respect et la préservation des écosystèmes forestiers, permettant même de favoriser la conservation des milieux naturels rémanents par la réhabilitation[1] des forêts dégradées[2] et ce, sans perte de productivité.

Mais pour y arriver il importe de mieux connaître l'écologie des arbres plantés: leur établissement, leur survie et leur croissance en fonction de l'environnement naturel et aménagé.

Le bois et les produits forestiers de demain proviendront d'arbres plantés

Dans plusieurs régions du monde, notamment en Europe, mais aussi dans les régions où l'on a axé la production sur les espèces à croissance rapide comme les Eucalyptus et les Pins, le bois et les autres produits forestiers proviennent déjà d'arbres plantés. Par exemple, la FAO (*Food and Agriculture Organization of the United Nations*) publiait le 1er août 2006 une dépêche titrée ainsi sur son fil de presse:

> « - Les pays d'Amérique latine et des Caraïbes tablent sur les plantations forestières.
> - Persistance de taux élevés de déforestation. »

Deux informations en apparence contradictoires : les plantations devraient permettre une plus grande protection des forêts naturelles, et pourtant la déforestation se maintient à des taux alarmants. Dans la même dépêche :

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[1] Réhabilitation est ici entendu comme analogue à restauration, reconstruction (Hobbs et Norton 1996), et concerne ici la valorisation des forêts dégradées.

[2] « *Degraded forest: a secondary forest that has lost, through human activities, the structure, function, species composition or productivity normally associated with a natural forest type expected on that site. Hence, a degraded forest delivers a reduced supply of goods and services from the given site and maintains only limited biological diversity. Biological diversity of degraded forests includes many non-tree components, which may dominate in the under canopy vegetation.* » (Convention on Biological Diversity 2001).

> « D'ici à 2020, plus de 60 % de l'offre durable de bois en Amérique latine et aux Caraïbes proviendra des plantations forestières, ce qui permettra de garder intactes davantage de forêts naturelles. »
>
> « Les plantations forestières devraient augmenter, passant de 13,1 millions d'hectares en 2005 à 17,3 millions d'hectares en 2020. Même si la majorité de l'offre de bois proviendra des plantations, on estime qu'en Amérique latine et aux Caraïbes les forêts naturelles reculeront de 924 à 881 millions d'hectares durant la même période. Les causes principales de cette déforestation, selon l'étude, sont l'empiètement de l'agriculture et de l'élevage. »

Le même phénomène s'observe en fait un peu partout sur dans le monde (FAO 2006), et a été bien démontré récemment pour la Montérégie (sud-ouest du Québec, Canada), région dans laquelle ont été installés les dispositifs expérimentaux de la présente thèse. Près de la limite nord de la forêt décidue de l'est de l'Amérique du Nord, la région est restée relativement intacte et inhabitée jusqu'à la fin du 18^e^ siècle. La présence autochtone précolombienne a eu des impacts importants sur la composition des forêts en plusieurs régions de l'est de l'Amérique du Nord (Foster 1992, Litvaitis 2003, Lorimer et White 2003, Briggs *et al.* 2006). Par contre en Montérégie, les changements observés sont plutôt dus à l'exploitation forestière suivie par l'expansion des activités agricoles et le drainage des terres, suivie enfin au XX^{e} siècle par l'abandon des terres marginales pour l'agriculture (îlots morainiques de petite taille à pierrosité élevée) au profit des terres argileuses (Bouchard et Domon 1997, Brisson et Bouchard 2003). Ces abandons agricoles se présentent aujourd'hui comme des friches de tailles et âges variables, allant de la jeune friche herbacée à la forêt pionnière composée d'espèces héliophiles, en passant par la friche arbustive (Benjamin *et al.* 2005). La présente thèse s'intéresse aux stades les plus avancés de cet éventail de conditions, soit les peuplements pionniers de feuillus intolérants. Les stades herbacé et arbustif ont toutefois retenu l'attention d'autres travaux dans la région (Cogliastro *et al.* 2003, Fournier 2003, Paquette et Cogliastro 2003, Couture 2005, Cogliastro *et al.* 2006).

Dans cette région, les peuplements pionniers résultants de l'abandon agricole sont souvent déficients en termes de quantité et de qualité de la régénération et sont maintenant considérés fortement perturbés, voire dégradés. Des espèces autrefois abondantes telles le bouleau jaune (*Betula alleghaniensis* Britt.) et le hêtre (*Fagus grandifolia* Ehrh.) sont maintenant absentes, et la régénération est souvent sévèrement limitée par l'absence de semenciers (Brisson et Bouchard 2003). Des constats récents de l'état des forêts du Québec (Commission d'étude sur la gestion de la forêt publique québécoise 2004) et de l'avancée de l'agriculture sur la forêt (Savoie *et al.* 2002, Soucy-Gonthier *et al.* 2003) rendent nécessaires l'élaboration et la mise en place d'approches plus intensives de réhabilitation de ces forêts.

Pour le sud du Québec, cette situation a eu pour conséquence de faire passer la région d'exportatrice à importatrice de feuillus nobles. Cela est pour le moins paradoxal pour un pays dont la forêt était réputée inépuisable il n'y a pas tellement longtemps (Bouchard 2000). L'industrie québécoise du meuble en souffre et dénonce cette situation (Michaud 2000), et la récente Commission d'étude sur la gestion de la forêt publique québécoise (2004) a dénoncé l'état pitoyable de la forêt feuillue québécoise et la nécessité d'intervenir afin de promouvoir sa réhabilitation grâce, entre autres, à une sylviculture plus dynamique[3] et intensive et la plantation d'enrichissement sous couvert.

Planter des arbres pour protéger la forêt

Planter des arbres pour protéger la forêt : voilà une affirmation qui peut paraître paradoxale. C'est pourtant l'idée qu'avancent de plus en plus de chercheurs soucieux de trouver des solutions durables à la crise actuelle dans la gestion des écosystèmes forestiers. Le zonage fonctionnel (Triade), par exemple, permettrait la protection intégrale d'une partie importante du territoire et l'exploitation écosystémique de la forêt commerciale, par l'allocation d'une petite partie du territoire à la sylviculture intensive et à la culture d'espèces à croissance rapide comme les peupliers hybrides (Hunter 1990, Messier 2000, Commission d'étude sur la gestion de la forêt publique québécoise 2004).

Mais au fait, qu'est-ce qu'une forêt ? Est-ce qu'une plantation est une forêt ? Est-ce qu'un peuplement dans lequel sont plantées des espèces indigènes est encore une forêt ?

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[3] Sylviculture qui procède par des interventions multiples et fréquentes.

La FAO propose les catégories et définitions suivantes, de même que leurs surfaces relatives dans le monde[4] (FAO 2006) :

- Forêts primaires (36.4%) : forêts indigènes essentiellement sans trace d'activité humaine;
- Forêts naturelles modifiées (52.7%) : forêts indigènes avec des marques visibles d'activités humaines, essentiellement l'exploitation forestière; il n'est plus possible de distinguer si la régénération, indigène, est naturelle ou assistée;
- Forêts semi-naturelles (7.1%) : forêts composées d'espèces indigènes mais plantées, en tout ou en partie, ou établies à partir de régénération naturelle assistée; les pratiques sylvicoles intensives qui y sont pratiquées peuvent entraîner des changements dans la structure ou la composition du peuplement (pour favoriser certaines espèces par exemple);
- Plantations forestières productives (3.0%) : principalement des monocultures équiennes d'espèces introduites ou indigènes avec pour fonction principale la production de matière ligneuse;
- Plantations forestières de protection (0.8%) : plantations dont les fonctions sont autres, par exemple pour la protection des sols ou des ressources en eau.

À l'échelle mondiale, les deux premières catégories sont en régression (1990-2005), alors que les suivantes sont en progression. Malgré son intérêt évident, cette catégorisation est critiquée, en particulier à cause de l'impact négatif qu'ont eu, et continuent d'avoir, de trop nombreux projets de monocultures dans le monde, mis en place sans égard aux populations locales ni à la capacité de support des sols et ayant pour seule fonction la maximisation d'un rendement dont les profits ne sont pas distribués localement. De plus la mise en place de ces plantations se fait sans programme parallèle de conservation des forêts naturelles (Carrere 2004, Petermann et Langelle 2006).

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[4] La forêt couvre 3.54 milliards d'hectares, soit environ 1/3 de la surface émergée de la Terre

En somme, le problème est dans la façon dont sont conduites les plantations, les monocultures en particulier, et encore plus dans les régions où les sols sont fragiles. Mais il y a aussi un problème de perspective et d'échelle (Noble et Dirzo 1997). Il est en effet impossible de répondre à la question, volontairement naïve, de savoir si les plantations sont une bonne ou une mauvaise chose sans spécifier l'échelle à laquelle la question est posée. Au niveau de la plantation elle-même, quelques hectares par exemple, il est difficile de considérer une monoculture comme un élément intéressant du point de vue écologique. Mais au niveau du bassin versant, de l'unité d'aménagement, du paysage, si la monoculture a pour objectif de permettre une exploitation durable de la forêt, incluant la conservation intégrale d'une partie significative du territoire, tout en supportant l'économie au profit des communautés locales, alors on voit bien que la question n'est pas tant de savoir si la monoculture *est* une forêt, puisque ce n'est pas l'objectif poursuivi, mais bien de savoir si l'arbre planté peut *remplacer* la forêt comme fournisseur de biens.

La clé serait donc dans l'établissement et le respect de normes obligeant cette mise à l'échelle des enjeux (Dekker-Robertson et Libby 1998); concrètement il faut d'abord garantir la conservation de territoires importants avant de permettre l'établissement de monocultures. Nous croyons cependant qu'il est possible de changer les pratiques et d'obtenir de bons rendements tout en conservant une partie importante des caractéristiques et des fonctions de la forêt, notamment par la conservation d'une partie du couvert et de la structure et son maintien dans le temps.

« Anthropogenic activities need not necessarily result in degraded ecosystems. Traditional ecological knowledge and indigenous agroecological management can be combined to create highly diverse agroecosystems that rival natural ones in ecosystem structure and function, while simultaneously meeting human needs »
(Martínez *et al.* 2006).

Planter des arbres pour reconstruire la forêt

La sylviculture, ou culture de la forêt, est donc à la fois le problème et la solution (Bouchard 2000, Martínez *et al.* 2006). En effet dans plusieurs régions du monde la plantation d'arbres en milieu forestier perturbé par les activités humaines se fait dans un but de restauration. Les travaux peuvent être menés à des fins purement écologiques, par exemple par la réintroduction d'espèces indigènes disparues souvent associées à la forêt primaire (Ashton *et al.* 2001, Martinez-Garza et Howe 2003, Gardiner *et al.* 2004) ou à des fins de biodiversité (Carnevalea et Montagnini 2002, Scherer-Lorenzen *et al.* 2004), ou alors essentiellement commerciales, afin de reconstruire le potentiel socio-économique de la forêt (Montagnini *et al.* 1997, Harrington 1999). Mais ces deux objectifs, écologique et socio-économique, ne s'opposent pas obligatoirement et de plus en plus de travaux poursuivent d'ailleurs des objectifs qui se situent à la frontière des deux (Noble et Dirzo 1997, Potvin *et al.* 2003). Ces travaux s'inscrivent dans le modèle de développement durable (Fig. 1.1), en répondant aux besoins du présent sans compromettre la capacité des générations futures de répondre aux leurs (Brundtland 1987). Au Canada le développement forestier durable est défini ainsi (Canadian Forest Service 2001) :

> « *Management that maintains and enhances the long-term health of forest ecosystems for the benefit of all living things while providing environmental, economic, social and cultural opportunities for present and future generations.*»

Plantation sous couvert

La plantation sous couvert s'inscrit très bien dans la perspective de reconstruction du potentiel forestier et du développement durable. La plantation sous couvert cherche un compromis entre la protection offerte par un couvert forestier résiduel, le *shelterwood* [5], et les ressources disponibles (particulièrement la lumière),

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[5] Bien que le terme puisse faire référence à une technique de régénération particulière (voir Johnson *et al.* 1986), il est ici utilisé pour décrire le couvert forestier résiduel sous lequel une régénération naturelle ou artificielle est aménagée après une coupe d'éclaircie (Sauvageau 1995, Ashton et Peters 1999, Langvall et Orlander 2001).

afin de favoriser l'établissement des plants de reboisement. La technique du shelterwood vise essentiellement la formation d'un environnement lumineux de compromis, cherchant à limiter la compétition par une atténuation du climat lumineux, tout en assurant une quantité suffisante pour l'établissement de la régénération (Lieffers et Stadt 1994). Une grande variété de conditions lumineuses peuvent être induites par un gradient de rétention des arbres du peuplement (Drever et Lertzman 2003).

Cette approche est attrayante et généralement mieux acceptée puisqu'elle combine une approche artificielle (la plantation) à l'aménagement du peuplement en place. Elle permet de maintenir une structure végétale composée de différentes strates et assemblages complexes de végétaux de tailles et de fonctions diverses, et ayant pour effet le maintien de l'ambiance forestière (Lahde *et al.* 1999, Pommerening 2002, Pommerening et Murphy 2004). Plusieurs avantages de l'ambiance forestière sont mentionnés. Elle favoriserait la survie des plants en réduisant l'évapotranspiration, les extrêmes de vent et de température, et les dommages associés (Barg et Edmonds 1999, Man et Lieffers 1999, Langvall et Lofvenius 2002, Pommerening et Murphy 2004). L'herbivorie par les ongulés pourrait être limitée par la conservation du couvert (Buckley *et al.* 1998, Agestam *et al.* 2003). La compétition aussi serait réduite (Lieffers et Stadt 1994, Truax *et al.* 2000, Carnevalea et Montagnini 2002), ce qui permettrait une installation efficace des plants et une réaction positive à l'ouverture éventuelle du peuplement résiduel (Johnson 1984, Gordon *et al.* 1995, Buckley *et al.* 1998). La croissance en hauteur et la forme des plants seraient améliorées par auto-élagage (Schütz 2001, Pommerening et Murphy 2004). Maintenir une structure forestière pourrait contribuer à préserver la diversité biologique et les fonctions de l'écosystème dans les peuplements aménagés (McComb *et al.* 1993, Hansen *et al.* 1995). Le développement accéléré de caractéristiques associées aux forêts matures pourrait être facilité par des éclaircies modérées favorisant l'établissement d'une vigoureuse régénération naturelle ou artificielle (McComb *et al.* 1993, DeBell *et al.* 1997). Elle est aussi bien adaptée à la forêt habitée, et se pratique essentiellement à petite échelle, favorisant la prise en charge par les petits propriétaires du développement forestier local.

La plantation d'enrichissement pour sa part est définie comme l'introduction d'arbres dans un milieu dégradé en préservant une partie de la végétation en place (Montagnini *et al.* 1997). Elle peut être faite sous couvert, mais aussi par bandes ou trouées. L'enrichissement est pratiqué là où la régénération naturelle est insuffisante ou pour réintroduire des espèces disparues à la suite d'une mauvaise exploitation. La plantation d'enrichissement, surtout si elle est pratiquée sous couvert, est un outil intéressant et performant de restauration (ou réhabilitation) d'écosystèmes forestiers dégradées (Aide *et al.* 2000, Ashton *et al.* 2001, Martinez-Garza et Howe 2003). À la condition de bien identifier les causes de la dégradation et de fixer des objectifs mesurables et réalistes (Hobbs et Harris 2001), il est possible d'intervenir artificiellement, par exemple à l'aide de la plantation, afin de stopper la dégradation et de favoriser le rétablissement (Dobson *et al.* 1997). Cette intervention est même souhaitable et justifiée étant donné l'ampleur des dommages causés par les activités humaines et notre dépendance aux écosystèmes de la planète (Vitousek *et al.* 1997, Hobbs et Harris 2001, Hobbs *et al.* 2006).

Écologie des arbres plantés

Face à la raréfaction de la ressource et la dégradation accélérée des écosystèmes forestiers force est de constater qu'il nous faut rapidement développer et mettre en place des solutions adaptées et basées sur une connaissance approfondie des nouveaux écosystèmes ainsi créés (Vitousek *et al.* 1997, Hobbs *et al.* 2006). Ces solutions incluent forcément la plantation d'arbres, mais peu de connaissances existent encore à ce jour quand à l'écologie des systèmes plantés en tout ou en partie, de leurs interactions avec les écosystèmes naturels, et plus spécifiquement de l'écologie des arbres plantés et de leur réponse aux conditions amenées par l'aménagement du couvert. L'intention manifeste de l'introduction d'un arbre dans une communauté végétale est d'influer sur le cour de la succession en vue d'accélérer le retour à un écosystème fonctionnel et productif. Le succès de l'opération dépend de la mise en place et du maintien de conditions favorables à l'établissement et à la croissance des espèces choisies. Il s'agit d'optimiser les effets de facilitation induits par le couvert résiduel et d'en minimiser les effets de compétition. L'effet facilitateur des plantes dans certains contextes fait l'objet d'une attention toute récente en écologie végétale, alors que seuls les effets négatifs de compétition étaient habituellement retenus (Callaway et Walker 1997, Holmgren *et al.* 1997). Des travaux sont en cours pour utiliser ces principes afin d'augmenter le succès d'établissement d'arbres dans les milieux difficiles (Gómez-Aparicio *et al.* 2004, Padilla et Pugnaire 2006) ou pour augmenter la performance et l'intégration des plantations équiennes dans le paysage (plantations mixtes plutôt que monocultures) (Lahde *et al.* 1999, Pommerening et Murphy 2004).

Les besoins des plants changent avec la croissance, et le peuplement d'accompagnement poursuit une évolution qui peut être particulièrement dynamique quand il s'agit de jeunes peuplements de transition. Ainsi les conditions de croissance des plants doivent-elles être suivies et possiblement modifiées pour qu'elles permettent aux arbres d'atteindre la strate supérieure de la canopée, ce qui est le but recherché (Johnson 1984, Gordon *et al.* 1995, Buckley *et al.* 1998). L'optimum de conditions, particulièrement au niveau de la lumière, devrait en principe être fonction du degré de tolérance à l'ombre et du stade successoral des espèces utilisées. Ainsi les espèces réagiront-elles différemment aux conditions offertes et présenteront plus ou moins de plasticité morphologique afin de maintenir un bilan en carbone positif assurant la survie de l'arbre. Mais des travaux récents en écophysiologie ont échoué à démontrer un lien clair entre le statut successoral des espèces et leur plasticité en fonction des conditions lumineuses (*e.g.* Walters *et al.* 1993, Beaudet et Messier 1998, DeLucia *et al.* 1998, King 2001). Il faut probablement élargir la notion classique de tolérance à l'ombre qui n'est peut-être pas suffisante pour l'élaboration de scénarios sylvicoles adaptés aux différentes espèces.

Principaux buts et objectifs, ainsi que plan de la thèse

L'aménagement forestier repose en bonne partie sur la tradition, elle-même basée sur une approche empirique; cette thèse tente d'apporter une base quantitative plus solide, de même qu'un cadre théorique pour l'analyse (1) de techniques sylvicoles en fonction d'objectifs mesurables d'aménagement et de conservation des ressources naturelles, et (2) de la réponse des espèces (croissance, écophysiologie) en fonction des conditions environnementales. Un manque important de connaissance sur l'écologie des espèces et de résultats probants empêche présentement les techniques de réhabilitation, telle que la plantation sous couvert, de s'étendre à d'autres régions que celles, restreintes, où elles ont été traditionnellement utilisées. La présente thèse poursuit donc les buts généraux suivants, essentiellement d'ordre écologique, assortis d'objectifs spécifiques dans chacun des chapitres :

- Mesurer l'efficacité de la plantation sous couvert à assurer le maintien d'une structure forestière et des bénéfices associés pour la régénération et les fonctions forestières, et ce sans perte de productivité;
- Identifier les conditions nécessaires à l'atteinte de ces objectifs;
- Tester la technique dans le contexte particulier des forêts tempérées décidues dégradées du sud-ouest du Québec;
- Obtenir les connaissances écologiques essentielles quant aux espèces utilisées en plantation sous couvert; tester les modèles de tolérance à l'ombre et de stades de succession pour les systèmes plantés; et contribuer à l'élaboration de nouveaux outils théoriques pour l'étude des systèmes plantés;
- Développer et tester des techniques adaptées d'évaluation des conditions de croissance, particulièrement au niveau de la lumière;
- Contribuer à l'élaboration de normes d'application de la technique pour le Québec par un transfert de connaissances vers les gestionnaires et professionnels du milieu forestier, particulièrement au niveau de la forêt feuillue privée.

Quatre chapitres, rédigés sous forme d'articles scientifiques, forment le corps de la thèse. Le premier de ces textes est une revue de littérature exhaustive et la méta-analyse des travaux de plantation sous couvert dans le monde, suivie des résultats de l'application sur six ans de la technique dans deux peuplements pionniers du sud-ouest québécois avec test d'un dégagement partiel. Le troisième texte teste les modèles théoriques d'écologie des semis pour l'analyse de la plasticité morphologique et de la croissance des arbres en aménagement sous couvert. Un dernier texte propose et teste différentes méthodes d'évaluation de la lumière disponible en sous-bois, un élément important des travaux en écologie forestière, particulièrement en plantation sous couvert. Une conclusion générale est proposée à la suite de ces chapitres.

CHAPITRE 2

Survival and growth of under-planted trees: A meta-analysis across four biomes

Alain Paquette, André Bouchard et Alain Cogliastro

Ecological Applications 16(4): 1575-1589

L'objectif poursuivi dans ce chapitre était d'évaluer l'étendue des activités et des objectifs poursuivis en plantation sous couvert, et d'analyser la survie et la croissance en fonction du degrés d'ouverture de la canopée, et inversement, de conservation de la structure forestière. Les questions posées étaient celles-ci :

- Existe-t-il une relation significative entre le densité du couvert et la survie ou la croissance des semis plantés?
- Le cas échéant, est-ce qu'un niveau optimum d'ouverture peut être identifié?

Dans le cas où un couvert partiel serait optimal, cela viendrait appuyer les efforts en sylviculture alternative visant la préservation du couvert forestier et des structures. Pour répondre à ces questions nous avons fait une revue de littérature et la méta-analyse des travaux en plantation sous couvert dans le monde. Quatre biomes présentant des données en quantité et qualité suffisantes ont été retenus pour l'analyse (forêt tempérée décidue, forêt côtière tempérée pluvieuse, forêt tropicale, et forêt boréale). Des techniques statistiques permutationnelles ont été adaptées pour répondre aux questions posées. L'analyse de la relation entre la survie ou la croissance et la densité du couvert a été faite par régression multiple sur variables factices binaires et testée par permutations. Les différentes classes étaient ensuite recodées pour permettre la construction d'une table de comparaisons multiples. L'importance de ces travaux réside dans une synthèse de données quantitatives sur une technique communément utilisée, mais peu justifiée. C'est à notre connaissance la seule étude exhaustive sur l'utilisation du *shelterwood* et de la plantation sous couvert à travers le monde, et l'une des trop rares études à faire usage de la méta-analyse en écologie (Osenberg *et al.* 1999).

CHAPITRE 3

Successful under-planting of red oak and black cherry
in early-successional deciduous shelterwoods of North America
Alain Paquette, André Bouchard et Alain Cogliastro
Annals of Forest Science (sous presse, accepté le 12 mai 2006)

Dans le troisième chapitre nous avons utilisé la plantation sous couvert pour évaluer sa capacité à enrichir avec des feuillus nobles de jeunes peuplements issus d'abandon agricole en Montérégie (sud-ouest du Québec, Canada), une zone où la forêt feuillue est particulièrement mal en point et où la régénération en place est insuffisante. Très peu d'information est disponible sur les semis plantés sous le couvert de jeunes peuplements pionniers quant à la densité optimale de rétention du couvert (et de lumière disponible), le choix et la performance des espèces, l'effet de l'herbivorie, et l'effet de la position de la compétition par rapport au plant sur sa croissance. Plus particulièrement les questions suivantes sont traitées dans ce chapitre :

- Est-ce que la plantation sous couvert est une technique efficace pour l'installation de feuillus nobles dans de jeunes peuplements dominés par les feuillus intolérants?

- Est-ce qu'un dégagement appliqué quelques années après la plantation est nécessaire pour maintenir une croissance intéressante?
- Est-ce que la prédation par le cerf de Virginie (*Odocoileus virginianus*) sera augmentée par le dégagement?
- Si un dégagement est nécessaire, à quelle(s) strate(s) végétale(s) devrait-il être appliqué?

