Effet des interactions entre la coupe partielle, les facteurs de site, et le type d’essence sur la résistance des arbres hôtes à la tordeuse des bourgeons de l’épinette (*Choristoneura fumiferana* (Clem.)).

Thèse

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Résumé

La tordeuse des bourgeons de l'épinette (TBE), *Choristoneura fumiferana* (Clem.), est le ravageur le plus important des forêts de l'Amérique du Nord. L'éclaircie a été souvent recommandée pour réduire les pertes ligneuses causées par les épidémies de TBE. Ceci est basé sur l'hypothèse que l'impact positif de cet outil sylvicole sur la vigueur des arbres résiduels devrait les rendre plus résistants aux défoliations de TBE. Cependant, les résultats de différentes études sont contradictoires. Le but de cette étude consiste à mieux cerner les impacts de ce traitement sylvicole sur l'insecte et sur ses hôtes selon diverses situations et de suivre ces impacts dans le temps. Pour y parvenir, des élevages sur le terrain de TBE et des analyses chimiques foliaires des essences hôtes ont été effectués selon un gradient d'éclaircie (réduction de 0, 25 et 40% de la surface terrière du peuplement) et de qualité de drainage du site (mésique avec drainage oblique, subhygric, hydrique). Des élevages ont aussi été effectués sur des sites à drainage rapide. L'ensemble des travaux a été conduit dans le domaine de la sapinière à bouleau blanc. Les résultats de cette étude démontrent que l'éclaircie réduit à court terme la résistance des sapins à la TBE et que ce phénomène est lié à des baisses significatives de certains monoterpènes dont les concentrations dépendent fortement de la qualité de drainage du site. Cependant trois ans après le traitement, celui-ci entraîne une forte augmentation de la résistance des sapins baumiers à l'insecte. Cette augmentation de résistance est essentiellement due à une augmentation de production foliaire (accroissement de la tolérance) et est particulièrement marquée dans les peuplements évoluant sur des sites hydriques soumis à des intensités d'éclaircie de 40% de réduction de surface terrière. Cette résistance accrue se maintient pour au moins 6 ans après l'application du traitement. Ces résultats suggèrent que cette technique sylvicole pourrait être utilisée comme mesure préventive visant à réduire l'impact négatif de TBE sur les forêts québécoises.

Abstract

Spruce budworm (*Choristoneura fumiferana* (Clem.)) is the most destructive insect pest in the maritime and boreal forests of North America. Thinning has been recommended to reduce damage caused by spruce budworm. The positive impact of this silvicultural procedure on the vigour of the residual trees should, in theory, render them more resistant to budworm defoliation. However, various research projects focused upon effects of this silvicultural tool on host tree resistance have yielded equivocal results. The main objective of this project was to clarify the real effect of thinning on host tree resistance to spruce budworm attacks. Field-rearing experiments with spruce budworm were conducted, together with foliar chemical analyses, along a gradient of stand thinning density (0%, 25%, and 40% stand basal area reduction) and drainage class (mesic with seepage, class 3; subhygric, class 4; hydric, class 5) in balsam fir–paper birch association stands. Rearing experiments were also conducted in rapidly drained sites (class 2). The results showed that resistance to spruce budworm of balsam fir, unlike white and black spruce, was significantly reduced one year after thinning. This response was likely due to increased defoliation linked to reduction in certain monoterpene concentrations and to decreased foliage production, except on drainage class 5, where the treatment increased fir resistance. However, three years after treatment we observed the opposite response. High thinning intensity (40%) positively affected balsam fir and white spruce tolerance to damage and, therefore, tree resistance by increasing foliage production and the amount that remained after budworm feeding. This increased resistance persists for at least 6 years after the treatment was conducted. These results suggest that this silvicultural technique could be used as a preventive control measure to reduce the negative impact of spruce budworm on Quebec's forests.

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Avant-propos

Cette thèse comprend une introduction et une conclusion générales, ainsi que quatre chapitres principaux (2 à 5) rédigés et présentés dans un format approprié pour la publication scientifique.