Deux espèces ont été utilisées, le chêne rouge (*Quercus rubra* L.) et le cerisier tardif (*Prunus serotina* Ehrh.). Bien qu'une quantité importante de littérature soit disponible sur le chêne rouge en régénération naturelle et artificielle, elle fait surtout référence aux chênaies matures mal régénérées du nord-est de l'Amérique du Nord. Plus encore que pour le chêne, les connaissances concernant le cerisier tardif en plantation sont presque absentes. La croissance des deux espèces a ainsi été suivie sur deux sites de plantation jusqu'à la sixième année de croissance. Un dégagement manuel appliqué deux ans après la mise en terre y est comparé à un témoin sans intervention. Des inventaires annuels de la lumière disponible à trois hauteurs à partir du sol, de même que juste au-dessus des plants, ont été faits. La compétition herbacée et arbustive autours des plants et la prédation par le cerf de Virginie ont aussi été évaluées, et un indice de densité de la compétition de sous-bois a été construit à partir des données de lumière.

CHAPITRE 4

Morphological plasticity in seedlings of three deciduous species under shelterwood under-planting management does not correspond to shade tolerance ranks

Alain Paquette, André Bouchard et Alain Cogliastro

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La quantité de lumière disponible influence non seulement la croissance des semis en sous-étage, mais aussi leur architecture, et la façon dont ils disposent l'appareil photosynthétique dans l'espace. La plasticité morphologique des semis d'arbre est posée comme un des éléments importants impliqués dans la tolérance à l'ombre et dans la dynamique de succession végétale. La survie est de plus en plus reconnue comme étant le principal facteur relié à la tolérance à l'ombre (Kobe *et al.* 1995, Canham *et al.* 1999), mais la survie ou la mort sont la conséquence d'un long processus d'adaptation au climat lumineux, réussie ou non, dont certains traits seulement sont reconnus (Walters et Reich 1996, Kaelke *et al.* 2001). Des études récentes comparant des espèces décidues tempérées n'obtiennent pourtant pas de correspondance entre leur plasticité et leur rang de tolérance à l'ombre ou statut successoral (Walters *et al.* 1993, Beaudet et Messier 1998, King 2001). Au quatrième chapitre il est donc question de l'écologie des espèces, et plus particulièrement de leur plasticité morphologique en fonction de la lumière disponible, de même que de l'utilité des rangs successoraux pour l'aménagement sylvicole par plantation sous couvert.

Nous avons mesuré la plasticité morphologique des semis de trois espèces d'arbres de la forêt décidue tempérée de l'est de l'Amérique du Nord selon 13 paramètres allométriques associés à la croissance, la géométrie de cime, la branchaison et la disposition de la surface foliaire, en fonction d'un important gradient de lumière dans de jeunes forêts de transition aménagées par la plantation sous couvert. Les espèces analysées sont l'érable à sucre (*Acer saccharum* Marsh.), très tolérante à l'ombre, le cerisier tardif, intolérant, et le chêne rouge, une espèce de tolérance intermédiaire associée au feu dont les difficultés de recrutement naturel et artificiel sont préoccupantes. Selon le modèle d'équilibre en carbone (Bazzaz 1979, Givnish 1988), les trois espèces à l'étude devraient se positionner sur un gradient de plasticité morphologique allant de grande (érable à sucre) à faible (cerisier tardif), correspondant à leur statut successoral respectif. Associé au feu et relativement tolérant en bas âge, le chêne rouge devrait se placer entre les deux autres espèces. La réponse des espèces au climat lumineux est analysée à l'aide de régressions et analyses de covariance. L'importance relative de la lumière et de la taille des arbres pour différents groupes de réponses morphologique est déterminé à l'aide de la partition de variance. Il s'agit d'une des rares études à appliquer les techniques et principes de l'écologie forestière pour l'analyse des systèmes plantés, appelés à prendre de plus en plus d'importance dans les milieux forestiers mais pour lesquels nous sommes encore mal outillés.

CHAPITRE 5

A less restrictive technique for the estimation of understory light in high replication or multiple site designs

Alain Paquette, André Bouchard et Alain Cogliastro

Forest Ecology and Management (soumis pour publication le 19 octobre 2006)

La lumière est une ressource limitante pour les plantes du sous-étage forestier, dont les semis qui constituent la régénération de la forêt (Chazdon et Pearcy 1991). C'est donc fréquemment pour l'optimisation de la disponibilité de cette ressource que sont conduits les aménagements forestiers tels que les éclaircies et la plantation sous couvert, incluant les travaux de la présente thèse. La recherche en écologie forestière a donc mis au point différentes techniques pour évaluer la disponibilité de cette ressource de façon aussi précise que possible. Bien qu'en apparence simple, la mesure de la lumière disponible fait l'objet de débats à la fois aux niveaux des concepts et des méthodes utilisées. De plus, certaines méthodes très utilisées, plus particulièrement la photo hémisphérique (Canham 1988, Rich *et al.* 1993) et la mesure instantanée sous ciel couvert (Messier et Puttonen 1995, Parent et Messier 1996), présentent des contraintes importantes à leur utilisation. Deux questions sont principalement investiguées au chapitre 5 :

- Existe-t-il des alternatives efficaces, précises, et moins contraignantes aux méthodes de références?
- Est-ce que ces méthodes peuvent efficacement prédire la croissance et la morphologie des semis?

Trois méthodes d'évaluation du climat lumineux ont ainsi été utilisées et comparées à l'aide de corrélations et de la régression orthogonale. Les méthodes sont la photo hémisphérique (indice GLI et les fractions diffuse et directe) et la méthode sous ciel couvert, de même qu'une sonde linéaire d'un mètre par temps ensoleillé. Une technique inédite a aussi été développée et testée, faisant appel à une sonde hémisphérique existante permettant de s'affranchir des conditions de ciel. Les différentes méthodes ont été utilisées sous quatre sites contrastés, allant de l'érablière mature au jeune peuplement de transition sous aménagement. Les mesures ont été prises à deux mètres du sol au dessus de semis naturels d'érable à sucre de taille comparable dont la pousse annuelle et le ratio de longueur de cime sur sa largeur ont été mesurés afin de tester la capacité des différentes méthodes à prédire la croissance et la morphologie des semis. Alors que d'autres études présentent des comparaisons de méthodes entre elles, ou contre le standard de pourcentage saisonnier, aucune autre étude n'a à notre connaissance fait une telle comparaison utilisant la réponse des arbres comme témoin de la qualité des mesures. Nous apportons aussi une méthode inédite, sans contrainte de ciel, et particulièrement intéressante pour la mesure des conditions lumineuses en forêt, un problème fondamental en écologie forestière qui demande beaucoup d'efforts et d'attention.

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Chapitre 2 : Survival and growth of under-planted trees: a meta-analysis across four biomes

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Ce chapitre a fait l'objet d'une publication :

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Abstract

The transformation of natural forest regeneration processes by human activities has created the need to develop and implement new models of forest management. Alternative silvicultural systems such as variable retention harvest, partial and patch cuts, and older forest management practices such as under-planting, are used in many forests around the world, particularly in North American oak stands, the boreal and coastal temperate rain forests of Canada and the USA, and in many degraded tropical regions of Asia and of the Americas. Specific objectives are pursued in each of these biomes, but some are common to most regions, such as preservation of cover and structure and their associated benefits for natural or artificial regeneration due to moderation of the micro-climate, development of optimal light and competition conditions, and reduced predation by herbivores. Shelterwoods are often presented as an alternative to clear-cutting to improve the survival of planted trees. A meta-analysis of published results with randomization tests was performed to test the relationship between overstory density and planted seedling growth and survival. Multiple comparisons were also used to reveal optimal levels of overstory density, if they exist. A majority of studies show that survival and growth improve as stand density decreases to an intermediate level, below which they either drop or stabilize. This level seems optimal in most conditions, as it is also more apt to fulfill other objectives imposed on today's forest activities, such as the conservation of forest processes and structures, and the reconstruction of degraded stands through the accelerated return of mid- to late-successional species.

Keywords

Alternative silvicultural systems; ANOVA-like multiple regressions; enrichment planting; forest regeneration; meta-analysis; overstory density; permutation test; seedling height growth; seedling survival; shelterwood; under-planting

Introduction

The interruption or changes in forest regeneration processes induced by human activities is prevalent in many places around the world (Kozlowski 2002). Many stands show regeneration problems even several decades after harvesting or agricultural abandonment. These problems range from the simple lack of regeneration to a shift to species composition that is less desirable economically and ecologically. In response, we have seen during the last decades the emergence of ecosystem management and alternative techniques such as variable retention harvest, patch or partial cutting, and the recycling of older practices such as under-planting in shelterwoods, two-storied or mixed stands, and continuous cover forestry.

This new forestry is presented as a valuable alternative to forestry practices which have, in many places, not been able to fulfill their dual role of providing developing economies with a much needed resource and ensuring adequate regeneration for a sustainable harvest (Rowe 1992, Greene *et al.* 2002, Mitchell *et al.* 2004). These silvicultural approaches are used in biomes as different as tropical or boreal forests, and deciduous or coastal temperate forests (Fig. 2.1). They share the common objective of the preservation of forest cover and structure and their associated benefits for natural or artificial regeneration. Silvicultural practices such as two-storied and uneven-aged stand structures are proposed to achieve structural objectives, as well as those of timber production and aesthetics (Brandeis *et al.* 2001). They are a response to situations where the natural recovery of forest composition is compromised or too slow and unpredictable to provide the forest products and services required by increasing population growth (Tappeiner *et al.* 1997, Kozlowski 2002).

Transformations of natural landscapes by human activities have profound implications for future resource management (Bouchard and Domon 1997, Kozlowski 2002), and current demands on the world's forests for social, environmental and economic benefits require new approaches and rapid implementation of relevant results (Harrington 1999, Burley 2004). Forest plantations now have the potential to provide wood and non-woody products, as well as to promote the conservation of natural forests (FAO 2001).

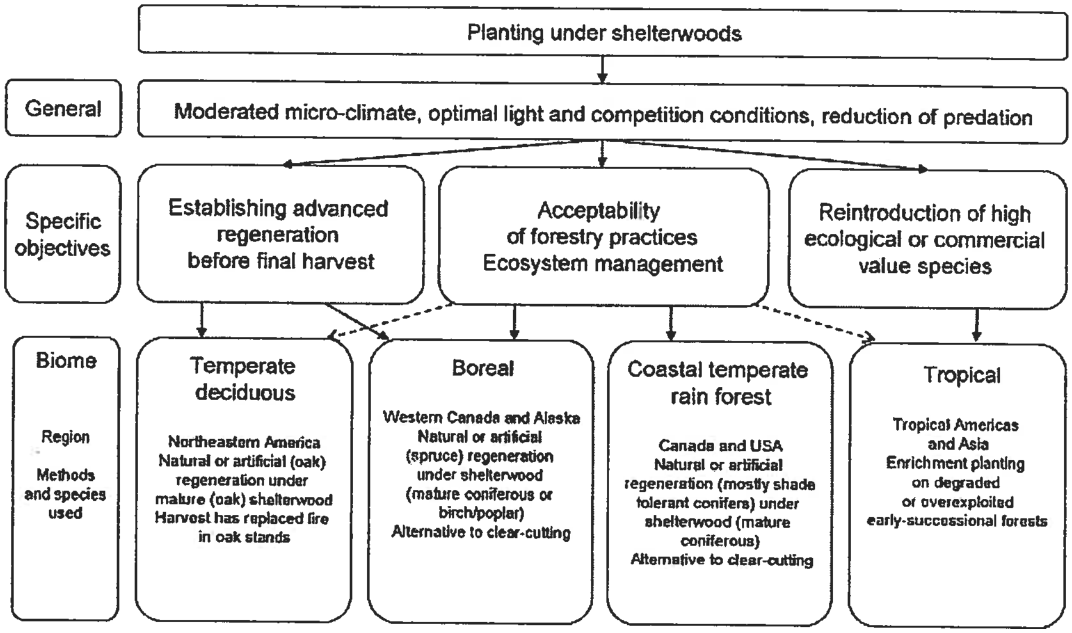

Figure 2.1. Planting under shelterwoods: general and specific objectives for the different biomes covered in this paper.

Shelterwoods – common and specific objectives

Although "shelterwood" can refer to a specific silvicultural technique used particularly in northeastern US oak forests (regeneration cut followed by overstory removal, see Johnson *et al.* 1986), the term is also used to describe the residual forest cover under which natural or artificial regeneration is managed after a partial cut (Sauvageau 1995, Ashton and Peters 1999, Langvall and Orlander 2001); the latter is used in the present work. The alternative silvicultural systems share the common features of producing an environment, the shelterwood, that is favorable to tree regeneration (Fig. 2.1). Many subscribe to the general concepts of ecosystem management and continuous cover forestry, as a response to criticisms of forest overexploitation, monocultures and clear-cuts in particular (Rowe 1992, Kenk and Guehne 2001, Rojo and Orois 2005). The methods associated with these concepts have the potential to achieve the objectives of sustainable development described in the Rio / Helsinki accords and of the certification of forest products (Pommerening and Murphy 2004), although these objectives of acceptability of forest practices are explicitly stated only in the boreal and coastal temperate forest literature (Fig. 2.1) (Lieffers *et al.* 1996, Barg and Edmonds 1999, Greene *et al.* 2002).

Shelterwoods are used in the boreal and American oak forests to establish regeneration before overstory removal by commercial harvesting (*e.g.* Brose *et al.* 1999, Spetich *et al.* 2002, Zaczek 2002). Regeneration of white spruce (*Picea glauca* [Moench] Voss) by the management of naturally occurring or planted seedlings following clear-cutting often proved difficult and expensive (Youngblood and Zasada 1991, Lieffers *et al.* 1996, Stewart *et al.* 2000), and is increasingly challenged in the boreal forest for aesthetic reasons, real or perceived environmental damage, and its variable efficiency at establishing the next cohort of conifers. Fire, naturally associated with the oak forests of northeastern America, is now controlled and has been replaced by the harvest of mature stands as the major perturbation (Lorimer *et al.* 1994, Buckley *et al.* 1998). Traditional, single cut harvesting, however, has proven ineffective in ensuring adequate regeneration of oak stands, which are often replaced by less desirable species after harvesting. The proposed solutions involve a preparation cut to create a shelterwood under which natural or artificial regeneration can establish prior to the removal of the residual overstory (Fig. 2.1) (Johnson 1984, Loftis 1990).

Enrichment planting can be used under a thinned overstory where the objective is the introduction of valuable species in degraded forests. It may be useful in areas where natural regeneration is insufficient, for reintroducing species that have disappeared following overexploitation, or to establish forest species that are inappropriate in open plantations. It may include planting of species of commercial or local value, using different approaches such as under-, gap- or strip-planting. Such is often the case with overexploited, early successional tropical forests of Asia, and Central and South America, in stands no longer offering the possibility of a harvest in the mid-term, and where ecological restoration is an objective (Fig. 2.1; Aide *et al.* 2000, Ashton *et al.*

2001, Martinez-Garza and Howe 2003). Rehabilitation of non-productive stands or former natural ecosystems using enrichment planting is also used in the southern United States for the restoration of bottomland hardwood forests (Gardiner *et al.* 2004), and in the eastern United States to restore the once important chestnut (*Castanea dentata* Marsh. [Borkh.]) (McCament and McCarthy 2005). It is also used for the conversion of even-aged plantation monocultures into mixed or two-storied stands and generally more complex systems (Truax *et al.* 2000, Kenk and Guehne 2001, Parker *et al.* 2001).

Under-planting is generally better accepted because it combines an artificial approach (planting) with the management of the existing natural stand (the shelterwood). It allows for the maintenance of a vegetation structure composed of different layers and complex assemblages of plants of various sizes and functions, and as a result retains a forest character (*e.g.*, Lahde *et al.* 1999, Pommerening 2002, Drever and Lertzman 2003). Maintaining a forest structure may contribute to conserving biodiversity and ecosystem functions in managed stands (McComb *et al.* 1993, Hansen *et al.* 1995). Accelerated development of mature forest characteristics can be facilitated by moderate thinning or partial harvesting to favor the establishment of natural or artificial regeneration (McComb *et al.* 1993, DeBell *et al.* 1997).

Several advantages of a forested environment, such as a shelterwood, are stated in the literature for the developing natural or artificial regeneration and are schematized in Figure 2.2 as a function of residual density. The forested environment, as opposed to a clear-cut or very thin density retention, would improve the survival of planted trees by protecting them from excessive evapotranspiration, wind and temperature extremes, and associated damage (*e.g.*, Langvall and Lofvenius 2002, Agestam *et al.* 2003, Pommerening and Murphy 2004) (Fig. 2.2). Predation, particularly by deer in temperate forests, could be reduced by the retention of cover (Buckley *et al.* 1998, Agestam *et al.* 2003). Competition by herbaceous plants and understory shrubs should also be reduced (*e.g.* Lieffers and Stadt 1994, Truax *et al.* 2000, Carnevalea and Montagnini 2002) (Fig. 2.2), which would allow an effective establishment of the planted trees and their positive reaction to an eventual opening of the residual stand (Johnson 1984, Gordon *et al.* 1995, Buckley *et al.* 1998). Height growth and trunk shape should be improved by the preservation of a vertical structure (Schütz 2001, Pommerening and Murphy 2004). These alleged advantages of a shelterwood are not always documented by formal experimental testing in the literature, and when they are, results are not always conclusive.

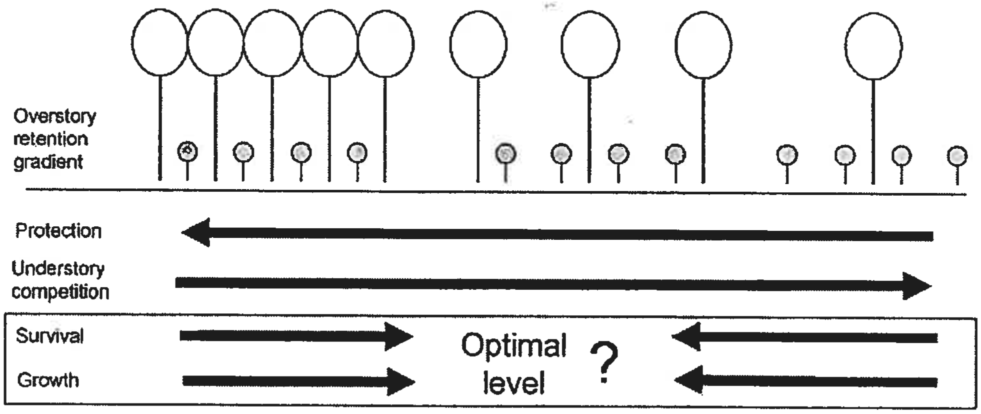

Figure 2.2. Diagram model of the effect of overstory density on several factors, based on assumptions found in the literature. The residual density of the overstory decreases from left (unmanaged forest or dense shelterwood) to right (light shelterwood or clear-cut). The effect on the factors is shown by increasing or decreasing arrows.

The shelterwood method essentially seeks to create a compromise in the light environment, to reduce competition by decreasing available light, while still ensuring a sufficient quantity for tree regeneration establishment (Lieffers and Stadt 1994). A wide range of light conditions can be induced by a gradient of tree retention (Drever and Lertzman 2003), and will impact differently on several factors. While many studies discuss some or all of these issues, conservation and succession usually remain as concepts, and are not subjected to experimentation. Some studies do present data on protection (from extremes in temperature, frost, wind, etc.) (*e.g.* Barg and Edmonds 1999, Man and Lieffers 1999, Langvall and Orlander 2001), and predation (*e.g.* Gordon *et al.* 1995, Buckley *et al.* 1998, Truax *et al.* 2000). The bulk of papers presenting results from field trials, however, are concerned with growth (mostly height growth) and survival of under-planted trees. Survival and growth are what practitioners are looking for from forest management, but they can also be used as indicators of the success of the shelterwood technique to protect the planted trees from climate extremes, predation, and understory competition, and to improve future stand composition and productivity.

Survival and growth as indicators of the success of the under-planting approach

Because of the potential for generalization from these two indicators and their relative accessibility in the literature, we chose published results of survival and height[6] growth for the basis of this investigation of the success of the under-planting technique. The conservation of residual forest cover by thinning prior to under-planting has been suggested as a method of improving the survival of planted trees. It is often simply proposed as an alternative to clear-cuts, in which survival would be reduced, especially in boreal ecosystems (Man and Lieffers 1999, Langvall and Orlander 2001), but it is rarely discussed as a function of the whole range of residual densities (Fig. 2.2).

Annual increments that are below the potential of the species planted are often deemed satisfactory, as the emphasis is put on the successful establishment of planted trees and their capability, at the appropriate time, to respond positively to the opening created by the overstory removal or successive partial releases (Johnson 1984, Spetich *et al.* 2002). Nevertheless, researchers and forest practitioners tend to predict better growth under a managed partial overstory than in a clear-cut; best growth is predicted where an optimal compromise is reached between controlling competition and allowing enough resources (mostly light) to reach the planted trees (Lieffers and Stadt 1994, Buckley *et al.* 1998, Truax *et al.* 2000) (Fig. 2.2). A considerable body of data from under-planting trials is available, but only rarely do any of the published studies cover the whole range of overstory densities, from a fully stocked unmanaged stand to zero residual overstory, that would be necessary to fully demonstrate the effect of the methods involved. This demonstration is facilitated by the use of already published data of survival and growth in a meta-analysis, a powerful tool which allowed us to bring together data from several

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[6] Height growth is most important in the early years to overcome understory competition, which is why most papers report data on height or height increments and very few report diameter or biomass data.

studies conducted under a wide range of overstory densities, and to reveal patterns that are not obvious when single studies are examined (Goldberg *et al.* 1999, Gómez-Aparicio *et al.* 2004). By testing survival and growth of under-planted seedlings for five classes of overstory densities in four documented biomes, we used meta-analysis to answer the following questions: (1) Is there a significant relationship between overstory density and survival or growth of artificial regeneration?, and (2) if significant, can an optimal density of residual overstory be identified? If the partial retention of forest cover is found optimal, that would lend support to alternative forestry practices targeting the preservation of forest cover and structure.

Methods

A common basis for comparison was needed to complete the meta-analysis. Residual density levels, either applied or recommended, are often defined using basal area, canopy cover, line opening width (in the case of strip- or line-planting), or even stocking, a qualitative expression of the adequacy of tree cover on an area, in terms of crown closure, number of trees, basal area, or volume, in relation to a pre-established norm (Haddon 1988). This can make the interpretation and comparison of thinning prescriptions very difficult (Dey and Parker 1996). We constructed an overstory density index from canopy opening values, stocking values, the ratio of opening width to neighboring trees or original canopy height, or available light values, using the cases where two or more of these measurements were given (Kim *et al.* 1996, Buckley *et al.* 1998, Man and Lieffers 1999, Parker *et al.* 2001, Peña-Claros *et al.* 2002, Drever and Lertzman 2003, Maas-Hebner 2005). We also used our own data of light and canopy openness (Paquette *et al.*, *in press*). Special care was used in cases for which measurements did not match, for example when light was measured some years after the silvicultural treatment was applied (*e.g.* Drever and Lertzman 2003), giving enough time for at least some vegetation layers to partly recover (Paquette *et al.*, *in press*). We then combined these data to create the overstory density index presented in Table 2.1. This index allows for a classification of the literature according to results obtained in terms of survival and height growth in relation to overstory density (Tab. 2.2).

Table 2.1. Overstory density index developed according to four descriptive variables used in the literature

Overstory density	Available light (%)	Stocking (% of original basal area)	Canopy cover (%)	Opening width : canopy height
Uncut "control" (UC)	≈ 0	100	≈ 100	0
Dense shelterwood (Dsw)	< 25	> 60	> 75	< 0.25
Intermediate shelterwood (Isw)	25 – 50	40 – 60	50 - 75	0.25 – 0.40
Light shelterwood (Lsw)	> 50	< 40	< 50	0.40 – 2
Clearcut (CC)	≈ 100	≈ 0	≈ 0	> 2

Five classes of overstory density were used in close association with the literature. We begin with trials conducted under uncut (UC), unmanaged closed canopies, often referred to as "control" treatments. This is followed by three contrasting levels of shelterwood densities for which trials were conducted in most biomes. These levels are arbitrary but they were chosen because they represented the range of conditions used in the literature while still offering as much contrast as possible. Studies presenting results for several levels mostly used contrasting levels that fell within those used here. We complete this index with trials conducted in clear-cuts (CC), which is also a point of comparison often used in under-planting literature.

We then reviewed all recent papers reporting growth or survival data for planted trees under shelterwoods around the globe. Data in sufficient numbers could be collected for only four biomes: the temperate deciduous forest of northeastern United States, where mostly red oaks (*Quercus rubra* L.) are used; the boreal forest of western Canada and Alaska, using white spruce; the tropical Americas and Asia, using several species of economic or ecological value; and the coastal temperate rain forest of British Columbia (Canada) and Oregon, USA, using mostly the typical conifers of these forests (Tab. 2.2). We included results from peer-reviewed articles in which survival or growth could be calculated and overstory densities used were given or could be calculated. We found no evidence of paper bias according to journal quality, such as measured by an "impact factor" (ISI Journal Citation reports 2004) (Murtaugh 2002). After careful review, 24 papers presented usable data and were retained for the meta-analysis of survival and growth of under-planted trees according to the overstory density level used. Many of these studies presented results for several species, overstory densities, or sites; a total of 191 entries of survival results and 165 entries for growth were recorded (Tab. 2.2).

Some measure of "effect size" is ordinarily used in meta-analysis where, for example, the absolute or relative difference between "control" and "treatment" are presented (Osenberg *et al.* 1999). We do not have a clear "treatment effect" here, but rather a range of overstory conditions under which trials were conducted, sometimes comparing results between levels, sometimes between one shelterwood and some "control", uncut forest or, at the other end of the gradient, a clear-cut, or even simply reporting results for one shelterwood treatment. Raw data of growth and survival were therefore used to compare results between overstory density levels.

Published results varied in time span from plantation establishment, which could be a problem in meta-analysis (Goldberg *et al.* 1999, Osenberg *et al.* 1999). All efforts were made to recover initial heights and calculate yearly height increments (Equation 2.1), for example from histograms, when annual height increments were not published per se, so that experiments could be compared on a common basis.

$$Annual\ height\ increment\ (cm) = \frac{Total\ height - Initial\ height}{Number\ of\ years} \tag{2.1}$$

The difference in time is more challenging for published results of survival, because mortality is often reported to be concentrated almost exclusively in the first year or first few years after plantation (Tworkoski *et al.* 1986, Cogliastro *et al.* 1990, Cogliastro *et al.* 1993), which would tend to suggest the use of an overall mortality (at the end of the experiment). However, other studies reporting detailed survival data (per year or even month), especially in the tropical biome, present rather regular, continuous patterns of mortality for the duration of the study (Ramos and del Amo 1992), or reported annual rates directly (Peña-Claros *et al.* 2002), lending support to the use of a yearly survival rate. In Table 2.2 we reported survival as a final rate at the end of the study, and the number of years during which the study was conducted. For the meta-analysis we used both forms of survival rates, which will be discussed further. The annual rate of survival is obtained from final rates following Equation 2.2, which is easily reversed to obtain final rates from annual data.

$$Annual\ survival\ rate = final\ survival\ rate^{(1/number\ of\ years)} \tag{2.2}$$

As a general rule one entry is made in Table 2.2 for each independent observation. For studies reporting results of multiple manipulations, experiments were considered independent observations if (1) they involved different species, or (2) different (independent) levels of overstory density, or (3) different sites were used (Englund *et al.* 1999). Replicates within the same site are not considered independent observations (an average is then used). Only results for planted trees are used; direct seeding or natural regeneration trials are excluded because their growth and survival cannot be compared with planted seedlings in the first years. When different planting stocks of the same species were used, an average was made. Treatments of fertilization and/or post-planting competition control using herbicides are excluded, but studies using herbicides for stand preparation before planting are included. Open field trials are not included since they are different from clear-cuts. However, some treatments not intended as clear-cuts, for example some “green tree retention” or “patch-cut” trials, were included in that category because they had almost no canopy cover left or openings that were greater than twice the height of the neighboring forest (Tab. 2.1). In the case of studies where the reduction of the stand density was incremental, we retained the most pertinent level, defined as the level at which planted trees made the greater part of their recorded growth. When animal browsing or other mechanical damage was measured and significant, only damage-free seedlings were retained here.

Table 2.2. Published results of under-planting trials for four different biomes. Results of survival and growth increment are classified per overstory density used (according to Tab. 2.1).

Biome/Source	no. overstory treatments	no. sites	no. years		Species planted	Survival (%)[1]					Annual height increment (cm)				
			survival	growth		UC	Dsw	Isw	Lsw	CC	UC	Dsw	Isw	Lsw	CC
Temperate deciduous															
Johnson 1984	3	1	5	5	*Quercus rubra*		84		84	84		6		13	18
Lorimer *et al.* 1994	2	2	5	5	*Quercus rubra*	26;28	94;93				0;0	7;3			
Gordon *et al.* 1995	1	1	6	4	*Quercus rubra*			83					9		
Dey and Parker 1997	2	1	2	2	*Quercus rubra*	89		99			2		10		
Tworkoski *et al.* 1986	2^2	1	3^3	3^3	*Quercus rubra*	90		89			2		17		
					Quercus alba	94		87			3		10		
					Pinus strobus	100		97			29		43		
Truax *et al.* 2000	1	4^4	8	2^5	*Quercus rubra*		98;92;85	25				28;23;18	20		
					Quercus macrocarpa		100;90;90	87				23;20;15	43		
					Fraxinus pennsylvanica		95;95;45	97				13;10;1	35		
					Fraxinus americana		97;87;65	68				13;18;1	33		
Buckley *et al.* 1998	4	2	2	1	*Quercus rubra*	99;99		100;100	99;99	98;98	4;5		4;5	4;4	10;7
Larrick *et al.* 2003	3	1	4	4	*Quercus rubra*	76		76		76	2		7		20
Bardon *et al.* 1999	1	2	5	5	*Quercus rubra*			73;72					7;5		
Parker *et al.* 2001	5	1	5	5	*Fraxinus americana*	95	98;98;95;95	97			2	4;8;0;1	9		
					Quercus rubra	50	90;72;75;80	85			1	5;8;4;6	20		
					Pinus strobus	77	87;90;90;90	95			4	8;11;8;11	16		
Teclaw, Isebrands 1993			3	3	*Quercus rubra*			98	95	95			10	13	10
Mean					**All**	**77**	**88**	**85**	**94**	**90**	**5**	**10**	**17**	**9**	**13**
Boreal															
Man and Lieffers 1999	4	1	3	3	*Picea glauca*	78		92	91	87	5		10	10	8
Youngblood, Zasada 1991	3	3	3	$3;5^7$	*Picea glauca*				98;98;96	99;98;96				8;8;8	6;8;11
Mean					***Picea glauca***	**87**	**-**	**97**	**96**	**95**	**6**	**-**	**7**	**9**	**8**

Table 2.2. Continued.

Biome/Source	no. overstory treatments	no. sites	no. years		Species planted	Survival (%)					Annual height increment (cm)				
			survival	growth		UC	Dsw	Isw	Lsw	CC	UC	Dsw	Isw	Lsw	CC
Tropical															
Montagnini *et al.* 1997	1	4	4-7	4-7	*Cordia trichotoma*			70;67;95;61					35;30;59;39		
					Enterolobium contortisiliquum			80					86		
					Bastardiopsis densiflora			63;50;95					149;97;66		
					Ocotea puberula			47;40;75					47;29;34		
					Euterpe edulis			27					37		
					Peltophorum dubium			30					59		
					Balfourodendron riedelianum			47;100					18;29		
					Parapiptadenia rigida			40					17		
					Nectandra lanceolata			63					64		
					Didymopanax morototoni			35					19		
					Jacaranda micrantha			94					27		
Peña-Claros *et al.* 2002	5	1	4	4	*Bertholletia excelsa*	62	91;95	89	95		13	63;69	108	111	
Ådjers *et al.* 1995	4	1	2	2	*Shorea johorensis*	45		58	45;35		22		59	60;36	
					Shorea leprosula	70		85	75;78		23		50	72;58	
					Shorea parvifolia	40		78	50;53		21		60	70;78	
Ramos and del Amo 1992	3	1	6.7	6.2	*Cordia alliodora*		18	50	45			32	34	137	
					Swietenia macrophylla		18	56	25			40	38	65	
					Brosimum alicastrum		35	45	3			10	16	12	
Ådjers *et al.* 1997	2	1	3	3	*Durio zibethinus*				83	55				60	64
Ådjers *et al.* 1996	1	1	3	3	*Shorea johorensis*				56					127	
					Shorea leprosula				67					114	
					Shorea parvifolia				48					89	
					Shorea faguetiana				55					54	
					Shorea fallax				67					51	
					Shorea polyandra				24					64	
					Hopea sangal				78					84	
					Dipterocarpus cornutus				6					28	
					Dipterocarpus kunstleri				38					34	
					Shorea ovalis				41					63	
Mean					**All**	**54**	**51**	**63**	**51**	**55**	**20**	**43**	**50**	**70**	**64**

Table 2.2. Continued.

Biome/Source	no. overstory treatments	no. sites	no. years		Species planted	Survival (%)					Annual height increment (cm)				
			survival	growth		UC	Dsw	Isw	Lsw	CC	UC	Dsw	Isw	Lsw	CC
Coastal temperate															
Brandeis *et al.* 2001	4	1	4	4	*Pseudotsuga menziesii*		10	20;37	37						
					Abies grandis		50	70;88	95						
					Thuja plicata		72	77;94	95						
					Tsuga heterophylla		12	40;45	50						
Maas-Hebner *et al.* 2005	4	1[8]	4;8[9]	8	*Tsuga heterophylla*	5	94	94	94		-[10]	61	61	61	
					Picea sitchensis	0	90	90	90		-	44	44	44	
					Pseudotsuga menziesii	0	87	87	87		-	38	38	38	
					Abies grandis	0	94	94	94		-	34	34	34	
					Thuja plicata	35	90	90	90		-	13	13	13	
					Alnus rubra	0	94	94	94		-	90	90	90	
					Acer macrophyllum	1	64	64	64		-	-[11]	-	-	
Mitchell *et al.* 2004	4	1	7	7	*Abies amabilis*				82	90;93;94				10	15;15;14
					Tsuga heterophylla				82	87;92;93				18	25;26;26
Mean					**All**	**15**	**71**	**72**	**81**	**92**	**5**	**43**	**47**	**39**	**20**

Notes: Key to abbreviations: UC, uncut; Dsw, dense shelterwood; Isw, intermediate shelterwood; Lsw, light shelterwood; and CC, clear-cut.

[1] Most often reported survival (at the end of the study)

[2] A third treatment was available but could not be used here since the release was applied three years after the trees were planted (see Methods)

[3] The trees were under-planted three years prior to treatment; only the following three are used

[4] Six sites were used, but two of them were old fields (not clear-cuts – see Methods)

[5] Trees were under-planted three years prior to treatment, then a shelterwood was applied for two more years, after which the trees were completely released; only the years under shelterwood are used for growth (mortality occurred within the first years)

[6] Six sites were used, but only means were published

[7] Results are given for third and fifth years; an average of these two results was used here

[8] Three sites were used, but only means were published

[9] Survival under the "no thin" treatment (UC) was given after four years (eight years are used elsewhere)

[10] Due to the high mortality of trees planted under the "no thin" treatment (UC), growth data were not presented

[11] Severe browsing by elk prevented the authors from testing for a treatment effect on *Acer macrophyllum*

Statistical analysis

Although a weighted analysis would have been preferable (weighing of each entry by the inverse of its sampling variance) (Gurevitch and Hedges 1999), only some papers gave any measure of growth variance (including error bars on histograms). This is often the case in ecology, but should not preclude the use of meta-analysis given the importance of the body of literature (Goldberg *et al.* 1999, Gurevitch and Hedges 1999). Variances are almost never given for survival data since it is an absolute value, unless replications of treatments are used (with blocks for example). Unweighted randomization tests (Goldberg *et al.* 1999, Gurevitch and Hedges 1999) were therefore done on published results to test for a significant relationship between survival or growth and overstory density, within each biome. This is a simple one-way ANOVA problem that can be reformulated as a multiple regression analysis once the classification criterion is recoded with dummy variables (one dummy for each of the five classes of Tab. 2.1) (ter Braak and Looman 1987, Legendre and Legendre 1998). The ANOVA-like multiple regressions were computed with the R software using the "rda" and the "anova.cca/permutest.cca" functions of the "vegan" package (Oksanen *et al.* 2005, R Development Core Team 2005) using 99,999 permutations (plus one for the original data) of the residuals under the reduced model (Anderson and Legendre 1999). This allowed for the computation of a pseudo-*F* statistic (the ratio of constrained to unconstrained inertia from a redundancy analysis) and corresponding probability with one degree of freedom for both the model and the residuals.

Within each biome, only those density classes with two or more entries were used for the analysis. More randomization tests were then computed where significant relationships were found to further test for differences between classes of overstory density. These *a posteriori* multiple comparisons were performed by recoding the datasets so as to contrast density levels (sum of contrast coefficients equals to zero). The computation is the same as the above multiple regressions, and is repeated for all possible pair-wise comparisons within a biome. A multiple comparisons table was then constructed using the appropriate Dunn-Sidak corrected alpha levels found with

Equation 2.3 (Sidak 1967) where α is the global Type I error (0.05) and c the number of possible comparisons :

$$p_{corrected} = 1 - (1 - \alpha)^{1/c} \tag{2.3}$$

Both the *a posteriori* approach for all possible comparisons and the Dunn-Sidak correction are considered conservative.

Results and discussion

Survival

Overall survival (at the end of the experiments) of under-planted trees did not show a significant relationship with overstory density levels in most biomes (except coastal temperate) (Tab. 2.3). This could be due to much variation in study durations (Tab. 2.2) which could preclude the use of this response variable for the analysis of otherwise comparable studies. Annual survival rates, on the other hand, are free from this variation and offer the possibility of comparing results on a common basis (one year). Significant relationships are then detected for all biomes except the boreal forest (Tab. 2.3). Although differences seem small (in absolute values), the survival rates are annual, and mortality differences will compound over the years and could become important as is the case here. Within-group variances are also very small, and differences can be effectively detected (Tab. 2.3). In the temperate deciduous forest of northeastern America, survival seems constant throughout the range except in the deepest shade (uncut, or control trials) where it drops to 93%, but a trend is not easily identified because only two opposite levels of shelterwood (dense and light) give results significantly different than those from an uncut forest (UC) (Fig. 2.3).

In tropical forests, the maximum annual survival of planted trees is reached with an intermediate shelterwood and it is significant (Fig. 2.3). The greatest increase in annual survival was found to be between the uncut forest and the dense overstory (Tab.

2.3). The gain is smaller from dense to intermediate densities, and drops under a light shelterwood or clear-cut (this last level was not included in the statistical analysis because only one observation was available, Tab. 2.2). Tropical survival data are more variable and show lower survival rates than in other biomes (Tab. 2.3), probably because of the greater number of species and poor knowledge of their light requirements (*e.g.* Ådjers *et al.* 1995, Davidson *et al.* 2002).

In this biome, many authors presented results for several species, the survival rates of which were sometimes very different, even nil (in such cases that species was not retained for assembling Tab. 2.2). It is interesting to note that Montagnini *et al.* (1997) report results for 11 species, none of which could be found in an earlier review by Weaver (1987) of 160 species used in enrichment planting trials in tropical America alone (only three genera were common to both papers). In the present review, out of the 15 species reported for the tropical Americas (Tab. 2.2), only five are included in Weaver's review, three of which had previous success in enrichment planting (*C. alliodora*, *D. morototoni* and *S. macrophylla*). All species used in Asia are *Dipterocarpaceae*, with one exception (*D. zibethinus, Bombacaceae*). Although Dipterocarps are a major source of prime wood in tropical Asia, little is known about their silviculture and light requirements which cover a wide range of shade tolerance (Ådjers *et al.* 1996, Tuomela *et al.* 1996).

A significant increase in survival (both overall and annual) is detected in the coastal temperate rain forest biome between the unmanaged forest and the dense shelterwood (Fig. 2.3). Survival then rises slowly all the way to the clear-cut but no significant differences could be detected between these classes, even after re-running the analysis without the entries for the uncut level (which could have masked other, smaller, differences between the remaining levels). The largest gain by far, and the only significant one, is again observed with only a small reduction in density (between an uncut forest and a dense shelterwood) already ensuring adequate survival of under-planted trees (Fig. 2.3).

Table 2.3. Means (SE) of survival rates and annual height increment for different overstory densities in four documented biomes, and meta-analysis statistical results.

Biome / Overstory density	Overall survival (%)	Annual survival[1] (%)	Annual increment (cm)
Temperate deciduous			
Uncut	77 (7.9)	93 (2.4)	5 (2.3)
Dense	88 (2.3)	98 (0.42)	10 (1.5)
Intermediate	85 (4.3)	97 (0.92)	17 (3.1)
Light	94 (3.5)	98 (0.48)	9 (5.2)
Clear-cut	90 (4.4)	97 (1.1)	13 (2.5)
Results	**$N = 66$; $p = 0.2901$**	**$N = 66$; $p = 0.0368$**	**$N = 66$; $p = 0.0169$**
Boreal			
Uncut	87 (9.0)	96 (3.5)	6 (0.7)
Dense	-	-	-
Intermediate	97 (1.5)	99 (0.50)	7 (1.1)
Light	96 (1.7)	99 (0.50)	9 (0.5)
Clear-cut	95 (2.7)	98 (1.1)	8 (1.0)
Results	**$N = 14$; $p = 0.2303$**	**$N = 14$; $p = 0.4210$**	**$N = 14$; $p = 0.2390$**
Tropical			
Uncut	54 (7.1)	75 (6.0)	20 (2.3)
Dense	51 (17)	87 (4.6)	43 (10.7)
Intermediate	63 (4.3)	91 (1.2)	50 (6.2)
Light	51 (5.3)	77 (3.1)	70 (7.0)
Clear-cut	*55*	*82*	*64*
Results	**$N = 56$; $p = 0.3515$**	**$N = 56$; $p = 0.0012$**	**$N = 56$; $p = 0.0146$**
Coastal temperate			
Uncut	15 (10)	31 (14)	*5*
Dense	71 (9.1)	90 (4.6)	43 (9.9)
Intermediate	72 (6.5)	92 (2.6)	47 (11)
Light	81 (5.2)	96 (1.9)	39 (16)
Clear-cut	92 (1.1)	99 (0.17)	20 (2.5)
Results	**$N = 54$; $p < 0.0001$**	**$N = 54$; $p < 0.0001$**	**$N = 27$; $p = 0.2397$**

Notes: Analysis results are based on 99 999 permutations (plus original data). N = number of entries used for statistical analysis; only those overstory densities, within a biome, with two or more entries are used (*italics* are excluded). [1]See Methods for survival equations.

No overstory density effect on planted tree survival could be detected in the few papers available for boreal forests. Other results from direct seeding (Youngblood and Zasada 1991) and natural regeneration trials (Wurtz and Zasada 2001), found no effect of overstory density on survival. Scarification, on the other hand, which reduces understory competition, is generally recognized as an effective method of promoting the establishment and survival of naturally regenerated or direct seedings of spruce (Stewart *et al.* 2000). More research is needed, therefore, to identify optimal residual density for reducing understory competition and promoting seedling survival in that biome. Lieffers and Stadt (1994) successfully achieved understory competition reduction and optimal spruce growth with an intermediate shelterwood, but they counted on natural regeneration and did not provide survival results.

It could be argued that the overall survival reported in many studies mostly occurred in the early years of establishment and could be artificially reduced with the use of annual data in the case of studies that were run over several years. This could be a serious problem if studies largely different in time span were reported under different overstory levels (short studies at one end of the range and longer ones at the other end, for example). This is not the case here, and several studies present results over two or more overstory levels (with the same duration) (Tab. 2.2). Also it seems that contrary to survival in traditional open field plantations, mortality under a partial overstory occurs over a longer time period, many studies still reporting significant losses after more than five years, which would support the use of annual survival rates.

Survival of planted trees generally increases with decreasing stand density, but this is significant only between the uncut control trials and any level of shelterwood, after which no gain is observed. Reduced survival with further thinning of the overstory is only observed in the tropical biome. However, several studies have measured less favorable microclimates in clear-cuts under many forest types (Man and Lieffers 1999, Langvall and Orlander 2001, Langvall and Lofvenius 2002). Only Ramos and del Amo (1992) and Buckley *et al.* (1998) have succeeded in showing a decrease in survival (accompanied by an increased growth of the surviving trees) with a major reduction of the stand's density. Agestam *et al.* (2003), studying beech seedlings (*Fagus sylvatica* L.), have measured greater damage to plants after a clear-cut, particularly by frost, but also better growth. Explanations considered for this phenomenon mostly concern climate, the extreme effects of which would be moderated by a shelterwood, even when sparse (Barg and Edmonds 1999, Man and Lieffers 1999, Langvall and Lofvenius 2002, Agestam *et al.* 2003, Pommerening and Murphy 2004).

Growth

There is a definite progression and significant relationship of annual height increments with decreasing stand density in the deciduous and tropical biomes for the first levels of density (Tab. 2.3). As with survival, the greatest absolute gains in growth are observed with only a small thinning to the dense level. The *a posteriori* tests performed on the temperate deciduous biome results, although conservative and already showing significant differences (Fig. 2.3), may not be very relevant because the somewhat predictable results from the uncut trials could mask the more important differences between thinning densities. We tested that by contrasting the intermediate shelterwood, which demonstrated maximum growth, against the dense and light shelterwoods and the clear-cut together, with a significant result (p=0.0124). Growth is at a maximum in the temperate deciduous forest under intermediate shelterwoods and is significantly reduced with further thinning of the stand. Most studies report results for red oak, which is moderately shade tolerant (Sander 1990) and intolerant of understory competition as demonstrated by Smidt and Puettmann (1998). The intermediate level of overstory density, where maximum growth is observed, offers a good compromise and corresponds to the model of Buckley *et al.* (1998), where optimal growth should be obtained at an intermediate level of overstory density. The growth values reported for the deciduous forest are not very high, however, and are below the minimum levels suggested by Johnson (1984) for ensuring the establishment of red oak in shelterwoods. It could be that height growth is decreased but diameter growth increased in lower density stands and clear-cuts, which is actually one of the alleged benefits of under-planting. Better height growth for red oak is often reported in open fields on former farm land when weed control (chemical, mechanical, or physical barrier) is applied (Cogliastro *et al.* 1990, Lambert *et al.* 1994, Cogliastro *et al.* 2003), but a comparison with a clear-cut is inappropriate and these results were not included here.

In the tropical biome the maximum growth is reached with light shelterwoods (Fig. 2.3 - only one entry was made under the clear-cut category and it was not included in the analysis). The height increments are higher as expected, but results are again highly variable (Tab. 2.2), probably for the same reasons as for survival (a great number of species used and poor knowledge of their ecology). In the tropical biome, growth does increase with decreasing stand density, but the greatest gains are acquired with only a small thinning from uncut, control forests (20 cm) to a dense shelterwood (40 cm) (Tab. 2.3). Ådjers *et al.* (1995) do not report any additional gain in growth when cut strips exceed two meters in width in a three meter high young tropical stand. Although some efforts are being made to better understand the species requirements for tropical reforestation purposes (see Davidson *et al.* 2002), this knowledge is incomplete. Weaver (1987) found that only about 15% of the 160 species reviewed for enrichment planting purposes had any success.

In the boreal biome no significant relationship could be detected between growth and density, but the maximum absolute height growth is reached with a light shelterwood (Tab. 2.3). Reported growth of planted white spruce is generally small, as is expected from this biome. Partial-cuts are often proposed as alternatives to clear-cuts in the boreal forest to control understory competition and maintain mixed species composition to mimic natural stand dynamics (Lieffers and Stadt 1994, Greene *et al.* 2002). According to Lieffers and Stadt (1994), acceptable leader growth of 9 to 25 cm for mid-tolerant white spruce can be obtained at light levels between 15 and 40% transmission, and no differences in height growth are noted between seedlings growing at 40% and those in open, clear-cut sites.

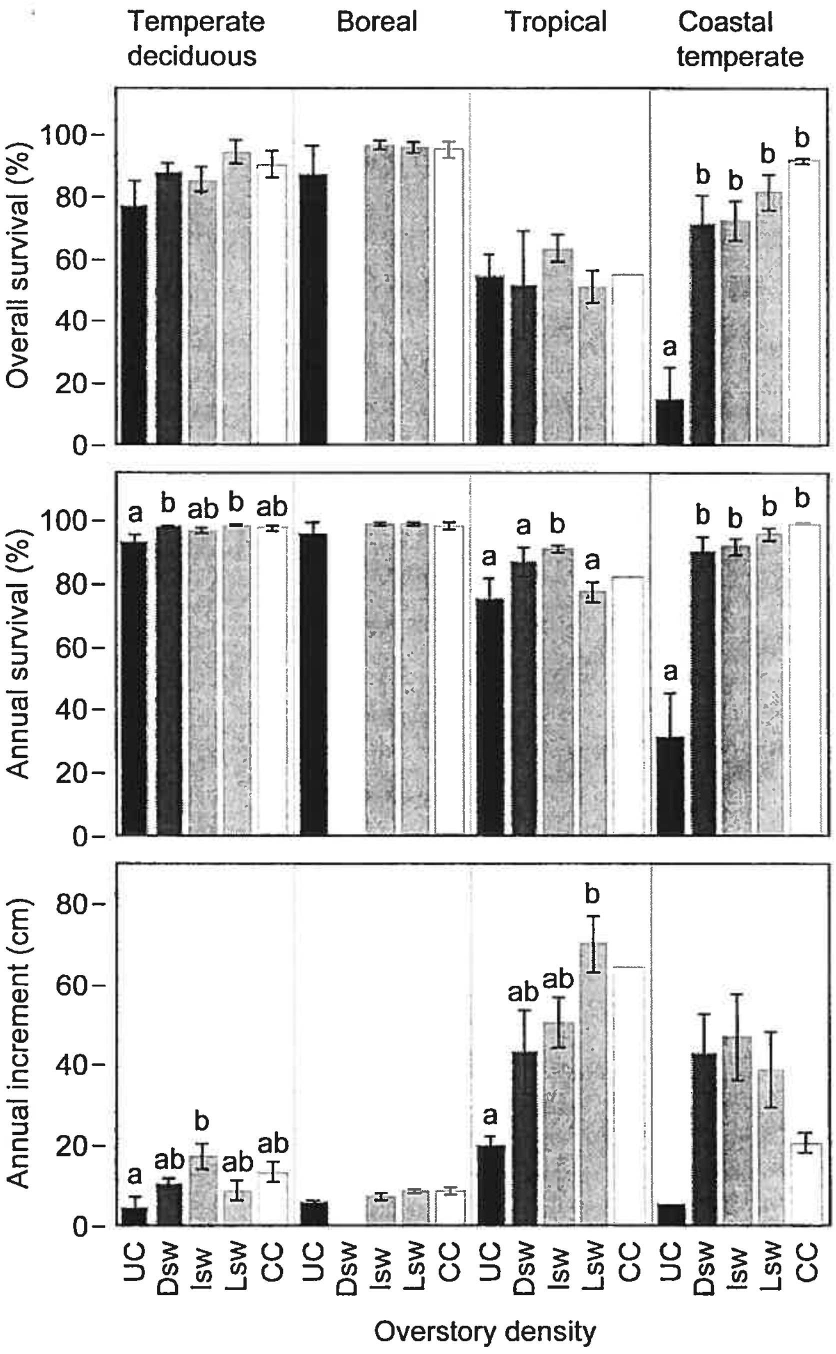

Figure 2.3. Survival rates and annual height increment (mean ± SE) for each overstory density within four documented biomes. Results of multiple comparison analyses are given (means not sharing the same letter are different) for a global Type I error of 0.05 (critical Dunn-Sidak corrected values are 0.0051 and 0.0085 for comparisons of five or four levels, respectively). Multiple comparison tests were computed only on significant relationships (Tab. 2.3); all classes are otherwise considered equal.

Four levels of density had sufficient data for the analysis in the coastal temperate biome, but no density effect could be detected (Tab. 2.3). The decrease in height growth in clear-cuts is not significant, and all results from that level came from a single study (Mitchell *et al.* 2004) in which the light shelterwood treatment actually produced lower growth than in the other more open treatments presented, including a clear-cut. Only one study reported results under an unmanaged overstory (it was not included in the analysis); at 5 cm of annual height growth it is very much lower than the average. Because most or all trees died under the control (uncut) treatment in the study by Maas-Hebner *et al.* (2005), height growth of the few survivors was not reported and could not be used here, though it was probably very low and would have confirmed the trend we observed, which is a highly probable, significantly reduced growth under uncut stands. Brandeis et al (2001) reported growth increments in volume, and these data could not be included in the statistical analysis either, but they showed a gradual increase for all four species with the thinning of the stand (from dense to light shelterwoods).

As with other biomes, the greatest gains in growth were obtained at relatively dense levels of overstory. All conifer species used in this biome are considered shade tolerant or even very tolerant (except *P. menziesii*, sometimes described as intermediate). But several studies on natural regeneration found that these species generally grew best under full or nearly full light (reviewed in Brandeis *et al.* 2001). Few data are available for planted seedlings, although they are used in great numbers, and the few results reviewed here do not concur with natural regeneration trials, as both growth and survival were not improved significantly with further decreases in the stand density past a dense shelterwood. This points to a probable "planting shock" experienced by conifer seedlings in clear-cuts due to increased understory competition, unfavorable microclimate, and the newly planted seedling's inability to compete in the year or years immediately following plantation (Man and Lieffers 1999, Maundrell and Hawkins 2004). Although naturally regenerated conifers can perform well in clear-cuts and under other light density management such as patch cut or green tree retention, some partial shade is needed to protect the planted seedlings initially and allow them to get established before the final cut or additional reductions of the residual overstory.

Conclusion

Under-planting activities have proven to be effective methods of artificial regeneration in many forested habitats around the globe. In temperate deciduous forests, tropical forests and coastal temperate rain forests, increased survival of under-planted trees is ensured by only a moderate thinning of the stand to a dense or intermediate density. Survival is stable or improves slightly with further decreases in overstory density, except in the tropical biome, the only one where a significant decrease in survival rate is observed at lighter densities, pointing to an optimum intermediate level. Growth follows a similar pattern in most biomes, with a sharp increase with only a moderate thinning to a dense shelterwood. Growth keeps improving slightly with further thinning of the stand to a light shelterwood in tropical forests. The growth of under-planted trees is significantly reduced in the temperate deciduous biome under shelterwoods thinned beyond an intermediate density, pointing again to an intermediate density for this biome.

In general, the greatest gains in survival and growth are achieved before or at an intermediate level of shelterwood and stabilize or decrease under thinner stands. Under thinner shelterwoods and clear-cuts, protection from climatic stresses such as frost and wind, as well as from predation, is diminished, while undergrowth competition is higher. An intermediate level of overstory density seems to be a good compromise in most cases, where resources and protection are balanced. Forest managers should note that any level of shelterwood is temporary, and light levels will decline as the stand recovers. This will occur at varying rates, fastest in tropical biomes and slowest in boreal biomes. In most cases regular maintenance is strongly suggested, at intervals that vary according to biome and species under-planted. The keys to sustained growth are an optimal intensity of the initial thinning to ensure successful establishment, and the correct timing of the subsequent interventions.

In the biomes surveyed, light shelterwoods and clear-cuts present no definite advantages in growth or survival over denser conditions, which are often better accepted and are apt to fulfill the other objectives now imposed on forest management, such as the conservation of structure and processes in a forested landscape. Our analysis suggests an optimal thinning density for the growth and survival of under-planted seedlings. However, further research is needed to demonstrate whether sustainable management objectives can also be achieved through thinning and under-planting.

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Chapitre 3 : Successful under-planting of red oak and black cherry in early-successional deciduous shelterwoods of North America

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Une version antérieure a fait l'objet d'une publication, ce chapitre intègre les modifications demandées par le jury d'évaluation de cette thèse de doctorat :

Paquette, A., A. Bouchard et A. Cogliastro. 2006. Successful under-planting of red oak and black cherry in early-successional deciduous shelterwoods of North America. Annals of Forest Science (sous presse; accepté le 12 mai 2006).

Abstract

Under-planting early-successional forest stands with red oak and black cherry was tested on abandoned agricultural land of North American temperate deciduous forests. A partial release treatment was applied during the third growing season and compared to a control. The growth increment after six years is analyzed with respect to treatment and the vertical position of the competition (upper *vs* lower layers). Although the release treatment reduced competition at all vegetation layers, growth was mostly determined by the density of the upper layer. Deer herbivory was not increased by the release. The release treatment succeeded in significantly increasing available light for the duration of the study, while the understory recovered quickly. Planted trees, particularly red oak, responded well to the release treatment.

Keywords

Under-planting; light; early-successional forests; deer herbivory; thinning treatment

Introduction

Under-planting while preserving part of the existing vegetation to serve as shelterwood has been proposed as a means of increasing valuable timber production in impoverished forest environments (Montagnini *et al.* 1997, Harrington 1999). The present study tested the method under common but poorly understood young pioneer stands within agroforested landscapes. The North American temperate deciduous forest has been highly transformed by human activity over the last four centuries, following European colonization. The forest slowly started to recover during the 20th century due to the reduction of agricultural activities on soils of marginal agricultural value (Brooks 2003, Litvaitis 2003). A number of recent studies have focused on vegetation, human disturbance, and reforestation with valuable hardwoods in the southernmost part of the St-Lawrence River Valley in eastern Canada (Domon *et al.* 1993, Bouchard and Domon 1997, Cogliastro *et al.* 2003). Some species found in large numbers at the beginning of the colonial period are now rare, while community composition has changed significantly (Simard and Bouchard 1996, Brisson and Bouchard 2003). Many of these early-successional forest communities show serious regeneration problems or interruption of succession even after several decades (Benjamin *et al.* 2005) and are still generally negatively perceived by their owners (Luginbühl 1999, Askins 2001, Benjamin *et al.* 2006). However, they can be considered as new opportunities to restore the forest to its former productivity (Kozlowski 2002).

Artificial regeneration under a shelterwood (under-planting) is relatively recent in eastern North America (Johnson *et al.* 1986). The technique is based in part on the long experience of American foresters in promoting the establishment of advanced natural regeneration prior to harvesting in fire adapted oak stands (Hannah 1988), and in the boreal forest as an alternative to clear-cutting (Greene *et al.* 2002). In Europe it was proposed as a technique for reconstructing forests damaged by the great windthrow of December 1999 (Boulet-Gercourt and Lebleu 2000), for converting even-aged plantation monocultures into mixed or two-storied stands (Kenk and Guehne 2001), and for promoting natural regeneration (Agestam *et al.* 2003). We believe the technique should be successful in degraded young successional temperate forests in agroforested landscapes where the standing trees have no commercial value and instead could help promote the establishment of a new cohort of high-value species, a technique which resembles enrichment under-planting in tropical forests (Montagnini *et al.* 1997, Martinez-Garza and Howe 2003).

The environment created by a shelterwood is a compromise between resource availability (mostly light) on the one hand, and protection from understory competition, herbivory from ungulates, and climatic extremes on the other (Paquette *et al.* 2006). Available light for tree regeneration establishment (natural or artificial) is increased through thinning (Drever and Lertzman 2003), but not so much as to promote competition by understory shrubs or herbaceous plants (Lieffers and Stadt 1994, Carnevalea and Montagnini 2002), or climatic stress (Man and Lieffers 1999, Langvall and Lofvenius 2002, Agestam *et al.* 2003). These conditions should allow an effective establishment of the trees and their positive reaction to an eventual release (Johnson 1984, Gordon *et al.* 1995).

Herbivory by white-tailed deer (*Odocoileus virginianus*) is an increasing problem for natural and artificial regeneration in eastern North America (Hix *et al.* 1994, Larrick *et al.* 2003). It is hypothesized that herbivory, in addition to damages caused by climatic conditions, will increase with the thinning of stands, whereas a denser shelterwood would better protect the planted trees (Gordon *et al.* 1995, Buckley *et al.* 1998).

Little information is available specifically for seedlings planted under young successional forest stands as to (1) the density of canopy retention (shelterwood) and light levels required, (2) the growth rates to expect, (3) the choice of species to use, (4) the effect on herbivory, and (5) the singular and combined effects of competition from above or below. Based on six years of growth, we tested red oak (*Quercus rubra* L.) and black cherry (*Prunus serotina* Ehrh.) performance under two levels of shelterwood density.

Although there is quite a large body of literature on natural and artificial regeneration of red oak in north-eastern North America, it deals mostly with poorly regenerated mature oak stands (Lorimer *et al.* 1994). Moreover, very little data is available concerning black cherry in shelterwood environments. The planted species have a shade tolerance that ranges from intermediate (red oak) (Sander 1990) to low (black cherry) (Marquis 1990); red oak is more shade tolerant when young (Kaelke *et al.* 2001). Marquis (1990) mentions that a partial cover is required for optimal establishment of black cherry, but that full sunlight is necessary afterwards to ensure continued growth, which can be vigorous. On average, red oaks in a variety of shelterwood densities (excluding unmanaged control treatments and clear-cuts) reviewed in Paquette *et al.* (2006), grew 10 cm per year (varying from 4 to 28 cm), which is well below the recommended success criterion of at least 30 cm proposed by Johnson (1984).

In this study we test the effectiveness of the under-planting technique for the establishment of hardwoods, namely red oak and black cherry, in degraded early-successional temperate forests. Specifically, we ask the following questions: (1) Is a release treatment necessary for the sustained growth of the planted trees? (2) Should this treatment be applied to the upper layers of competing vegetation or to the layers in the understory? (3) Will the treatment increase predation by white-tailed deer?

Methods

Study sites and stand characteristics

Two sites located in the St. Lawrence River Valley, an important agricultural region in eastern Canada, within the sugar maple - hickory bioclimatic domain (Thibault 1985), were selected for this study. The region has a humid continental climate with mean annual temperatures of 6 °C, and monthly means of 21 °C in July and -10 °C in January. Mean annual total precipitation is 1030 mm (of which 18% falls as snow), and is well distributed throughout the year (Environment Canada, climatological normals 1971-2000). Stands at both sites share similar soils (Tab. 3.1) and originate from recent

(1962) agricultural abandonment (pasture), which followed extensive deforestation and high grading.

The St-Chrysostôme site (45°09'N; 73°45'W) is dominated by grey birch (*Betula populifolia* Marsh.), which comprises 67% of the stand's basal area. Hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) and white elm (*Ulmus americana* L.) are also present (22%), but late successional species are almost absent from the canopy and rare in the undergrowth, mostly scattered sugar maple (*Acer saccharum* Marsh.) seedlings. Tall shrubs (*Crataegus* spp. and *Malus pumila* Mill.) are also present and form dense thickets under which regeneration is greatly reduced. A major ice storm (January 1998) seriously damaged the site and most grey birch stems were bent. With a basal area of 21 m^2/ha (all species DBH>1 cm), this site was deemed to be sufficiently open to be under-planted directly in the spring of 1998, without prior site preparation (Tab. 3.1).

Table 3.1. Summary of site characteristics and silvicultural work

	St-Chrysostôme	Ste-Clotilde
Area	2.5 ha	3 ha
Soil (15 cm)	Sandy loam; pH 5.15	Sandy loam; pH 5.87
Composition	*Betula populifolia*, *Ostrya virginiana* and *Ulmus americana* High shrub density	*Betula populifolia*, *Ostrya virginiana*, *Fraxinus americana*, *Carpinus caroliniana* and *Ulmus americana*
Basal area[1]	21 m^2/ha	16 m^2/ha
Density[1]	6500 stems/ha	6100 stems/ha
Canopy height	11 m	12 m
Origin[2]	1962	1962
Preparation	None	Thinning (fall 1997)
Planting	April 28th and 29th 1998; 900/ha (3 m x 3 m)	
Release	Summer 2000; 1 m around planted seedlings	

Notes : Stand height, composition, density and basal area, as well as soil pH and texture were evaluated in summer 2000, prior to the release treatment. [1] All species DBH>1 cm. [2] Approximate year of abandonment of agricultural activities (pasture), based on growth ring counts of sampled trees.

The Ste-Clotilde site (45°08'N; 73°38'W) is of the same age, and grey birch is still dominant in the upper vegetation layer, but less so than on the St-Chrysostôme site (26% of total basal area) because this species was the primary target of a preparation thinning. It is accompanied by hophornbeam, white ash (*Fraxinus americana* L.), hornbeam (*Carpinus caroliniana* Walt.) and white elm (63%). Shrubs are less abundant, and valuable hardwood regeneration is somewhat greater and composed mostly of sugar maple, white ash and black cherry seedlings, but restricted to the vicinity of a few remaining large seed trees of the same species pre-dating agricultural abandonment and heavily damaged by the ice storm. The Ste-Clotilde site was prepared during fall 1997 by thinning approximately 30% of the stand's basal area without creating major openings in the canopy, primarily targeting early successional species. The residual basal area was 16 m^2/ha, which is lower than that of the St-Chrysostôme site without preparation (21 m^2/ha), with comparable stem densities of over 6000 stems/ha and average stand height of 11 m (Tab. 3.1).

Under-planting of black cherry and red oak seedlings

Under-planting was carried out in spring 1998 (hereafter noted as year 1) using one-year-old black cherry and red oak in containers (340 ml). Mean height and diameter at the root collar for black cherry were 34 cm and 4 mm, respectively, and 27 cm and 6 mm for red oak (nursery data). Black cherries were planted in greater numbers than red oaks on both sites (2:1 at St-Chrysostôme and 6:1 at Ste-Clotilde) due to limited supplies at the nursery. Trees were planted every three meters, on parallel planting lines spaced at three meters. Species were distributed on alternate planting lines, according to their respective proportions. Inadequate micro-sites, due in particular to small depressions with drainage problems or fallen trees from the ice storm, were avoided for an approximate final density of 900 trees per hectare.

Experimental design and treatment

This study started in 2000, 2 years after the trees had been planted as a first time trial under the supervision of the *Agence forestière de la Montérégie*. No other trials of this kind (hardwoods planted under a shelterwood of intolerant, pioneer species) were available at the time. The sites had been planted according to new guidelines only recently introduced in the silvicultural norms manual (AFM 1999). This was a great opportunity for evaluative research as the technique was being proposed and applied by a few progressive foresters and producers. The research questions investigated in this study were the same as those of the foresters and policy makers involved in the project.

We choose to conduct this research on those sites instead of planting new ones in a more classical experimental design because we could benefit from two more years of growth and thus learn more on the effectiveness of the method, especially given that the release treatment cannot be applied too early. Although we had to work around unsuitable or unplanted sectors of the sites to construct experimental plots inside the blocks, this design could provide much needed answers for which we had no data at the time. The design is composed of a large number of trees, on two sites, and it covers a greater time scale (6 years), especially following the treatment, than any comparable studies in temperate forests (average = 3.5 years ; Paquette *et al.* 2006). The sites were also managed using the tools and financial incentives already available to small producers through the regional Agency and the *Programme de mise en valeur des resources du milieu forestier* (MNRF Québec) so the conclusions could be readily translated into applicable norms and instructions, and have a positive impact on forest policies and activities in the region and elsewhere.

On each site we delineated two replication blocks to account for possible spatial heterogeneity (Hulbert 1984). Inside these blocks, in early spring of 2000 (year 3), experimental rectangular plots were delineated so as to contain areas which were completely planted without interruption and with visually homogenous vegetation composition. They were scattered over the planted areas of each block and buffers of at least 20 m were kept between them. Plots vary from 400 to 600 m^2. Eleven were established at the St-Chrysostôme site for a total area of 0.62 ha (25% of the total planted area), and twelve at the Ste-Clotilde site for a total area of 0.56 ha (19%). Plots were then randomly assigned to either "control" or "thinning treatment". Four replication blocks (two on each site), each containing the two treatments, thus composed the complete randomized block design for this study.

In the treated plots, all trees and shrubs (1 cm < DBH < 10 cm) were cut within a one-meter radius around the planted trees, whereas the herbaceous vegetation and small woody stems (<1 cm) were cut flush with the ground within a smaller radius (50 cm), in proportion to their smaller size. Larger trees (>10 cm) within the same one-meter radius were devitalized with glyphosate herbicide capsules (E-Z-Ject system, Waynesboro, MS, USA) and left standing to prevent damage to seedlings. The vegetation of control plots was left untouched.

All trees in each plot were inventoried early in the spring of year 3 ; damaged or diseased trees were excluded, as well as a number of trees with bad drainage microsite conditions that were not identified at the time of plantation. The 593 trees used in the analyses, 149 red oaks and 444 black cherries, are distributed as follows: at St-Chrysostôme, 66 red oaks and 73 black cherries in control plots, 48 and 112, respectively, in released plots, and at Ste-Clotilde 15 red oaks and 139 black cherries as controls, and 20 and 120, respectively, in released plots.

Planted tree growth and herbivory

Herbivory by white-tailed deer still occurred, but was reduced by the application twice annually (May and October), as of year 3, of a deer repellent (Deer-Away, IntAgra Inc., Minneapolis, MN, USA). Deer herbivory was recorded as a semi-continuous variable according to whether it was heavy, particularly on the leader (2), weak or on the lateral shoots (1), or absent (0) (Baker *et al.* 1999, Truax *et al.* 2000).

Total height and diameter at ground level of planted trees for year 2 was measured in early spring of year 3 (before bud burst) and at the end of growing seasons 3 through 6. Before the release treatment was applied, black cherries were taller, on average, than were red oaks ($p<0.0001$) (Fig. 3.1). Although plots were chosen randomly between control and treatment groups, control black cherries were significantly taller than those that were to be released ($p<0.0001$), but not red oaks. Treatments were assigned to plots, not individual trees, so that the releases would not affect the trees in control plots.

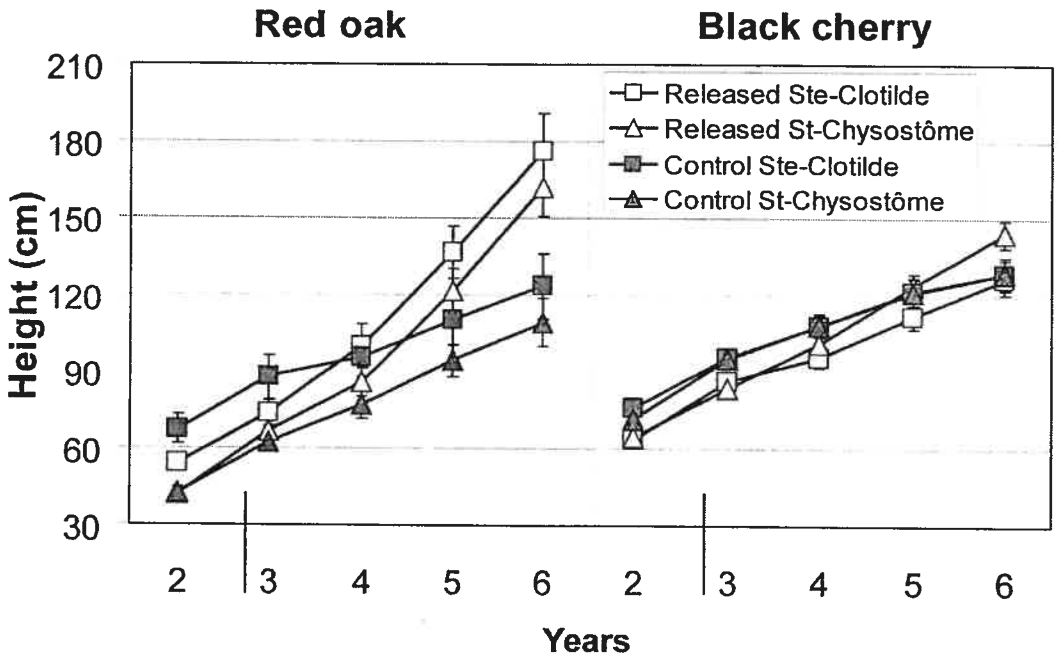

Figure 3.1. Mean tree height in relation to time since year 2 (1999), site and treatment. Timing of the release (summer of year 3) is represented by a vertical bar. Error bars are ± standard error (SE; some error bars are smaller than the corresponding symbol).

Competition and light availability

Inventories of trees and large shrubs around planted trees were done at year 3 before the release treatment in all plots, and repeated at year 4 in the treated plots. DBH of all woody stems (trees and shrubs >1 cm) was recorded within a radius of three meters around each planted tree and basal area values were computed. No significant differences were found in basal area between designated control and release plots before the release treatment, on both sites.

Available light was measured before (year 3) and after the release treatment of planted trees (year 4), and again in years 5 and 6. Light measures were used as they integrate the effects of all plants around the seedlings and so are accurate descriptors of a seedling's growing environment. They also measure the actual result of the thinning treatment, accounting for prior heterogeneity and possible variability in its application, including the presence of devitalized trees that were left standing. The instantaneous measurement of available light (%PPFD) was made according to Parent and Messier (1996), using two quantum sensors (li-190, LiCor, Lincoln, NE, USA) on a cloudy day (solar disk invisible), between July 1st and August 31st of each year. One sensor was located in a nearby open field as a reference and the other *in situ*. Light measurements were taken at each seedling location at 50 cm, one, and two meters above ground, and finally just above their crown, in the prolongation of the main axis for measurements taken above the crown, and at its margin for lower ones to prevent self-shading.

Because required light measurement conditions (overcast sky) were difficult to obtain within a short period of time for such a large number of measurements (593 trees, at four heights), we limited the first measurements to only those plots which were to receive the release treatment in order to obtain pre-treatment values (year 3). At year 4, especially difficult for light measurements, we measured available light in all plots and for all trees at one meter, but only on a sample of trees for the other heights. Measurements at all fixed heights (50 cm, 1 m and 2 m) were taken on all trees at years 5 and 6. Finally, crown level values were measured at year 6 and were predicted for all other years using linear regressions computed for each year from data at fixed heights from the same site and treatment. Sample sizes are given where appropriate and should be considered when interpreting light measurement results, especially at year 4 where values at 1 m should be used preferably. We computed an understory density index as a function of the light extinction coefficient of that layer (Aubin *et al.* 2000) (Eq. 3.1) :

$$understory\ density\ (UD) = 1 - (\%PPFD_{50cm} / \%PPFD_{200cm}) \qquad (3.1)$$

Statistical analysis

The experimental design is composed of four replication blocks (two on each site), two treatments (released and control) and two species[1]. Sites are thus considered random effects (Hooper *et al.* 2002) and eventual differences between sites, or among them, can be investigated using contrast tests on blocks[2]. ANOVA with random effects was used to test (1) the effect of the release treatment on stand characteristics (available light, understory density, basal area and stem density), and (2) the effect of treatment on tree growth. The effect of time and treatment on available light was investigated using MANOVA on repeated measures. The effect of treatment on herbivory was tested using ordinal logistic fit and likelihood ratio tests (proportional odds assumption for the model being the same for each class was met). The effect of competition from above (%PPFD at 2 m) and from below (understory density index) on tree growth was tested using multiple regression. Rank transformations were used, where appropriate, to meet assumptions of normality and homoscedasticity in parametric analyses (Iman et Conover 1979, Conover et Iman 1981, 1982, Potvin et Roff 1993). Analyses were carried out on JMP software (SAS 2003).

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[1] Species are not used in the analyses, but are treated independently to facilitate the interpretation of the treatment effect.

[2] Contrasts were carried only when a significant block effect was detected. The sites are first compared by contrasting their respective blocks. Then blocks from each sites are contrasted among themselves to detect within site differences. This allows for the detection of eventual differences between or among sites, but does not imply that sites are a replicated and testable effect.

Results

Because the planted trees are relatively close to each other (3 m x 3 m), the combined effects of individual releases around each of them in the 3rd year of growth in the treated plots were such that they allowed for a significant increase in the range of available light conditions. The light available at one meter above ground rose from 10% to 22% on average (Tab. 3.2). This increase in available light is due to a significant reduction in total basal area (24% at St-Chrysostôme and 40% at Ste-Clotilde), and stem density (49% and 39%, respectively), although the Ste-Clotilde site had a somewhat lesser initial basal area following the preparation cut in 1997 (contrast test - Tab. 3.2). A "Block x Treatment" interaction was observed for light levels, and is related to a weaker treatment effect in one of St-Chrysostôme's blocks (contrast test).

The light available at 50 cm, one meter and two meters above ground increased significantly after the release treatment in treated plots, and with the same intensity at all heights (approximately 12 percentage points; the non significant result at 2 m in the 4th year is due to under-sampling - Fig. 3.2). Starting in the 4th year, however, available light decreased until in year 6 it reached levels comparable to those prior to the release (Fig. 3.2). Control plots followed the same trend, with a regular decrease in available light at all measurement heights. We tested the overall effect of time (year 3 through 6), and since the release (year 4 through 6), on light availability (repeated measures MANOVA), and found it highly significant at all fixed heights (F-test ; $p<0.0001$).

Table 3.2. Treatment effect on light availability and stand characteristics in year 4 (2001) (means and SE).

Site		Light at 1 m (%PPFD)	Basal area (m^2/ha)	Density (stems/ha)
St-Chrysostôme	Control	11 (0.9)	20.3 (1.0)	7155 (332)
	Released	20 (0.6)	15.4 (0.9)	3669 (197)
Ste-Clotilde	Control	9 (0.5)	16.2 (0.7)	6197 (248)
	Released	24 (1.1)	9.7 (0.7)	3750 (203)
ANOVA	*d.f.*	*F (p>F)*	*F (p>F)*	*F (p>F)*
Model	7	62.04 (<0.0001)	12.38 (<0.0001)	23.33 (<0.0001)
Block[1]	3	0.0239 (0.9842)	10.07 (0.0448)	0.7861 (0.5760)
Treatment	1	25.31 (0.0178)	42.13 (0.0026)	73.88 (0.0015)
Block x Treatment[1]	3	14.98 (<0.0001)	0.9812 (0.4012)	1.608 (0.1864)
Whole model R^2 (*N*)		0.46 (517)	0.13 (590)	0.22 (590)

Notes: Available light and stand characteristics are rank transformed prior to analysis.
[1] Random effects.

The effect on released trees of both species was observed at their crown, which received more light after the treatment (Fig. 3.2). Because of their small size in the 3rd year, released red oaks received less light than that available at one meter, but the situation was much improved in the following years as their sustained growth (Fig. 3.1) kept them at 20% available light on average. Because they grew more slowly, released black cherries could not maintain the light levels attained at their crown after the release (Fig. 3.1). In the control plots, light at crown level decreased each year for trees of both species, following the same trend observed at fixed heights, because they did not grow enough to overcome the natural growth and densification of the stands (Fig. 3.2).

The release treatment strongly increased the mean annual height increment of both species in the last two years at both sites (Tab. 3.3). Increments of 13 to 16 cm were observed in control red oaks, which is slightly higher than in black cherry under the same conditions (10 cm). The increment was 38 cm, more than double, for released red oaks, whereas it only increased by 15 to 22 cm in released black cherries (Tab. 3.3). The effect on diameter growth was even stronger; on average close to six times greater for released red oaks and about half as much for black cherry (Tab. 3.3).

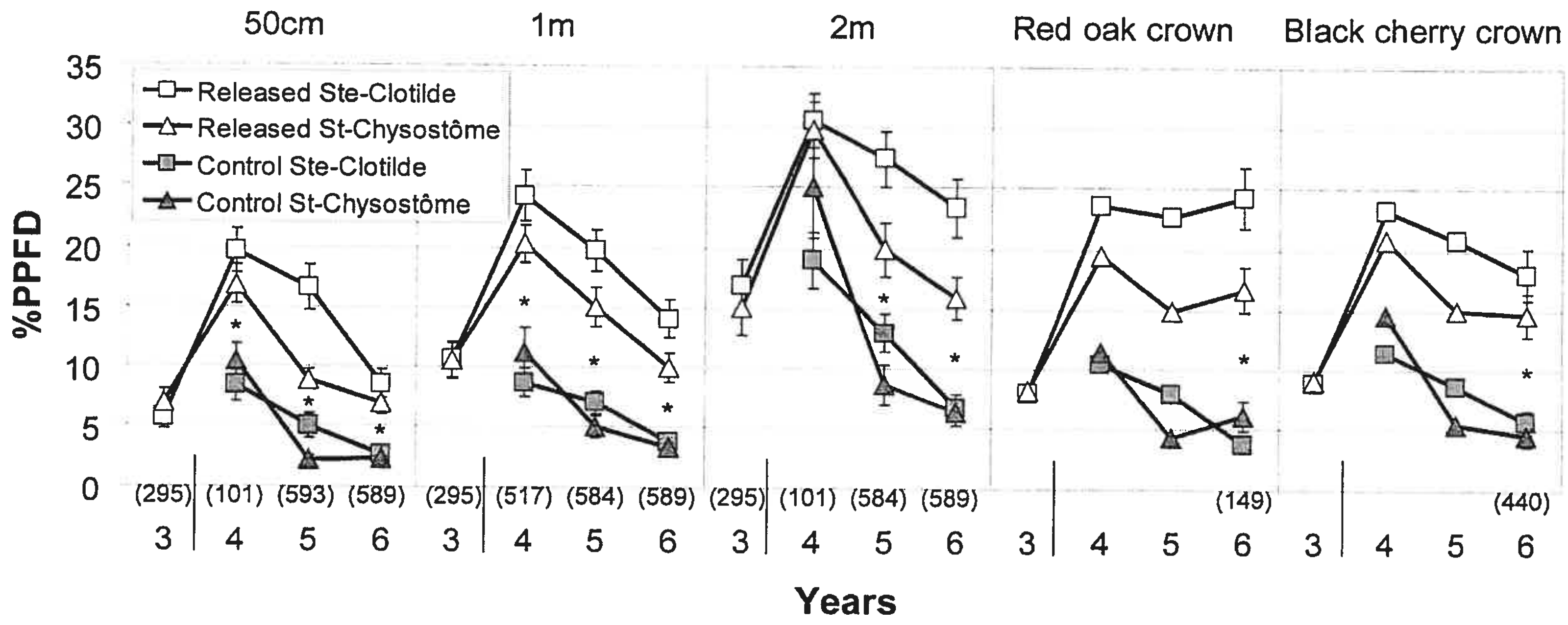

Figure 3.2. Mean available light (%PPFD) in relation to time according to site, treatment, and measuring height (50 cm, 1 m and 2 m above ground, and just above the crown of planted trees). Timing of the release (summer of year 3) is represented by a vertical bar. Sample size is given between parenthesis. * Significant treatment effects for each year are noted with an asterisk (model as in Tab. 3.2). Error bars are ± two standard deviations (some error bars are smaller than the corresponding symbol). No error bars or test results are presented for years 3 through 5 at crown level because they are predicted values at mean tree height.

Annual increments during the year immediately following the treatment (4th), did not show any significant treatment effect on both species (not shown). The change in growth curves is easily observed for red oak and occurred later, during the 5th growing season (Fig. 3.1). For black cherry, a change in growth was observed on control trees, which started to show signs of stagnation during the 4th growing season, whereas released trees, which started smaller, overcame the stagnation and maintained a regular but slow growth rate thereafter (Fig. 3.1). By the end of the experiment, control and released red oaks were on average 112 cm and 166 cm tall, respectively, while black cherries were 128 cm and 134 cm, and released trees had finally reached or overcome the controls (Fig. 3.1).

The release treatment performed in year 3 targeted all vegetation layers around the seedlings, from the ground up. Its effect on available light was still significant three years later at all heights (Fig. 3.2 – year 6). The treatment effect on understory density (UD), as evaluated by the ratio of the light measured at 50 cm and that at 2 m (Eq. 3.1), was not as important. By the end of the experiment (year 6), no treatment effect on understory density (UD) could be detected (Tab. 3.4), because that layer had recovered from the release, fueled by the increased light available at higher levels.

Though red oaks seemed to have suffered heavier herbivory in the control plots (Tab. 3.4), the release treatment had no detectable effect on herbivory, and deer damage did not vary between or among sites.

The range of competition conditions, naturally present and amplified by the treatment, created ideal conditions for testing the single and combined effects of competition from above (available light at 2 m) and from below (understory density). Red oak and black cherry responded positively in height and diameter growth to higher light levels above them (Tab. 3.5). Again, as with treatment, the response was stronger for red oak than for black cherry. Competition from below (understory density) had no effect on red oak, while for black cherry better height and diameter growth is also associated with a thicker understory (Tab. 3.5).

Table 3.3. Treatment effect on mean annual height and diameter increments (SE) per species (4th to 6th year).

Site		Height increment (cm)		Diameter incr. (mm)	
		Red oak	Black cherry	Red oak	Black cherry
St-Chrysostôme	Control	16 (2.9)	10 (1.8)	0.5 (0.17)	0.4 (0.15)
	Released	38 (3.5)	22 (1.6)	2.8 (0.36)	1.6 (0.16)
Ste-Clotilde	Control	13 (4.1)	10 (1.8)	0.6 (0.23)	0.6 (0.14)
	Released	38 (4.8)	15 (1.9)	3.6 (0.41)	1.5 (0.18)
ANOVA	*d.f.*	*p>F* [2]	*p>F*	*p>F*	*p>F*
Model	7	<0.0001	<0.0001	<0.0001	<0.0001
Block[1]	3	0.4803	0.1777	0.3926	0.8262
Treatment	1	0.0107	0.0239	0.0110	0.0264
Block x Treat.[1]	3	0.4005	0.1021	0.0844	0.0108
Model R^2		0.27	0.12	0.43	0.12
(*N*)		(147)	(440)	(146)	(440)

Notes: Height and diameter increments were rank transformed prior to analysis. [1] Random effects. [2] Only probabilities are given for clarity.

Discussion

Light

The gradual decrease in light availability in treated plots can be explained by the gradual closing of the stands, but it does not seem to be related to the treatment because the same trend is observed in control plots (Fig. 3.2). It is instead a natural process of densification associated with the aging of these young stands.

The recommended shelterwood level reported in the literature for establishment of red oak under mature stands in north-eastern U.S. varies, but is often around 60% of original basal area (40% removal) (Johnson 1984, Gordon *et al.* 1995). In a recent review of published results from under-planting studies, an optimal intermediate density (40% to 60% basal area) was identified for the growth of under-planted trees (mostly red oak) in that region, corresponding to levels of 25% to 50% available light (Paquette *et al.* 2006).

Table 3.4. Means (SE) and treatment effect in year 6 on understory density index (Eq. 3.1) and herbivory intensity.

Site		Understory density index	Herbivory (%)[1]	
			Red oak	Black cherry
St-Chrysostôme	Control	0.54 (0.026)	44	10
	Released	0.50 (0.022)	19	13
Ste-Clotilde	Control	0.54 (0.025)	21	20
	Released	0.59 (0.019)	10	14
Tests	*d.f.*	*F* (*p*>*F*)	*chi*^{2} (*p*>*chi*^{2})	*chi*^{2} (*p*>*chi*^{2})
Model	7	2.74 (0.0084)	14.2 (0.0484)	7.87 (0.3442)
Block[2]	3	3.14 (0.1861)	3.91 (0.2710)	3.93 (0.2688)
Treatment	1	0.65 (0.4699)	0.042 (0.8372)	0.053 (0.8160)
Block x Treatment[2]	3	1.46 (0.2233)	1.68 (0.6417)	4.00 (0.2616)
Model R^2 (*N*)		0.03 (589)	0.07 (148)	0.02 (441)

Notes: ANOVA results are presented for rank transformed understory density index. Herbivory (three classes) is tested using ordinal logistic fit and likelihood ratios. [1] Classes 1 (weak) and 2 (heavy) of herbivory intensity were combined only for computing percentage of predated trees. [2] Random effects.

The under-planting experiment we conducted in young shade-intolerant hardwood stands had light intensities at one meter above ground in control plots (approximately 10%), as well as in treated plots (22%), which would rank our design in the dense shelterwood category. We must go up to two meters above ground, in released plots, to find light intensities greater than 25%, but they decreased to below that level in less than two years (Fig. 3.2).

Growth increments

Black cherry, an early-successional species, should have responded to the release treatment with greater growth increments than red oak, of intermediate shade tolerance. The opposite results were obtained; red oak reacted more strongly to the release than did black cherry (Fig. 3.1). It is possible that light availability even in treated plots was not sufficiently high for black cherry, never providing the necessary conditions for its optimal growth, which can be substantial. Very little literature exists on this species in spite of its high economic value. With annual height increments of 10 cm (control) and 18 cm (treated), black cherry results are within the averages reported in the literature for hardwood species in North America (Paquette *et al.* 2006). The fact that control black cherries started taller did not give them an advantage that would compromise our analysis of annual growth increments.

Our results for released red oaks are nearly four times the average reported, with 38 cm of mean annual height increment (Tab. 3.3), whereas results from control plots are comparable to the ones recorded for managed shelterwoods. Our results for released red oaks also stand up well to comparison with open field experiments conducted within the same region with the use of herbicides (Truax *et al.* 2000, Cogliastro *et al.* 2003). While Kaelke *et al.* (2001) raise doubts about the capacity of red oak to respond effectively to this type of silviculture, due to its alleged low plasticity, the species reacted well to the release treatment applied at the 3rd growing season under a young forest cover of intolerant deciduous species.

Table 3.5. Multiple regression analysis of available light at two meters (%$PPFD_{2m}$) and understory density (UD) effect on red oak and black cherry mean annual height and diameter increments (4th to 6th year).

		Height increment		Diameter increment	
		Red oak	Black cherry	Red oak	Black cherry
Test	*d.f.*	*p>F* [1]	*p>F*	*p>F*	*p>F*
Model	3	<0.0001	<0.0001	<0.0001	<0.0001
%$PPFD_{2m}$	1	<0.0001	<0.0001	<0.0001	<0.0001
UD	1	0.0947	<0.0001	0.6705	0.0265
%$PPFD_{2m}$ x UD	1	0.5787	0.3850	0.8266	0.0024
Model R^2 (*N*)		0.45 (147)	0.12 (436)	0.55 (146)	0.13 (436)

Notes: Growth increments, available light and UD were rank transformed prior to analysis. See Equation 3.1 for UD ratio. [1] Only probabilities are given for clarity.

Competition stratification

Planted trees with good annual growth were positively associated with a thinner upper layer of vegetation (Tab. 3.5). Although it is generally recognized that growth increases with decreasing competition, few studies have looked at the vertical position of this competition. Lorimer *et al.* (1994) observed that the density of the intermediate layer of vegetation (understory trees > 1.5 m) negatively affected the growth and survival of oak seedlings, while understory vegetation (all vegetation < 1.5 m) competition had no effect. Other researchers working on red oak, conifers, or even tropical species, all found similar results, namely the predominant effect of competition produced by the overstory canopy on that of the lower vegetation layer (Ådjers *et al.* 1995, Buckley *et al.* 1998, Smidt and Puettmann 1998, Curt *et al.* 2006). Grassi and Giannini (2006), working on conifers, found strong growth and morphological relations with available light (canopy induced), but none with competing sapling's density. For Brandeis *et al.* (2001), also working on conifers, and Spetich *et al.* (2002) (red oak), growth increased with a decrease in the density of the shelterwood stand and of the understory competition. Although light is not the only factor explaining growth in forest understories (below-ground competition is another important one), it is a good integrator of most competition and resource factors in all but the most nutrient poor or dry conditions (Ricard *et al.* 2003). In the present study, it seems clear that within the range of light conditions experienced, the density of the layer above the seedlings is of prime importance in explaining growth of planted red oak and black cherry.

The density of the understory did not affect growth of planted red oaks, while a denser understory, following an increase in light availability at higher levels, was associated with increased growth of black cherry. Both height and diameter growth were increased. This points to an increase in available light at the top of the seedlings (which would also explain the denser understory), and possibly better protection from deer browsing (see below), rather than an increased height to diameter ratio following the seedlings adaptation to overcome understory competition by allocating more resources to height at the expense of diameter growth (Cogliastro *et al.* 2006). Thus planting under successional forest stands, followed in the 3rd growing season by a partial release, increased light availability and growth, at least for a time, and avoided the successional setback and competition problems associated with thinner stands and clear-cuts (Lieffers and Stadt 1994, Truax *et al.* 2000, Carnevalea and Montagnini 2002, Rose and Rosner 2006).

Herbivory

Apart from some browsing by cottontail rabbit (*Sylvilagus floridanus*), especially in the early years following planting, and trees crushed by branches or stems of dead trees, we did not observe serious damage other than herbivory by white-tailed deer, especially on red oak (Tab. 3.4). Red oak suffered more predation than black cherry, but whereas the herbivory level remained unaffected by treatment for the latter species, it more than doubled (in percent of affected trees) for red oaks in control plots, though that was not statistically significant (Tab. 3.4). Deer behaviour is probably spatially dependent, but we did not detect any block or site effect. These results are important because they go against the accepted opinion that thinning the stand should increase herbivory. We observed no such increase, even in red oak which experienced the most browsing.

Three studies have reported that decreased stand density, which would have the effect of making planted trees more visible, resulted in greater deer herbivory (Gordon *et al.* 1995, Buckley *et al.* 1998, Truax *et al.* 2000). For two of these studies, however, that of Gordon *et al.* (1995) and of Truax *et al.* (2000), the determining factor was the understory vegetation, more than the overall openness of the stand. Indeed, in both of these studies the impact of deer browsing was greatest where understory vegetation decreased, but not the density of the upper canopy. Our observations concur; the trees that were the least damaged by deer were often those, well-released from above, that were surrounded, but not suppressed, by a vigorous re-growth of understory competition, especially raspberry (*Rubus* spp.). Those trees had good light conditions at their crown and were possibly better protected from deer. On the other hand, trees under a dense upper canopy are often fairly free of understory competition, and thus paradoxically more accessible to deer. Morgan (1991) draws similar conclusions from his study of a heavily browsed woodland in England, where vigorous seedlings could only be found under gaps within dense understory thickets, or near obstacles, where they were protected from deer herbivory. It is also possible that deer are more likely to be active under a dense canopy, where they can hide better, than in thinned stands where they are more vulnerable, especially in areas where hunting is allowed.

Conclusion

Our results support the idea of a dynamic silviculture in young intolerant hardwood stands of moderate height located in sensitive rural landscapes. Under-planting with possibly frequent, light cuts timed with the growth of planted trees can be used to achieve multiple objectives. It seems promising as an economically and ecologically sound alternative management technique for impoverished young stands following agriculture abandonment. We believe that such an approach should allow for the optimal establishment of planted trees initially, followed by sustained growth if regular maintenance is performed, and long term conservation of forest cover and its associated benefits to the landscape.

More long term research is required to demonstrate the effectiveness of the technique at establishing advanced hardwood regeneration in these young stands and bring them to canopy height. A better planning of such projects by a coordinated effort of foresters and researchers would greatly improve our knowledge and would facilitate the evaluation of innovative techniques, such as under-planting, to restore degraded, early-successional deciduous forests.

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Chapitre 4 : Morphological plasticity in seedlings of three deciduous species under shelterwood under-planting management does not correspond to shade tolerance ranks

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Abstract

The morphological plasticity of tree seedlings is considered to be an important factor in shade tolerance and plant succession dynamics. However, recent studies comparing temperate deciduous species have not found the expected relationship between plasticity and shade tolerance or successional status. We measured morphological plasticity in seedlings of three temperate deciduous species of northeastern North America, using 13 parameters associated with growth, crown geometry, branching, and leaf arrangement, as a function of a steep light gradient (0% to 40%) in young transition forests under shelterwood management. The effects of light and seedling height were investigated using variance partitioning. We studied naturally occurring seedlings of the very shade tolerant sugar maple (*Acer saccharum*), and planted seedlings of shade intolerant black cherry (*Prunus serotina*), and red oak (*Quercus rubra*), a species of intermediate shade tolerance. Contrary to expectations, sugar maple had the lowest light-induced plasticity and did not modify its morphology except as a function of height. It also produced relatively good growth. Moreover, black cherry displayed several unexpected characteristics, such as weak growth in response to increasing light and strong plasticity of several morphological characteristics, mostly light-induced. Although red oak had a low level of overall plasticity, it produced the largest height increments under these shelterwoods. The morphological plasticity we observed lends support to more complex models of shade tolerance. Those models, which include resistance to pathogens and herbivory, and the capacity to store reserves, still need to be supported with larger, integrated studies. Our results lead us to question how useful classic shade tolerance models based on morphological plasticity are for regeneration management and silviculture. At least under the pioneer stands we studied, both black cherry and sugar maple behaved in ways opposite to what was predicted.

Keywords

Morphological plasticity; successional status; shade tolerance; under-planting; variance partitioning; available light; *Acer saccharum*; *Prunus serotina*; *Quercus rubra*

Introduction

The objective of many silvicultural practices such as shelterwood management and under-planting is to optimize the availability of light for regeneration (Lieffers and Stadt, 1994), but it is often done with an inadequate knowledge of the tree species' requirements (Ådjers *et al.*, 1995; Paquette *et al.*, 2006b). The quantity of available light influences not only seedling growth in the understory, but also their architecture (Millet *et al.*, 1998). Only a few of the factors involved in these adaptation processes are understood (Walters and Reich, 1996; Canham *et al.*, 1999; Kaelke *et al.*, 2001), and the interpretation of observed differences between species as a function of forest dynamics is often ambiguous (Walters *et al.*, 1993a; DeLucia *et al.*, 1998).

Though it is not the only way plants acclimate to a changing environment, morphological plasticity in seedlings is thought to be an important adaptation to shade (Messier and Nikinmaa, 2000) and has received much attention in recent forest ecology literature (*e.g.* DeLucia *et al.*, 1998; Takahashi *et al.*, 2001; Delagrange *et al.*, 2004). In seedlings, crown architecture, namely the position, length, orientation and ramification of the branches, determines the light interception pattern of the leaves as well as the cost of constructing and maintaining this structure (Canham, 1988a). The carbon balance model (Bazzaz, 1979; Givnish, 1988) proposes that morphological adaptations allowing the plant to optimize its use of light in open areas will have a corresponding high metabolic cost under a dense canopy, eventually resulting in seedling death (Canham, 1988a; Walters and Reich, 1996). Thus, morphological plasticity should be greater in shade tolerant, late successional species (Canham, 1988a; Williams *et al.*, 1999).

However, studies comparing species of contrasting shade tolerance concluded that observed plasticity does not always correspond to successional status nor to the often oversimplified carbon balance model (*e.g.* Walters *et al.*, 1993a; Beaudet and Messier, 1998; King, 2001). Therefore, alternatives have been suggested (DeLucia *et al.*, 1998). Other studies show that at least some of the morphological plasticity of a tree is a function of its size or ontogenesis (Messier and Nikinmaa, 2000; Delagrange *et al.*, 2004).

Although an even greater proportion of the world supply of forest products will depend on planted trees in the near future and much of the needed restoration of degraded forests relies on planted trees (Dekker-Robertson and Libby, 1998; Ashton *et al.*, 2001; Kozlowski, 2002), little is known about the specific ecology of planted trees and the usefulness of classic forest dynamics models for managed artificial regeneration. Moreover, many species are routinely planted outside the natural range of conditions to which they have adapted.

Our main objective was to study the morphological acclimation of contrasting species to the specific conditions in the understory of young shade intolerant stands. The study was conducted in transition forests of shade intolerant hardwoods under shelterwood under-planting management with 12% available light on average (varying from ≈0% to 40%). The species used are common and co-occurring in the temperate deciduous forest of eastern North America. They vary in shade tolerance ranks from very tolerant, late succession sugar maple (*Acer saccharum* Marsh.) (Baker, 1949; Godman *et al.*, 1990), to shade intolerant, early-successional black cherry (*Prunus serotina* Ehrh.) (Marquis, 1990; Horsley and Gottschalk, 1993). The study also included red oak (*Quercus rubra* L.), whose shade tolerance decreases with age and size, but is usually reported as intermediate (Baker, 1949; Sander, 1990). It should be noted that the reported shade tolerance rankings for black cherry and red oak are quite variable (*e.g.* Baker, 1949; Abrams *et al.*, 1992; Canham *et al.*, 1999).

A secondary objective was to compare the observed morphological plasticity with that predicted by classical and alternative models of shade tolerance and successional status. According to the carbon balance model, the three species in this study should occupy different positions on a morphological plasticity gradient going from high (sugar maple) to low (black cherry). Because it is relatively shade tolerant, red oak should fall somewhere between these two species. Growth in late succession species (*e.g.* sugar maple) should plateau rapidly, while in early succession species (*e.g.* black cherry) it should reach high levels with increasing available light (Walters *et al.*, 1993a). Late succession species should have a crown architecture displaying a high degree of light-induced plasticity, being wide under shade and more elongate in open areas (Takahashi *et al.*, 2001). The crowns of these species should be less ramified, displaying a maximum of leaf area with a minimal investment in perennial tissue (Canham, 1988a). Finally, we also discuss the pertinence of shade tolerance rankings as decision-making criteria for accelerated regeneration of degraded temperate forests using techniques such as under-planting.

Methods

Description of sites

The study was conducted in the southwestern part of the St. Lawrence Valley (Québec, Canada), an important agricultural region in the sugar maple-bitternut hickory bioclimatic zone (Thibault, 1985). Several research projects have studied the impact of human activities on its vegetation (*e.g.* Bouchard and Domon, 1997; Brisson and Bouchard, 2003), as well as methods of forest rehabilitation (*e.g.* Cogliastro *et al.*, 2003; Cogliastro *et al.*, 2006; Paquette *et al.*, 2006a). Natural regeneration of several species of hardwood trees, once abundant in the region's forests, is now rare after two centuries of severe deforestation resulting in the loss of seed trees (Simard and Bouchard, 1996; Brisson and Bouchard, 2003).

The study was conducted using permanent plots established on two sites of recent agricultural abandonment (*circa* 1962) that had been planted under a shelterwood with one-year old seedlings of red oak and black cherry in spring 1998 (Paquette *et al.*, 2006a). The seedlings were nursery-grown[1] in containers (340 mL) and had mean heights of 27 cm for red oak and 34 cm for black cherry (nursery data). The two sites (45°09' N ; 73°45' W and 45°08' N ; 73°38' W) have a moderately drained, sandy loam

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[1] At the Berthier provincial nursery

soil of till origin in a landscape of cultivated marine deposits, which is typical of the region. They were damaged by the ice storm of January 1998, further increasing the natural heterogeneity of such stands. The sites share similar tree compositions dominated by *Betula populifolia* Marsh. of an average height of 12 m in 2000.

In treatment plots on each site, the competing vegetation was removed manually over a one-meter radius around the seedlings during summer 2000, and the other plots were kept as a control. Since all trees, planted every 3 m, were released in the treated plots, the individual releases resulted in a important increase in mean light availability. The original heterogeneity was conserved, however, thus increasing the range of light conditions for the study. Total basal area in 2001 (after the release treatment) was 20.3 and 15.4 m^2/ha (all species DBH > 1 cm) for the control and released plots on the first site, and 16.2 and 9.7 m^2/ha, on the second.

Inventory and measurement of control seedlings and light climate

Planted red oak (n=39) and black cherry (n=41) trees were selected in spring 2003 by random stratified sampling in three height classes using data from 2002. Red oak height classes were 1) less than 125 cm, 2) between 125 cm and 150 cm, and 3) over 150 cm. Black cherry class thresholds were 100 cm and 145 cm. The planted trees, after being checked for disease, bad drainage, pests, and physical damage due to falling branches or trees, were included in the study one by one *in situ* until each height classes was saturated with a third of the total for a given species and site. Naturally present sugar maple seedlings were first inventoried over the permanent plots. They were then added one by one (n=40), respecting the same quality criteria so as to cover the observed size variance, using bottom third, mean, and upper third visual height classes. A total of 120 trees (hereafter called 'seedlings') were used in this study, none of which died during the investigation. Height was not significantly different between sites except for sugar maple (Table 4.1). Red oaks were taller than the other two species. Although not released individually in 2000 in treated plots, sugar maples benefited from the same conditions as did the planted seedlings because of the overall effect of the close-set individual releases.

Table 4.1. Sample size (*N*), mean height (H) and standard deviation, for each species on each site, and mean comparison tests.

	St-Chrysostôme		Ste-Clotilde		Total	
	N	H (cm)	*N*	H (cm)	*N*	H (cm)
Black cherry	26	152 (49) *a*	15	145 (48) *a*	41	149 (48) *L*
Red oak	25	183 (67) *a*	14	189 (31) *a*	39	185 (56) *M*
Sugar maple	25	112 (26) *a*	15	158 (57) *b*	40	129 (46) *L*
Total	76	149 (57)	44	163 (50)	120	154 (55)

Notes : Means followed by the same letter are not significantly different at the 5% threshold (Tukey-Kramer HSD). Differences between sites for a given species are noted with lower case "*a*" and "*b*". Differences between species are noted with capital "*L*" and "*M*".

Available light was measured with hemispherical sensors (type BF2, Delta-T, Burwell, Cambridge, UK). This technique allows for the instantaneous measurement of the percent average seasonal available light regardless of sky conditions or time of day, and is well correlated with standard methods such as hemispherical image analysis (Canham, 1988b) (r=0.91) and the instantaneous estimation under overcast skies (Messier and Puttonen, 1995; Parent and Messier, 1996) (r=0.94), as well as with seedling growth and morphology (Paquette *et al.*, 2006, submitted). Measurements of *in situ* PAR were taken just above the crown of each seedling, in line with the main stem, while incident PAR was measured in a nearby open field. We used handheld two-way radios in order to get simultaneous measurements at both locations. The %PAR (L) is then simply the ratio of *in situ* PAR to incident PAR (Gendron *et al.*, 1998).

The 120 seedlings were measured at the end of the 2003 growing season. We measured the total height perpendicular to the ground (H; cm), the diameter of the crown projected on the ground (average of the maximum diameter and of the diameter perpendicular to the maximum; cm), the crown length (cm), and the length of the annual shoot (2003) of the main stem (AS; cm) (Fig. 4.1). The total length of the main axis (A1; cm) and of all second order axes (A2; cm) were also measured, while third order axes (A3) were counted (Fig. 4.1). The area of the crown projected on the ground (m^2) was calculated using the crown diameters (Eq. 4.1) where Dmax is the maximum diameter and D90 the diameter perpendicular to the maximum (Fig. 4.1).

$$Crown\ area = \frac{\pi}{4} \times D_{\max} \times D_{90} \qquad (4.1)$$

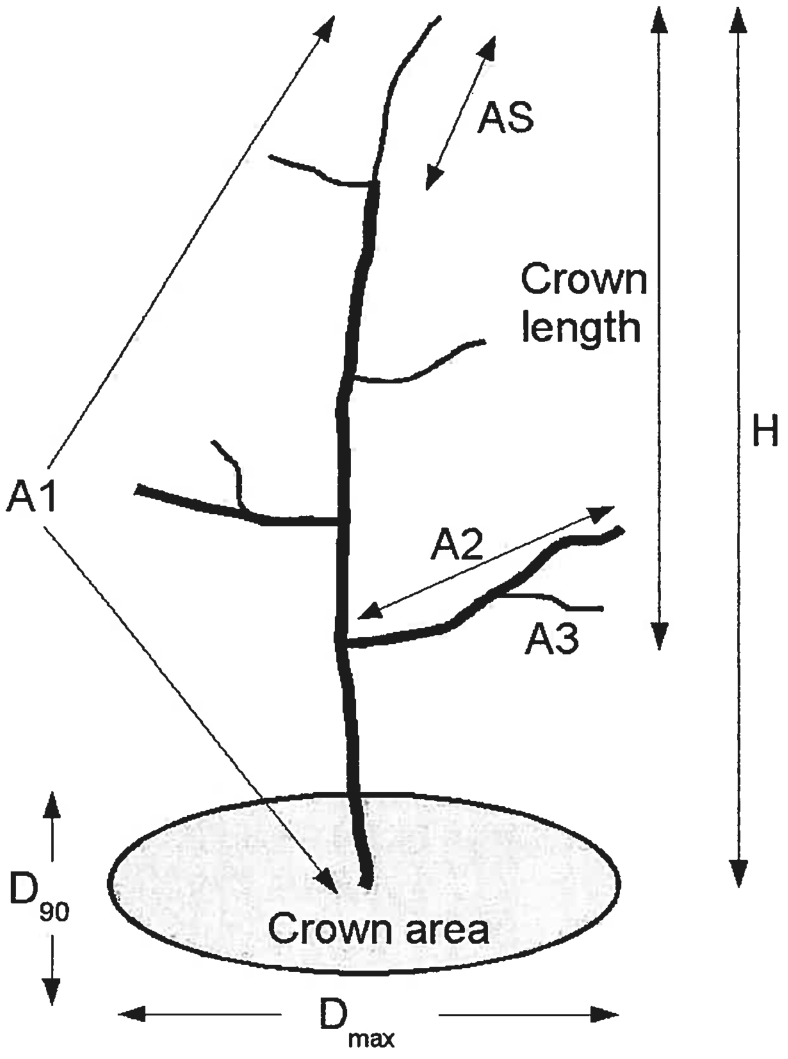


Figure 4.1. Seedling schematization and measurements taken in 2003; annual shoot (AS), total height perpendicular to the ground (H), crown length, maximum diameter (D_{max}) and diameter perpendicular to the maximum (D_{90}) of the crown, projected crown area, length of the main axis (A1) and 2nd order axes (A2), and number of 3rd order axes (A3).

All the leaves were counted, and the length of the leaf blade and the petiole of the most distal ten leaves from the top, starting with leaves from the main stem (A1), and the last ten leaves from the bottom of each seedling were measured (mm). Ten leaves per species per site, covering the range of observed sizes, were collected on seedlings of the same origin and comparable height growing just outside the perimeters of the permanent plots. Their individual leaf area (cm^2) was measured in the laboratory (DeltaT Area Meter). Predictive regressions of leaf area from blade length were constructed (Table 4.2). Average area per leaf (LA) could then be calculated from mean blade lengths per species using the equations in Table 4.2. The total leaf area equals the average leaf area multiplied by the number of leaves.

Table 4.2. Regression coefficients for the determination of unit leaf area (LA ; cm^2) from leaf blade length (BL ; mm). Equations are in the form $LA = b_0 + b_1 \times (BL/10)^2 + \varepsilon$. No differences could be detected between sites for any species.

Species	*N*	b_0	b_1	R^2
Black cherry	20	0.324	0.286	0.93
Red oak	20	-0.500	0.326	0.95
Sugar maple	20	7.452	0.652	0.78

Various ratios were constructed with the measured variables and were used to characterize the seedlings' response to light climate (Fig. 4.1). The extension growth index is the ratio of annual shoot to mean length of second order branches (Lei and Lechowicz, 1990). Stem straightness is the standard height to length ratio (H/L; where L = length of A1) (DeLucia *et al.*, 1998; King, 2001). Live crown ratio is the crown length to tree height ratio (Delagrange *et al.*, 2004). Crown shape index is the crown length to diameter ratio (L/D) (Beaudet and Messier, 1998; Delagrange *et al.*, 2004). Branching density was evaluated as the total length of second order branches to crown area ratio, and fine ramification as the number of third order branches per meter of second order branches. LA t/b and Petiole t/b are ratios of mean leaf area or petiole length from the top (t) of the crown to that of the bottom (b). The proportion of support structure in petioles (%Petiole) was evaluated as the total length of petioles (mean of top and bottom petioles times the number of leaves), divided by the sum of petioles, second order branches, and main axis lengths (Beaudet and Messier, 1998). Efficiency of leaf display is the total leaf area divided by the sum of the main axis and all second order branch lengths (Canham, 1988a; Lei and Lechowicz, 1990; Beaudet and Messier, 1998). Finally, the leaf area index (LAI) is the total leaf area to crown area ratio (Beaudet and Messier, 1998).

The 13 indices we used cover a large spectrum of seedling responses to light climate. They include growth (AS) and 12 seedling architecture parameters, which can be separated into three groups: crown geometry (extension growth index, stem straightness, live crown ratio and shape), branching (branching density, fine ramification), and leaf display (LA, LA and Petiole t/b, %Petiole, efficiency of leaf display and LAI).

Data analysis

Because seedlings were chosen by stratified sampling from both treated and control plots, no significant differences in height were found between treatments for any species, and so data were pooled by species. The species' morphological means were compared using HSD tests (Tukey-Kramer). An analysis of covariance (ANCOVA) was used to determine the effect of species, seedling height, available light (after natural log transformation), and sites (random effect) on seedlings' growth and morphological characteristics. We found no significant interaction with site so data were pooled and this effect removed from the analysis. These analyses were carried out using JMP 5.1 (SAS Institute Inc., Cary, NC).

Variance partitioning was done for each species on the previously normalized morphological variables to determine the fractions that could be attributed to the single and combined effects of available light (L; log transformed) and seedling height (H) (Legendre and Legendre, 1998), using adjusted R^2 ratios (R^2_a) (Peres-Neto *et al.*, 2006). The probabilities associated with the different fractions were computed using partial regressions and 10 000 permutations of the residuals under the reduced model, except for the common fraction, which cannot be tested (Anderson and Legendre, 1999). These analyses were carried out in the 'R' environment (R Development Core Team, 2005) using 'varpart', 'rda' and 'anova.cca' functions from the 'vegan' library (Oksanen *et al.*, 2006).

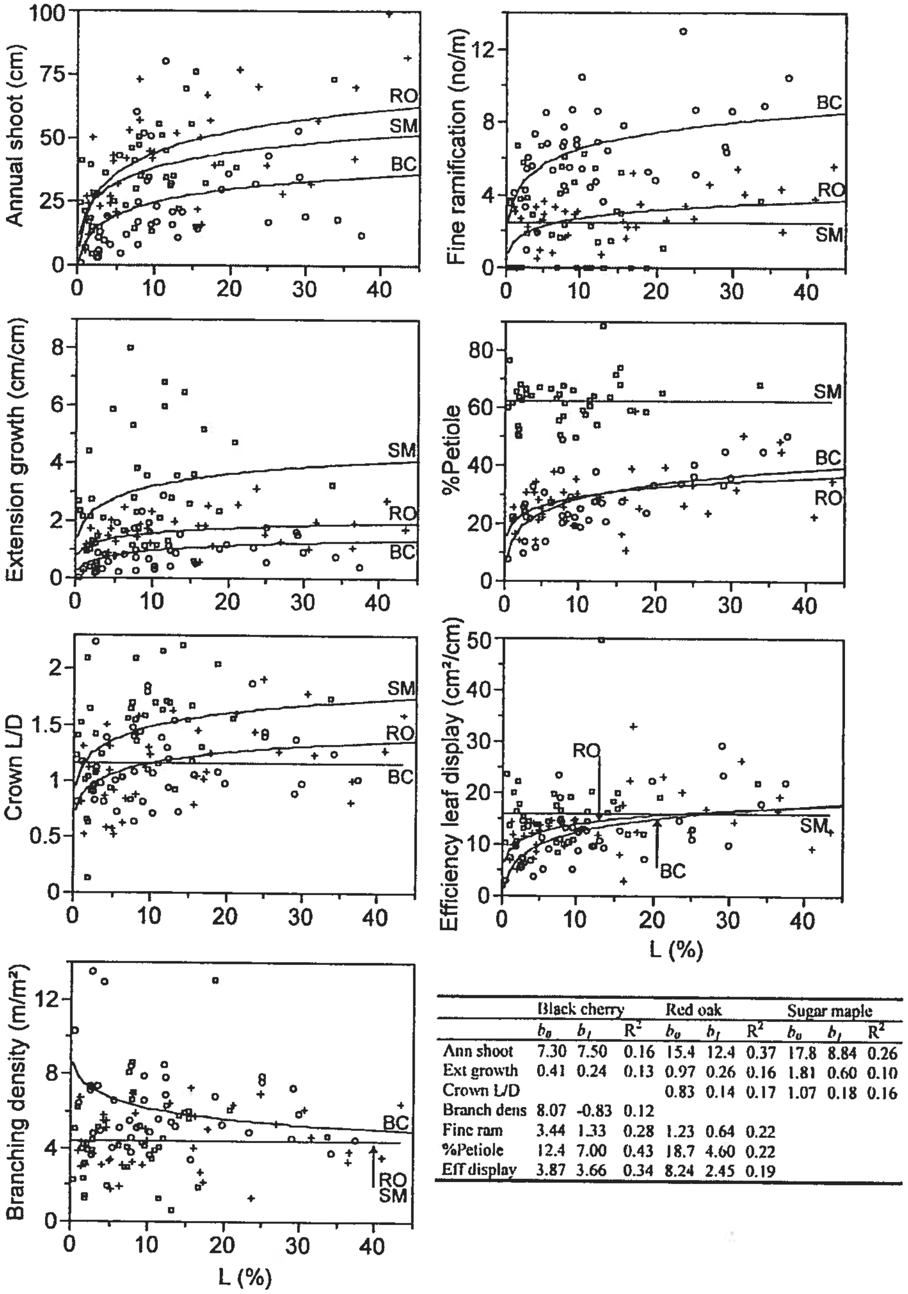
Results

Growth

Annual shoot growth (AS) as a function of available light at the crown varied with species. Maximum (Fig. 4.2) and average (23 cm ; Table 4.3) growth of black cherry as well as its relationship to available light (R^2=0.16 ; Fig. 4.2), were weaker than in the other two species. Red oak had the greatest maximum and average growth (43 cm), which was strongly related to available light (R^2=0.37). Sugar maple occupied an intermediate position regarding annual shoot length (33 cm) and its relation to available light (R^2=0.26).

Specific morphologies

Sugar maple had the highest extension growth index, live crown ratio (together with black cherry) and crown shape index (Table 4.3). Black cherry had the lowest level of stem straightness (0.94), the longest branch length (A2) per unit crown surface, and the highest fine ramification (Table 4.3). Black cherry had the smallest leaves on average and, like red oak, leaf size varied considerably within the crown (LA t/b). In both species leaves at the top were about twice the size of those at the bottom (Table 4.3), and their petioles were twice as long (Petiole t/b). The differences in leaf area and petiole length between the top and the bottom of the crown were significant in all three species ($p<0.0001$; not shown), but smallest in sugar maple (Table 4.3). The proportion of sugar maple's support structure invested in petioles was twice that of the other two species (Table 4.3). Sugar maple also had the highest efficiency of leaf display and leaf area indices.



	Black cherry			Red oak			Sugar maple		
	b_0	b_1	R^2	b_0	b_1	R^2	b_0	b_1	R^2
Ann shoot	7.30	7.50	0.16	15.4	12.4	0.37	17.8	8.84	0.26
Ext growth	0.41	0.24	0.13	0.97	0.26	0.16	1.81	0.60	0.10
Crown L/D				0.83	0.14	0.17	1.07	0.18	0.16
Branch dens	8.07	-0.83	0.12						
Fine ram	3.44	1.33	0.28	1.23	0.64	0.22			
%Petiole	12.4	7.00	0.43	18.7	4.60	0.22			
Eff display	3.87	3.66	0.34	8.24	2.45	0.19			

Figure 4.2. Growth and morphology of seedlings as a function of available light (L), according to species. (BC) black cherry (o); (RO) red oak (+); (SM) sugar maple (□). Equations are of the type Y = $b_0 + b_1 \times \ln(L) + \varepsilon$. Significant relationships ($p<0.05$) are plotted and parameters given in the inserted table; if not significant, a line is drawn at the mean.

Table 4.3. Growth and morphology mean comparison tests between species, and covariance analysis. Probabilities (p<F) are associated with the seedling responses as a function of species (sp), available light (L; natural log), height (H) and interactions.

Parameters	Black cherry (*N*=41)	Red oak (*N*=39)	Sugar maple (*N*=40)	sp	L	H	sp x L	R²
Growth								
Annual shoot (AS) (cm)	23 b	43 a	33 ab	**0.0027**	**0.0033**	**0.0000**	0.4532	0.51
Geometry								
Extension growth index (cm/cm)	0.9 b	1.5 b	2.9 a	**0.0000**	**0.0279**	0.7730	0.2696	0.43
Stem straightness (cm/cm)	0.94 b	0.97 a	0.98 a	**0.0050**	0.1418	0.1638	0.9610	0.30
Live crown ratio (%)	66 a	57 b	66 a	**0.0000**	0.1682	**0.0024**	0.5028	0.31
Crown shape index (L/D) (cm/cm)	1.2 b	1.1 b	1.4 a	**0.0000**	0.6409	**0.0000**	0.0760	0.43
Branching								
Branching density (cm/cm^2)	6.3 a	4.4 b	4.4 b	**0.0007**	0.6331	0.3050	0.0802	0.26
Fine ramification (no/m)	6.3 a	2.6 b	2.4 b	**0.0000**	**0.0357**	**0.0007**	0.2226	0.58
Leaf arrangement								
Unit leaf area (LA) (cm^2)	22 b	57 a	55 a	**0.0000**	0.3181	0.0755	0.7424	0.72
LA t/b	2.0 a	1.9 a	1.4 b	**0.0013**	0.3690	0.4116	0.2317	0.21
Petiole t/b	1.5 ab	1.8 a	1.3 b	**0.0002**	0.5703	0.4280	0.2156	0.22
Proportion of support in petiole (%)	27 b	29 b	62 a	**0.0000**	**0.0000**	0.1436	**0.0109**	0.82
Efficiency of leaf display (cm^2/cm)	12 b	14 ab	16 a	**0.0009**	**0.0003**	0.3325	0.1667	0.27
Leaf area index (LAI) (m^2/m^2)	1.0 b	0.97 b	1.4 a	**0.0000**	**0.0010**	0.1570	0.9301	0.35

Notes: Means from a given line followed by the same letter are not significantly different at the 5% threshold (Tukey-Kramer HSD). Significant effects ($p \leq 0.05$) are in bold characters. The L x H, sp x H, et sp x L x H interactions are not presented as they did not show any significant probability.

Height effect

Annual shoot length (AS) in the three species increased significantly not only with available light but also with seedling height (Table 4.3). Live crown ratio, crown shape index and fine ramification also varied significantly with height. These relationships were all positive and similar in all three species (no sp x H interaction ; Table 4.3). Black cherry and red oak had a larger fraction of the total variance in morphology due to light than did sugar maple (Table 4.4). Height alone (H | L) did not explain a significant fraction of the variance in red oak. The contrary was observed in sugar maple, in which the height effect was stronger, in general, than the light effect.

Plasticity as a function of light climate

Morphological plasticity due to available light was obvious in several traits. The extension growth and fine ramification indices, as well as the proportion of the support structure in petioles (%Petiole) and leaf arrangement indices (efficiency of display and LAI) all varied significantly with available light (Table 4.3). With the exception of %Petiole, these relationships to light were all positive and similar among species. The relationship between %Petiole and available light varied with species (Table 4.3 ; sp x L interaction). This proportion increased with light in black cherry and red oak, but remained stable in sugar maple (Fig. 4.2). The crown lengthened with an increase in available light in red oak and sugar maple, but not in black cherry (Fig. 4.2). While crown branching density strongly decreased as light increased in black cherry, it remained stable in red oak and sugar maple (Fig. 4.2).

Black cherry had the highest level of morphological plasticity explained by light or height (R^2_a=0.23), followed by red oak (R^2_a=0.17) and sugar maple (R^2_a=0.13) (Table 4.4 ; L □ H). Only sugar maple modified its crown geometry as a function of light (Table 4.5), and even so, the height effect was greater (not shown). Similarly height, not light, determined the plasticity of branching and leaf arrangement components of architecture in sugar maple. Red oak did not show any specific adaptation related to height, but its leaf arrangement had a high level of plasticity due to light. Black cherry also modified its leaf display to light climate, but was the only species to modify its branching characteristics in response to light. Crown geometry of black cherry varied with seedling height but not light (Table 4.5).

Table 4.4. Variance partitioning (R^2_a) and partial regression of the effect of light availability (L ; natural log) and seedling height (H), and their singular (L | H; H | L), common (L ∩ H) [1], and combined (L ∪ H) effects, on morphology [2] according to species.

Species	L	L | H	L ∩ H	H	H | L	L ∪ H
Black cherry (N=41)	0.174***	0.070***	0.104	0.156***	0.052**	0.226***
Red oak (N=39)	0.150***	0.061**	0.089	0.108***	0.019	0.169***
Sugar maple (N=40)	0.057**	0.026	0.031	0.107***	0.072***	0.133***

Notes: [1] The common fraction cannot be tested (see Methods). [2] Extension growth index, live crown ratio and crown shape index, branching density and fine ramification, proportion of support in petiole, efficiency of leaf display and leaf area index. The remaining morphological variables (Table 4.3) did not show any significant relation with either light or height.

Table 4.5. Importance of the single effects of light (L ; natural log) and seedling height (H) on crown geometry, branching, and leaf arrangement, according to species. Responses are tested using partial regression by removing the effect of height or light, respectively, and significant effects are flagged with an "x".

	Black cherry		Red oak		Sugar maple	
	L	H	L	H	L	H
Crown geometry		x			x	x
Branching	x					x
Leaf area	x		x			x

Notes: Crown geometry : extension growth index, live crown ratio and crown shape index; branching : branching density and fine ramification; Leaf arrangement: proportion of support in petioles, efficiency of leaf display and leaf area index.

Discussion

Growth

Black cherry's weak growth and weak response to light do not correspond to its successional status. This early succession species was expected to display strong height growth through the whole range of light climates except in deepest shade (Marquis, 1990; Horsley and Gottschalk, 1993; Walters *et al.*, 1993a, b). It might be suspected that as light became more available (up to about 40% - Fig. 4.2), growth became limited by another resource, such as nutrients or water. The relatively low pH and cation exchange capacity of the tills on both sites might support that hypothesis, although it would be surprising given the relatively good growth of the seedlings in the study and the limited demand for resources associated with their small size. We found no visual indication of nutrient stress in any of the species. Red oak and sugar maple showed stronger asymptotic growth responses to increasing light that concord with each species' successional status (Kaelke *et al.*, 2001) (Fig. 4.2). Planted red oak, a mid shade tolerant to shade intolerant species had the largest growth of the group, and responded most strongly to an increase in available light ($R^2 = 0.37$). Naturally occurring sugar maple, considered to be very shade tolerant, had weaker growth than red oak yet stronger than black cherry, and responded moderately to an increase in light conditions ($R^2 = 0.26$; Fig. 4.2).

Plasticity as a function of light climate

Sugar maple differed from black cherry and red oak in several ways. It had a more elongate crown and a higher leaf area index, and maximized its use of petioles (Table 4.3), which are less costly than branches as a support structure (Beaudet and Messier, 1998). However, the proportional investment in petioles and branches (branching density, fine ramification and efficiency of leaf display) did not show any light-induced plasticity (Fig. 4.2). With a comparable range of seedling heights, Beaudet and Messier (1998) found that the proportion of support in petioles increased with light in sugar maple. However, although only height strongly influenced sugar maple's morphology in our study (Table 4.5) as well as in other research (Delagrange *et al.*, 2004), it was not considered by Beaudet and Messier (1998). Although sugar maple is known for its extensive leaf area, with large leaves supported by long petioles on relatively few branches, in concordance with its high level of shade tolerance (Walters and Reich, 1996), the plasticity of these characteristics was low. Equally, we had anticipated a high level of crown shape plasticity in maple, producing a wide crown under shady conditions and an elongate one in more open areas. However, light-induced plasticity was again low, with the ratio of width to height almost never lower than one (Fig. 4.2). Interestingly, Bonser and Aarssen (1994) found an inverse crown ratio to that normally found in sugar maple (*i.e.* wide in shade, elongate in high light). In their study, the crowns were elongate with little ramification in shade, which the authors hypothesized would increase the seedlings' height relative to competing species. The crowns were wide in open areas, maximizing light interception.

The rigid morphology we observed in sugar maple may be specific to the young shade intolerant stands in our study. These are inherently different from the mature forest stands in which the majority of studies on sugar maple have been done. A mature sugar maple stand is generally very closed and admits very little, mostly diffuse, light (<5%) that is poor in the wavelengths that are most useful for photosynthesis (low red to far-red ratio). The canopy is located high above the seedlings (>20m), is uniform, and very stratified vertically. It is possible that the high level of plasticity usually associated with sugar maple is only expressed under such conditions, rather than under young pioneer stands such as those of the present study. The latter have a fully stocked, un-stratified vegetation continuum from seedlings right up to the canopy. They have higher light levels and are richer in direct light (high red to far-red ratio).

Black cherry had a high branching density, also observed by DeLucia *et al.* (1998). It was the only species in which the average growth in width was greater than the growth in height (extension growth index = 0.9 ; Table 4.3), a relationship that varied little with increasing available light (Fig. 4.2). Given its successional status, its morphology should not have been very plastic, but it was the species whose morphology varied the most with light (Table 4.4), particularly with regard to its branch and leaf arrangements (Table 4.5). However, this plasticity did not optimize leaf display, nor growth, while the investment in branches remained the highest in the group (6.3 m/m^2 ; Table 4.3), even when light levels were very low.

Black cherry had a poorer stem straightness than the two other species (Table 4.3), although we expected the opposite given its shade tolerance ranking (King, 2001). This was also observed by DeLucia *et al.* (1998) and could be due in part to the lower density of its wood, making it markedly less resistant to bending under the weight of snow. An analysis of the H/L ratio for black cherry alone revealed an increasing degree of straightness with increasing height but particularly with increasing available light (not shown), demonstrating an unexpected plasticity in this species. Indeed, King (2001) noted strong morphological plasticity and curved stems under shady conditions in species with short petioles, such as black cherry.

For black cherry and red oak, the relative increase in petioles with an increase in leaf area allows the leaves to be displayed further away from the stem and increases the distance between them. This allows these two species to reduce the risk of self-shading at a lower cost. Sugar maple was the only species to display a leaf area greater than the area of the crown (LAI>1), allowing some self-shading to occur.

Red oak had the best growth of the group with a low degree of plasticity except in regards to leaf arrangement (Table 4.5). Its morphology hardly varied with height. Only black cherry and red oak displayed within-crown plasticity, with leaves and petioles that were larger at the top of the crown. Under good conditions, red oak, a species with an episodic growth habit (Dickson *et al.*, 2000), can have several growth flushes per season, concentrated at the top (Sander, 1990). This could give it the capacity to adapt to different light conditions between the top and the bottom of the tree. Black cherry, with indeterminate growth (Horsley and Gottschalk, 1993; Fredericksen *et al.*, 1995), concentrates summer leaves at the top of the tree. These leaves could also be more adapted to higher light conditions. Black cherry can stop growing or prolong its growth period depending on light conditions (Canham *et al.*, 1999).

The main architectural characteristics as well as the plasticity of the three species are summarized in Figure 4.3. The species may have constructed specific architectures that were the result, in part, of past stresses that varied between planted and naturally occurring seedlings. But the red oaks and black cherries had been growing on these sites for six years, and were only one year old when planted, displaying a very simple, still very adaptable architecture. Also, the sugar maples were significantly smaller than the red oaks (Table 4.1), which could be important since most of sugar maple's morphological plasticity was size dependent. But again this would be surprising because light-induced morphological plasticity in this and other species actually decreases with increasing size (Messier and Nikinmaa, 2000; Delagrange *et al.*, 2004). Sugar maple seedlings were young and had established only recently in the understory of the young pioneer stands. They could only establish once the canopy had closed enough to substantially reduce herbaceous competition.

Observed morphological plasticity and alternative models of shade tolerance

Like others studying seedlings (Beaudet and Messier, 1998; Messier and Nikinmaa, 2000; King, 2001; Takahashi *et al.*, 2001), we did not find the expected relationship between species characteristics and shade tolerance on the one hand, and morphological plasticity on the other (Fig. 4.3). In fact, we observed the opposite of what was predicted by the carbon balance model for two of the species. The least shade tolerant species in our study, black cherry, displayed the highest level of plasticity as a function of light climate, while the most shade tolerant, sugar maple, had the lowest light-induced plasticity and did not modify its morphology except as a function of height (Fig. 4.3). This lends support to more complex shade tolerance models, although more work is required to clearly demonstrate them as we did not estimate carbon allocation directly, nor physiological plasticity.

DeLucia *et al.* (1998) proposed a more complex model that includes resistance to pathogens and predation as well as the capacity to store energy reserves, which is related to shade tolerance because it allows the seedling to survive periods of unfavorable conditions or to recover after stress (Canham *et al.*, 1999). Resistance to herbivory is also an important characteristic of shade tolerance because of the relatively high cost of replacing leaves in slow growing species (Givnish, 1988), and because the synthesis of the necessary secondary compounds to provide resistance competes with growth for resources.

Indeed, sugar maple is very resistant to pathogens and is usually little affected by predation, particularly by white-tailed deer (*Odocoileus virginianus*). Deer can cause serious damage to black cherry and red oak both in the region in which the present study was conducted (Truax *et al.*, 2000; Paquette *et al.*, 2006a) and elsewhere in North America (Buckley *et al.*, 1998). The latter two tree species are also attacked regularly by various pests (insects and fungal pathogens), which are much less frequent on sugar maple (Godman *et al.*, 1990).

By favoring long-term survival and lower mortality over strong growth in clearings, sugar maple would thus belong to the first group of the DeLucia *et al.* study (1998), and is in fact the representative species. Red oak, on the other hand, would belong to the second, moderately shade tolerant group, growing rapidly in clearings but being more susceptible to herbivory (Sander, 1990). Black cherry, used in both studies, would belong to the last group. It grows quickly in clearings but is also susceptible to herbivory, disease, and frequent mortality of the apex. Like red oak, black cherry can respond to stresses by producing vigorous sprouts (Marquis, 1990; DeLucia *et al.*, 1998). Its ability to store energy, measured by DeLucia *et al.* (1998), was unexpected in an early succession species.

Implications for forest management

Our results lead us to question whether classic carbon balance and shade tolerance models (Bazzaz, 1979; Givnish, 1988) of morphological, and perhaps physiological, plasticity are useful for regeneration management and silviculture. Shade tolerance rankings are often attributed to species after measurement of a few growth, survival or physiological traits in natural conditions, or from experience (Baker, 1949; Walters and Reich, 1996). It is questionable as to how applicable these rankings are when exported to a critically different environment.

For example, Kaelke *et al.* (2001) and Gottschalk (1994) developed recommendations for the use of red oak and black cherry for under-planting that contradict our observations. These recommendations were based on a classic interpretation of plasticity. In both studies, the data lead to the same classification of species according to their plasticity, low for red oak and high for black cherry. Gottschalk (1994) concluded that black cherry should be a strong competitor of red oak under a shelterwood because it should grow more quickly than the latter. Both studies predicted that red oak should perform poorly under a shelterwood, much like a late succession species such as sugar maple (Kaelke *et al.*, 2001). We observed the opposite. Red oak grew strongly and seemed to be well adapted to this regeneration technique, at least in pioneer stands. Black cherry grew less strongly than red oak and did not respond well to increased available light. This was unexpected but, in fact, is predicted by more complex models of shade tolerance. Black cherry is known to produce many small seedlings, which establish well but grow very slowly under dense canopy. They eventually die and are replaced by a new cohort unless the stand is opened following disturbance (Marquis, 1990). This species is also capable of producing vigorous sprouts, after a small fire for example, using reserves concentrated in a large hypogeal biomass, as reported by DeLucia *et al.* (1998) and Canham *et al.* (1999). Canham *et al.* reported that black cherry survived better after complete defoliation than red oak or sugar maple. Vigorous individuals reported in the literature, therefore, could have been seedlings planted in open areas or sprouts following disturbance. This would explain both the lack of consensus regarding black cherry's shade tolerance, which has been evaluated both as low and intermediate (Baker, 1949; Marquis, 1990; Abrams *et al.*, 1992; Canham *et al.*, 1999), and its high degree of morphological plasticity reported here and elsewhere. Black cherry's plasticity would only be found in shaded seedlings, while vigorous sprouts or trees planted in large clearings would display rapid height growth and a low level of morphological plasticity more in keeping with its successional status.

The management of red oak has been studied extensively because this species has difficulty regenerating after harvest, being naturally regenerated by fire in much of its range (Lorimer *et al.*, 1994; Buckley *et al.*, 1998). As a result, much of today's oak management relies on artificial regeneration. The sometimes disappointing regeneration results in northeastern North America could be due to heavy predation by white-tailed deer. But it can be successful, at least in young pioneer stands, in the absence of predation, or if herbivory is controlled (Paquette *et al.*, 2006a). We have found few trials of this kind on black cherry but our results indicate that regeneration of this species would be successful under a more extensive and earlier opening of the canopy, thus taking advantage of reserves accumulated during early establishment under a shelterwood. Greater disturbance, including clipping the seedlings to the ground, is perhaps required to allow black cherry to use its hypogeal reserves by producing a vigorous sprout. The results of the present study do underline discrepancies between observed and predicted plasticity, but are limited by the number of species used and the limited range of forest type. Clearly, larger integrated studies, covering the whole range of ways that seedlings adapt to light environments, are needed to thoroughly revisit the classical models of shade tolerance and their use for the management of forest regeneration, especially for planted trees.

Acknowledgments

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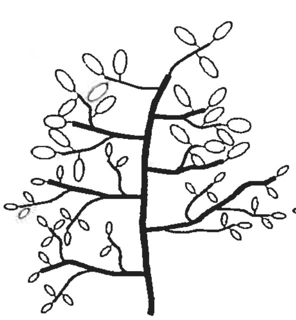
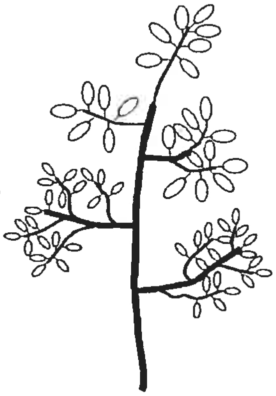
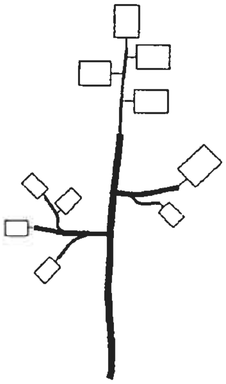
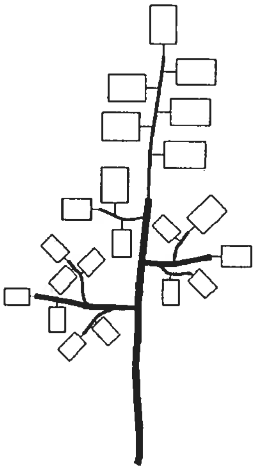
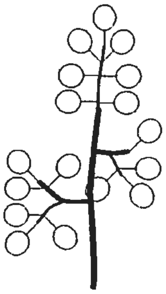
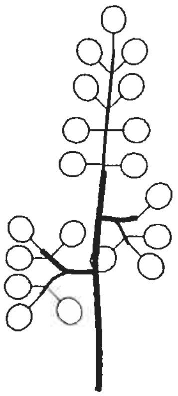
Light gradient		Morphological plasticity with increasing light
Low	High	
Black cherry		
		Weak growth and weak response to increased light. Architecture resulting in high maintenance cost. High level of plasticity : ↓ branching ; ↑ fine ramification ; ↑ % support structure in petioles ; ↑ leaf area.
Red oak		
		Strong growth and vigorous response to increased light. Low maintenance architecture. Low plasticity : ↑ % support structure in petioles ; ↑ leaf area.
Sugar maple		
		Average growth and response to increased light. Low maintenance, very efficient architecture. Very low plasticity : ↑ crown length to width ratio.

Figure 4.3. Schematization of species morphological characteristics and plasticity as a function of the light gradient found in the present study

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Chapitre 5 : A less restrictive technique for the estimation of understory light in high replication or multiple site designs

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Abstract

Many techniques have been developed to estimate mean available light in forest understories. The standard methods estimate average seasonal PAR by recording it *in situ* with quantum sensors or through simulation using hemispherical image analysis (HIA). Other techniques have been developed to overcome some of the drawbacks of the standard methods, such as high cost, cumbersome equipment, user bias, and limited replication. The "overcast" method allows rapid evaluation of average seasonal PAR in most situations by taking instantaneous measurements, but is restricted by the overcast sky conditions required. The present study proposes a new, less restrictive method (BF2), that uses a sensor array under a hemispherical dome to overcome the sky condition restrictions of the overcast method, and tests it against the overcast and HIA techniques. The study also evaluates the method's ability to predict seedling growth and morphology. The BF2 method provided rapid and precise estimations of %PAR under variable sky conditions, as well as good estimations of seedling's responses, and is suitable for multiple site or highly replicated designs. The methods were used under deciduous stands with contrasting structures.

Keywords

%PAR; %PPFD; available understory light estimation; BF2; hemispherical image analysis; overcast sky; beam fractions; diffuse light

Introduction

Understory light plays an important role in forest dynamics and over the years, forest ecology researchers have developed techniques for evaluating understory light availability as accurately as possible. Optimizing that resource for understory seedlings is the primary objective of many silvicultural practices (Drever and Lertzman, 2003; Paquette *et al.*, 2006b), hence the need for reliable light measuring methods adapted to that purpose.

The standard method of measuring the growing season percent transmittance of photosynthetically active radiation (PAR; 400-700 nm) involves leaving a quantum (PAR) sensor and a data-logger in a given understory location for a whole season, while another sensor is positioned above the canopy to measure incident PAR (Comeau *et al.*, 1998; Gendron *et al.*, 1998). Seasonal %PAR is simply the ratio of *in situ* PAR to incident PAR. Although simple in design, this method has limited use because it is time consuming and requires as many sensors as there are points to evaluate (Rich *et al.*, 1993). But it does provide a complete rendition of the complex light microclimate at a given location, including the frequency, intensity and duration of direct light events (sunflecks) allowed into the understory from gaps in the canopy.

Hemispherical image analysis (HIA) is an indirect method that has allowed researchers to overcome some of the above constraints by recording the geometry of the canopy above a given point in the understory in order to simulate the seasonal solar radiation flux using computer software (Canham, 1988b; Rich *et al.*, 1993). Except for the whole season standard, it is the only method that directly measures temporal variability. However, although HIA is a major improvement over the whole season method, it has its own limitations. The instantaneous evaluation of seasonal %PAR under an overcast sky has been a popular alternative in recent years (Messier and Puttonen, 1995; Parent and Messier, 1996). It is fast, reliable, and easy to use, but the overcast sky conditions required can be restrictive.

There are many studies relating plant performance to light availability evaluated by a single method, and some studies testing light methods against each other. The present investigation addresses both objectives. Three techniques, the much used HIA, the rapid "overcast" method, and a new technique using an existing sensor array device under an hemispherical dome, were tested (1) against each other for estimating seasonal %PAR, and (2) against natural sugar maple seedlings (*Acer saccharum* March.) for their performance at estimating seedling growth or morphology.

Methods

The study was conducted on four deciduous stands with contrasting structures within the North American temperate deciduous forest in 2003. The sites were chosen to display a succession gradient from young to mature forests, and contrasting light micro-climates. The first two sites (45° 08.7' N; 73° 44.6' W and 45° 07.6' N ; 73° 38.4' W) are young pioneer stands originating from recent agricultural abandonment (*circa* 1962). They have a low mean canopy height (~ 12 m) with no obvious stratification of vegetation layers. Both sites are dominated by early successional *Betula populifolia* Marsh., for a total basal area of 18 and 13 m^2/ha respectively (all species DBH > 1 cm). Tall shrubs (*Crataegus* spp. and *Malus pumila* Mill.) are present on the first site. These two sites are part of a larger study on under-planting during which half of each site's permanent plots were thinned in summer 2000 (Paquette *et al.*, 2006a), thus accentuating the light gradient and variance.

The third site (45° 06.2' N ; 73° 20.6' W) is a pure, dense young maple stand of low height (10 m), with an undergrowth mostly composed of sugar maple seedlings, for a total basal area of 13 m^2/ha. It is also of agricultural origin (*circa* 1967). The last site (45° 29.7' N ; 73° 47.6' W) is an old growth maple-beech stand with a very high canopy (some trees at 35 m) and a very stratified vertical organisation. Sugar maple is accompanied mostly by *Fagus grandifolia* Ehrh. for a total basal area of 39 m^2/ha. It has no obvious signs of perturbation other than the probable regular harvest of firewood since the beginning of European colonization. The larger trees are approximately 300 years old (<1712) (Boivin and Boily, 1991) and the site is now protected within a municipal park (*Bois-de-Liesse*).

Mean available light at one meter from the ground ranged from less than 1% in the old growth forest to 11% in thinned plots of one of the young pioneer stands. The same stands without thinning had 4% available light on average. Available light under the dense young maple stand was 2.5%.

On the four sites, a total of 95 naturally occurring sugar maple seedlings were inventoried in spring 2003 and used as light measurement points. Healthy seedlings free of serious problems were chosen. The 95 seedlings had an average height of 125 cm (standard deviation [SD] : 39 cm). The length of the annual shoot (2003) on the main stem (AS) was measured on each seedling at the end of the growing season (mean : 19 cm ; SD : 17 cm). A geometry ratio of crown length to mean crown diameter (Crown L/D) was also evaluated (mean : 1.1 cm/cm ; SD : 0.47 cm/cm) (Beaudet and Messier, 1998; Delagrange *et al.*, 2004). Being very shade tolerant (Godman *et al.*, 1990), sugar maple is a good candidate for discriminating measuring methods as it generally exhibits a high level of plasticity in response to light availability (Canham, 1988a).

Three methods of measuring light environments were applied to each of the 95 seedlings at several heights from the ground (0.5m to 4m). Only the results at 2 m (just above mean seedling height) are presented here because they displayed the strongest relations in the method comparison trial and against seedling response. Because the methods could not be used simultaneously, a permanent 60 cm steel stake was planted vertically to a depth of 30 cm at the foot of each seedling to insure spatially consistent readings. The light measuring instruments were attached to a photography tripod's head, which in turn was screwed to the tip of a steel rod of specific length so as to place the top of each sensor exactly 2 m from the ground. The rod was placed against the permanent stake and the tripod head adjusted so that the sensors sat horizontally on their support. The measurements were taken on all seedlings in July and August 2003. All sensors were new or recently (< 1 year) calibrated by the manufacturer.

Hemispherical image analysis (HIA)

Hemispherical photographs were taken at each location with a digital camera (Nikon Coolpix 990, Tokyo, Japan) and a hemispherical lens (Nikon fisheye converter FC-E8) using the maximum resolution (2048 x 1536 pixels x 16 million colors, normal [1:8] JPEG compression) (Englund *et al.*, 2000; Nobis and Hunziker, 2005). The north was aligned with the bottom of the image using a compass (Frazer *et al.*, 2001). Exposure was adjusted manually for the best contrast, and under- or over-exposed images were identified on site or at the lab and taken again. Images were taken when the sun was not visible through the canopy to limit light flecks and editing. Again, images with light flecks making the identification of foliage difficult were identified and taken again. Fewer images would have been rejected by only working under an overcast sky (Englund *et al.*, 2000), but stronger contrasts can be obtained under blue skies (Frazer *et al.*, 2001), and overcast days are scarce and were reserved for the overcast method (see below).

Color images were treated by the same person using the same protocol on an image editing software to get a binary image after manual correction, when required, of small light flecks. This method was preferred over the use of thresholds and color filters available in HIA software packages because it allows for the precise editing of color ranges within delimited areas of the image (such as white bark on *B. populifolia*). Gap Light Analyser (Frazer *et al.*, 2000) was then used to analyse the binary images with proper configuration for each site (Canham, 1988b). The season used for the calculations was the same as for the other methods compared, July 1st to August 31st (fully developed canopy), at a temporal resolution of one minute and a spatial resolution of 36 azimuth by 18 zenith sky regions. The gap light index (GLI) was then computed, as well as the direct and diffuse fractions (Canham, 1988b).

Editing and analysis of the acquired images can be done at any time, but require time, skill, and software, and much is done manually, thus introducing some user bias (Englund *et al.*, 2000; Nobis and Hunziker, 2005). The method is expensive and uses a cumbersome and fragile instrument needing *in situ* adjustments (Parent and Messier, 1996; Ferment *et al.*, 2001). The end product is very versatile though, and is not only a permanent record of a given forest location, but can be analysed to provide many indices other than GLI (%PAR), such as the diffuse and direct fractions, canopy openness, and the frequency and duration of sunflecks, as it accounts for temporal variability. The method has been proven successful at approximating the standard growing season percent PAR transmittance (Comeau *et al.*, 1998; Gendron *et al.*, 1998), and has been used extensively in forest ecology research (*e.g.* Canham *et al.*, 1990; Rich *et al.*, 1993; Easter and Spies, 1994).

Overcast method

The overcast method instantly estimates %PAR under diffuse light with full cloud cover (Messier and Puttonen, 1995; Parent and Messier, 1996). To evaluate relative available light, a quantum sensor (LiCor li-190, Lincoln, NE, USA) was placed *in situ* while a second reference sensor was placed as high as possible (using a large tripod and a vehicle if necessary) in a nearby (<300m) large open area. Both sensors were connected to portable data-loggers (LiCor li-1400). Measurements were taken at the two points simultaneously using radio communication thus limiting errors due to temporal variations.

The instantaneous measurement of relative light under an overcast sky is used when one is interested in approximating the seasonal PAR at several locations with a direct and rapid method that requires no adjustments in the field nor image processing (Messier and Puttonen, 1995; Parent and Messier, 1996). Although there is some doubt whether the method is accurate under very heterogeneous canopies (Messier and Parent, 1997; Stadt *et al.*, 1997), it has proven useful in many contexts (*e.g.* Beaudet *et al.*, 2004; Delagrange *et al.*, 2004; Cogliastro *et al.*, 2006). But the completely overcast sky condition upon which its application depends are restrictive and can be quite rare in certain regions during the data collection season (Comeau *et al.*, 1998). In multiple-site studies covering a large area, it is not always practical or even possible to return to each site after initial inventories to take light measurements when the conditions are right. The sensors and data-loggers are expensive but very rugged and require no special skills.

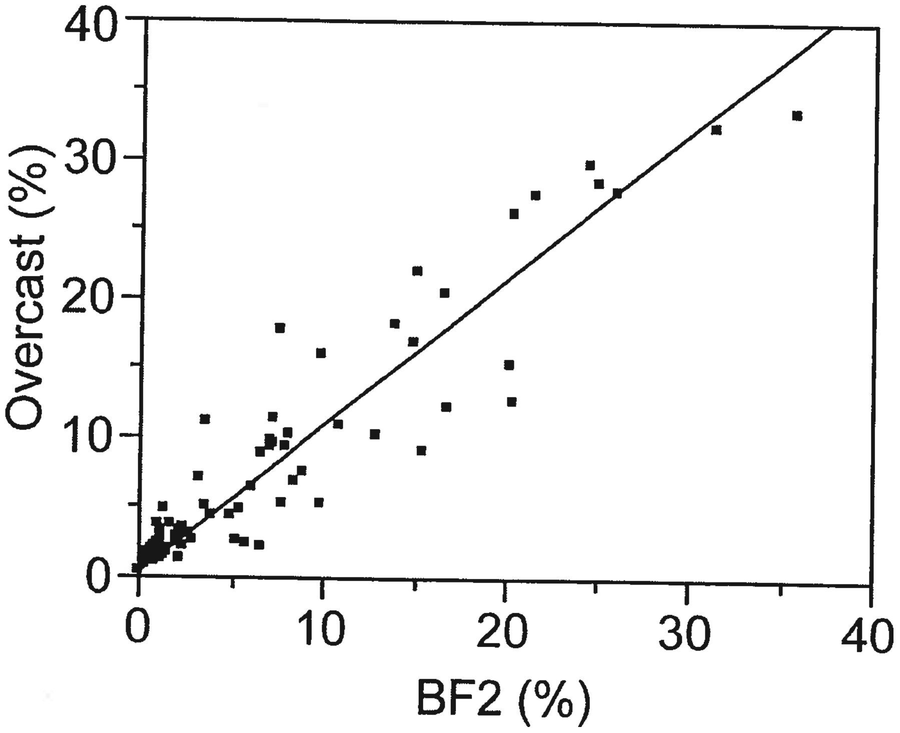
Beam Fraction Sensor (BF2)

The BF2 type Sunshine Sensor (Delta-T, Burwell, Cambridge, UK) was tested in an attempt to find an alternative to the overcast method which could also match the accepted reference of HIA. It comprises seven quantum sensors under an hemispherical dome (≈ 7.5 cm in diameter) with a pattern of clear and opaque areas (mask) such that at any given moment, in whatever direction the BF2 is oriented, at least one of the sensors will be in diffuse light (Wood *et al.*, 2003). Three signals are sent from the BF2 to a portable computer (PSION Workabout, Singapore): the quantity of diffuse and total light, and a binary signal indicating the presence of direct light (from a pre-established threshold). Only the diffuse signal is used here. The ratio of available light was obtained in the same fashion as in the overcast technique, namely by placing another BF2 in a nearby field and communicating by radio, except this time under clear or partly cloudy skies so as to evaluate the accuracy of the BF2 method under variable light conditions.

The BF2 sensor meets all the requirements established for meteorological stations (Wood *et al.*, 2003) and should behave identically to regular quantum sensors under overcast conditions. The price is roughly the same as for the overcast method and the equipment is easy to use, but not quite as rugged. At the time of writing this article, the BF2 has been replaced with a new, software upgraded model (BF3) with identical light measuring characteristics.

Previous attempts at evaluating relative seasonal PAR instantaneously using only diffuse light under clear or variable skies have been successful with the use of Plant Canopy Analysers (LiCor LAI-2000), with view restrictors and multiple readings during the day, each time masking the sun (Hanan and Bégué, 1995; Comeau *et al.*, 1998; Gendron *et al.*, 1998). But the instrument is very expensive (and two are required for relative PAR measurements), requires at least two measurements per point at different times, and does not measure PAR per se, but rather a fraction below 490 nm called "diffuse non-interceptance".

Figure 5.1. Relationship between the BF2 and the Overcast methods at two meters.



Notes: Linear orthogonal regression equation is : Overcast (%) = 0.379 + 1.059 x BF2 (%). Correlation = 0.94 ($p \leq 0.0001$; *N*=95).

Methods performance

The methods compared had strong (r > 0.9), highly significant pairwise correlations with each other (Tab. 5.1). The BF2 technique under clear or partly cloudy skies was a very good estimator of the mean seasonal %PAR assessed by the overcast method (r = 0.94). Further analysis of that relationship was carried out using orthogonal regression to account for measurement errors and allow predictive equations to be used both ways. With a slope close to unity (1.06) and a small intercept (<0.4 %) it can be used directly without calibration as an alternative to the overcast method (Fig. 5.1).

Table 5.1. Correlation table for the comparison of light measuring methods.

	HIA (GLI)	Overcast	BF2
HIA (GLI)	1	0.93	0.91
Overcast		1	0.94
BF2			1

Notes: All correlations are highly significant (*p*≤0.0001; *N*=95).

Each method was then used to predict growth (AS) and morphology (Crown L/D) of the maple seedlings, using least-squares regression and square-root transformations of the light values. The annual shoot length (AS) of sugar maple seedlings was strongly and significantly (p≤0.0001) associated with light measurements obtained with all tested methods (Tab. 5.2). The R^2 coefficients of multiple determination were weaker in the case of the morphology index (Crown L/D), while still being highly significant, a phenomenon also observed elsewhere for the same species (Beaudet and Messier, 1998; Messier and Nikinmaa, 2000). HIA (GLI), the overcast, and the BF2 techniques always performed well and explained more than 50% of the variability in growth and over 30% of that in morphology (Tab. 5.2).

The sites covered in this study differed greatly in composition and structure, from disorganised young stands (including tall shrubs), to a very stratified, high canopy mature forest. About half of the sample area of the two young pioneer stands had been thinned by small two-meter gaps three years earlier, creating even more heterogeneity in the canopy. Though such small regularly distributed gaps are quite different from larger ones with definite edge effects, we found the BF2 and overcast instantaneous methods to be quite resilient to at least some degree of heterogeneity, as compared with the standard HIA. It should be noted that we only tested the methods under broadleaved, deciduous stands, although instantaneous methods such as the overcast technique have been used successfully under mixed and coniferous stands (*e.g.* Messier and Puttonen, 1995; Messier *et al.*, 1998; Aubin *et al.*, 2000).

Table 5.2. R^2 coefficients from regression analysis of annual shoot growth (AS - cm) or crown length to diameter ratio (Crown L/D – cm/cm), to light microclimate (L) at two meters, according to the method used.

Method (L)	AS (cm)	Crown L/D (cm/cm)
HIA (GLI)	0.53	0.32
Overcast	0.56	0.34
BF2	0.51	0.32

Notes: Least-squares regression models is : Y (AS or Crown L/D) = $b_0 + b_1(\sqrt{L})$. All relations are highly significant ($p \leq 0.0001$; $N = 95$).

Heterogeneity has been the focus of recent work and has proven to be important to some processes in forest ecology, such as the use of sunflecks for photosynthesis (Naumburg and Ellsworth, 2000; Beckage and Clark, 2003). Distinguishing the respective effects of beam fraction (diffuse and direct light, from which heterogeneity is born) and mean availability on plant response, however, is not an easy task (Wayne and Bazzaz, 1993). The two are intrinsically associated under natural conditions, for as more sunflecks are allowed in from larger or more numerous gaps, so is diffuse light. We have attempted to evaluate the importance for maple seedlings of the relative contributions of direct and diffuse fractions of available light from HIA. Forward selection (α=0.25) of square-root transformed percent of direct and diffuse light only allowed the diffuse fraction to enter the model for both seedling responses. Furthermore, re-running the analysis of seedling response to light climate with the diffuse fraction alone, instead of GLI (which includes both fractions), revealed even stronger relations ($R^2 = 0.56$ [AS] and 0.33 [Crown L/D]; not shown). Sunflecks are important, as they compose a large part of understory light and impose important restrictions on plant processes especially at the leaf level (Wayne and Bazzaz, 1993; Valladares *et al.*, 1997). However, mean available light as evaluated from the diffuse fraction alone remains a good predictor of larger scale responses such as growth or crown morphology.

The BF2 method thus offers an efficient alternative to the technique proposed by Parent and Messier (1996) because it can be used under all sky conditions regardless of cloud cover. It can be used with minimal skills by different people on the same project as it is mostly automated and free of user input. These represent considerable advantages when many points are being evaluated, or for large scale studies that do not allow multiple visits to sites. The measurements taken with the BF2 gave not only an accurate evaluation of average seasonal %PAR but also an adequate assessment of the growing conditions of understory seedlings.

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Chapitre 6 : Conclusion générale

Conclusion générale

Les plantations ont pris une place importante parmi les écosystèmes forestiers du monde et sont en progression constante. Une partie de plus en plus importante des services économiques, sociaux et environnementaux rendus par la forêt le seront par des arbres plantés. Il est désormais acquis que les forêts naturelles ne seront pas, ne sont déjà plus, capables de répondre aux besoins d'une population de plus en plus importante. La question n'est plus de savoir si les plantations sont nécessaires ou désirables, mais bien comment elles devraient être conçues pour d'une part minimiser leurs effets négatifs et d'autre part garantir et maximiser les impacts positifs comme la conservation intégrale des forêts primaires résiduelles. Il faudra développer les connaissances relatives aux arbres plantés pour arriver à ces fins ; la présente thèse est une contribution au développement de modalités pour les plantations sous couvert par la connaissance de l'écologie des espèces en fonction des paramètres environnementaux induits par l'aménagement, et devrait favoriser l'utilisation de cette approche, particulièrement dans les forêts dégradées du sud-ouest québécois.

Le rendement des plantations sous couvert n'est pas diminué par le maintien d'une partie importante du couvert forestier

Il est possible de conserver une partie importante du couvert forestier sans diminuer la survie ou la croissance des plants de reboisement, voire même réussir à les augmenter. Dans la forêt tempérée, la forêt tropicale et la forêt pluvieuse côtière, la survie et la croissance des plants sont assurées avec seulement une ouverture modérée du couvert forestier. En général, les gains les plus importants sont obtenus avec un couvert de densité intermédiaire. Sous des couverts plus faibles, la protection des plants contre la prédation par les ongulés et les stress climatiques est moindre, alors que la compétition par les plantes herbacées est plus grande. Le niveau d'ouverture intermédiaire semble être un bon compromis dans une majorité de situations. Les coupes d'éclaircies plus importantes et les coupes totales ne présentaient aucun avantage sur des conditions plus denses, et ces dernières sont aussi plus susceptibles de répondre aux objectifs de conservation.

Les plantations sous couvert sont applicables au contexte particulier des jeunes forêts de transition appauvries de la partie nord de la forêt décidue

Les forêts de la partie nord de la forêt décidue de l'est de l'Amérique du Nord ressemblent étrangement, du point du vue de l'impact des activités humaines et de l'état de dégradation, aux forêts dégradées du biome tropical, et requièrent le même type d'intervention pour leur réhabilitation. L'enrichissement sous couvert avec dégagement partiel, deux ans après la plantation, s'est révélé être une méthode efficace d'établissement d'une régénération en feuillus nobles, particulièrement le chêne rouge, dans de jeunes peuplements mal régénérés d'origine agricole, et ce sans augmentation de la prédation par le cerf de Virginie. Les résultats supportent une sylviculture plus dynamique dans les paysages ruraux sensibles, là où la conservation des structures forestières est importante. Nous avons souligné l'importance d'une planification adéquate des opérations, en particulier quant à la stratification verticale de la végétation compétitrice et à l'ontogénèse des plants.

La méthode est applicable à l'échelle des petits producteurs régionaux dans une matrice agro-forestière. Un enjeu majeur pour la Montérégie et la forêt feuillue privée québécoise sera de bien informer les propriétaires des possibilités sylvicoles offertes et de l'importance de la conservation des structures forestières en place, même dégradées. Il faudra surtout les supporter adéquatement au cours du temps, puisqu'il en va non seulement de la santé financière de la filière forestière québécoise, mais aussi de la santé des écosystèmes de la forêt feuillue.

La plasticité morphologique des semis sous couvert ne correspond pas à leur statut successoral

La correspondance attendue entre d'une part, les traits et la plasticité morphologiques, et d'autre part, le statut successoral n'a pas été confirmée en situation de plantation sous couvert en jeune forêt de transition. L'inverse de ce qui était prévu par le modèle d'équilibre en carbone pour le cerisier tardif et l'érable à sucre a été constaté. Ceci tend d'une part à appuyer les modèles plus complexes sur la tolérance à l'ombre mettant en jeu d'autres paramètres tels que la résistance aux pathogènes et herbivores ainsi que le stockage de réserves, mais aussi remet en question la pertinence de l'utilisation unique du statut successoral à des fins d'aménagement sylvicole pour prédire le succès d'établissement et les besoins spécifiques des espèces en terme d'ouverture de la canopée.

Étant donnée la place que prendront les arbres plantés dans le paysage forestier futur et leur importance grandissante dans la livraison des produits forestiers, il est important de développer les connaissances quant à l'écologie particulière des arbres plantés. Ces connaissances sont nécessaires pour que les plantations puissent fournir les approvisionnements prévus et ainsi remplir les objectifs de protection des forêts naturelles sur lesquelles leur acceptabilité est fondée. Parce que les arbres plantés se développent dans un contexte particulier, en partie en dehors du spectre habituellement investi par les semis naturels de l'espèce, ces connaissances seront aussi utiles pour alimenter les connaissances sur l'écologie naturelle des espèces. En effet, en milieu naturel il est souvent difficile d'isoler les variables explicatives et pertinentes quand à l'écologie des espèces.

Mesure de la lumière disponible sans contraintes de ciel

La mesure de la lumière disponible aux plants de reboisement a représenté un effort important tout au long des travaux de cette thèse. Nous avons pu ainsi tester diverses techniques et les évaluer en conditions réelles sur le terrain. Les conditions de ciel requises par certaines techniques ont représenté un obstacle important à la réalisation des échantillonnages, qui n'ont pu être complétés certaines années. Certaines alternatives ont plutôt représenté des coûts importants en traitement et analyse d'images au laboratoire. Nous avons ainsi été amené à chercher une alternative à la fois précise, pertinente pour la tâche (l'évaluation des conditions de croissance des semis), avec un minimum de contraintes quant au ciel, rapide et peu coûteuse. Nous avons développé une telle méthode et l'avons testée avec succès en comparaison avec les standards en écologie forestière et avec la réponse de semis dans une large gamme de forêts feuillues.

Des pistes pour l'avenir

Au Québec, la foresterie a laissé peu de place à la sylviculture des forêts feuillues, tous les efforts portant essentiellement sur l'exploitation de la forêt boréale. Pourtant la grande majorité des Québécois habitent la forêt feuillue. Alors que les valeurs environnementales commencent à s'imposer dans les sociétés occidentales, fortement industrialisées, on peut prévoir que l'intérêt pour cette forêt va s'intensifier, et parallèlement les exigences et les attentes quant à sa gestion seront plus élevées. Du point de vue économique et culturel, accepterons-nous encore longtemps que l'industrie québécoise du meuble doive s'approvisionner de plus en plus loin pour obtenir du bois de qualité de moins en moins bonnes, alors que les feuillus précieux étaient ici autrefois abondants ? De quel bois seront faits les meubles de nos enfants ?

La plantation d'arbre est une avenue qu'il n'est plus possible d'ignorer pour réhabiliter la forêt feuillue du sud du Québec et de nombreuses autres forêts dégradées du monde. La plantation d'enrichissement sous couvert par exemple permet en effet la restauration et la réhabilitation de sites par l'introduction plus rapide d'espèces désirables des points de vue écologique et économique, tout en favorisant la conservation des structures et fonctions forestières par le maintien local et au niveau du paysage d'un couvert forestier permanent. Les plantations devront cependant être conduites de façon durable, en tenant compte des aspects économiques et environnementaux, évidemment, mais aussi des besoins des populations locales, actuelles et futures. Pour la forêt d'ici nous retenons un certain nombre d'enjeux et de questions de recherche pour les années qui viennent :

- Après la phase d'établissement des arbres, les interventions visant à assurer et maintenir la croissance et la qualité doivent être précisées en fonction des espèces et des conditions environnementales;
- La longueur du cycle de production implique des interventions répétées qui incomberont à plus d'une génération de propriétaires ; l'intérêt pour le peuplement doit être aussi durable et soutenu financièrement par des programme d'aide et de l'animation, visant le maintien du dynamisme des producteurs;
- Le savoir faire, encore peu développé, doit se répandre et déboucher sur la formation de personnel qualifié dans le domaine de l'aménagement de la forêt feuillue et plus particulièrement dans la régénération artificielle pour appuyer les producteurs;
- Quelques espèces seulement ont été utilisées pour le moment, et ce dans seulement quelques conditions parmi celles disponibles (sols et types de peuplement), mais déjà il semble que les traits connus de l'écologie naturelle des espèces soient de pauvres indicateurs de leur performance en plantation. Le cerisier tardif mérite plus d'attention, étant donné sa valeur économique, le peu de littérature disponible, et sa réponse imprévue aux conditions lumineuses ;
- Enfin il importe particulièrement de développer et tester des outils permettant de mesurer l'atteinte des objectifs de conservation de la biodiversité, des structures et des fonctions forestières, et d'accélération de la succession vers des stades plus avancés, poursuivis par les efforts de restauration par la plantation, et ce tant à l'échelle du peuplement aménagé qu'à l'échelle du paysage.

Les plantations mixtes seront appelées à remplacer les monocultures là où cela est possible et souhaitable. Ces plantations supportent une plus grande diversité à la fois en espèces mais aussi en structure, particulièrement si elles sont conçues en multi-cohortes de façon à favoriser le maintien permanent d'un couvert forestier (*continuous cover forestry*). Les plantations mixtes sont par ailleurs un environnement de recherche particulièrement intéressant pour la mesure précise des interactions de compétition et de facilitation afin d'alimenter les modèles théoriques sur la dynamique des communautés végétales. De façon plus pratique, les projets en marche tentent aussi de démontrer qu'il est possible d'optimiser les effets de facilitation afin d'obtenir des rendements supérieurs aux rendements des monocultures. Les plantations mixtes et la sylviculture intensive sont parties intégrantes de projets de zonage fonctionnel (Triade) qui sont en voie d'établissement ici et ailleurs et suscitent beaucoup d'intérêt.

Le Québec n'est pourtant pas seul face à la dégradation des écosystèmes forestiers ; les forêts tropicales par exemple sont particulièrement touchées par la surexploitation forestière et l'agriculture itinérante, et les techniques qui nous ont inspiré pour cette thèse, plus particulièrement au niveau des objectifs, viennent en bonne partie de ces régions. Les forêts tropicales supportent aussi une partie importante de la biodiversité de la planète, de même que plusieurs peuples indigènes. Dans de nombreuses régions des Amériques tropicales, en Afrique et en Asie, la conservation des écosystèmes passe nécessairement par la survie des traditions, langues et cultures des peuples qui les habitent. Malheureusement les efforts de reboisement dans ces pays ne sont pas toujours faits en tenant compte des besoins des populations locales, et encore moins en partenariat avec eux. Rarement les connaissances autochtones pourtant ancrées dans ces milieux depuis des millénaires sont-elles mises à profit. Au contraire de nombreux projets poursuivent dans le chemin tracé par des siècles de colonisation, détruisant les écosystèmes et les communautés humaines. Des projets de restauration et d'exploitation durable de la forêt, en partenariat avec les populations locales, sont pourtant en place partout dans le monde. Le Québec et le Canada doivent être solidaires de ces actions mais aussi s'en inspirer, comme nous l'avons fait, pour trouver des solutions novatrices et efficaces aux problèmes d'ici, étonnamment semblables du point de vue fonctionnel.