Le chapitre 1 est publié sous la référence : Fuentealba, A. et Bauce, É. 2012. Site factors and management influence short term host resistance to spruce budworm (*Choristoneura fumiferana* (Clem.)) in a species-specific manner. Pest Management Science: 68(2): 245-253. DOI: 10.1002/ps.2253.

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1. Introduction

La tordeuse des bourgeons de l'épinette (TBE), Choristoneura fumiferana (Clemens) (Lepidoptera: Tortricidae), est l'insecte ravageur le plus destructeur des forêts maritimes et boréales de l'Amérique du Nord. Les populations de ce défoliateur ont atteint des niveaux épidémiques sur de vastes zones boisées de façon assez régulière, au moins au cours des trois derniers siècles (Blais 1965, Jardon et al. 2003). Lors d'une épidémie typique, la défoliation sévère se répète sur une période de 5 à 25 ans, tant à l'échelle locale qu'à l'échelle régionale. Ces épidémies entrainent une baisse substantielle de la vigueur et une mortalité accrue chez les arbres touchés. La destruction répétée des pousses annuelles entraine souvent la mort des arbres hôtes, car ils deviennent incapables de produire les ressources nécessaires pour survivre (Blais 1981, MacLean et Ostaff 1989). En effet, les pertes globales pour l'industrie des produits forestiers au Canada pouvant être attribuées à la tordeuse des bourgeons de l'épinette lors de sa dernière épidémie s'élèvent à 44 millions de m3 de bois par année (Sterner et Davidson 1982). Au Québec seulement, la dernière épidémie de TBE (1968-1987) a causé des pertes de 283 millions de m3 suite à la mortalité des arbres et à la réduction de la croissance (Coulombe et al. 2004).

Malgré son nom, la TBE se nourrit de plusieurs conifères hôtes (Henningar et al. 2008), son préféré étant le sapin baumier (Abies balsamea (L.) Mill.), suivi par l'épinette blanche (Picea glauca (Moench) Voss), l'épinette rouge (P. rubens Sarg.) et l'épinette noire (P. mariana (Mill.) BSP). La protection des peuplements de conifères contre la TBE repose actuellement sur les pulvérisations aériennes de l'insecticide microbien Bacillus thuringiensis ssp. kurstaki (Btk) (van Frankenhuyzen 1990). Cette bactérie du sol à coloration de Gram positif produit un cristal protéique qui est spécifiquement toxique pour les lépidoptères. La bactérie doit être ingérée par l'insecte ciblé afin de provoquer des dommages dans l'intestin menant à la mort par septicémie (Höfter et Whiteley 1989). Étant donné le coût élevé et les dommages potentiels qui peuvent être causés à l'environnement, le contrôle direct avec les pesticides devient une option de moins en moins intéressante (Muzika et Liebhold 2000). Les manipulations forestières à l'aide de prescriptions sylvicoles représentent une alternative intéressante à la gestion des ravageurs forestiers, car elles peuvent être moins coûteuses, plus efficaces et durables, et elles ont une faible incidence sur l'environnement par rapport aux pesticides (Muzika et Liebhold 2000). L'éclaircie a souvent été recommandée pour réduire les dommages causés par la TBE (Crook et al. 1979, Bauce 1996, Bauce et al. 2001) et la tordeuse de l'ouest (Choristoneura occidentalis Freeman) (Mason et al. 1992). Cependant, plusieurs projets de recherche axés sur les effets de cet outil sylvicole sur la résistance des arbres hôtes ont donné des résultats contradictoires. Des études antérieures ont signalé que la résistance à la TBE pourrait augmenter (Batzer 1967, Bauce 1996, Bauce et al. 2001), diminuer (Piene 1989, MacLean et Piene 1995) ou rester inchangée (Crook et al. 1979) après l'éclaircie. Par conséquent, il est essentiel de comprendre l'effet réel de cette technique sylvicole sur la résistance des arbres hôtes à la TBE, ce qui permettrait d'exercer un meilleur contrôle sur les populations de ce ravageur (épidémies), tout en conservant un approvisionnement permanent en bois pour l'industrie forestière du Québec. En plus, il est très important d'évaluer l'effet de la qualité nutritionnelle de la nourriture fournis par les principales essences hôtes sur la performance de ce ravageur forestier, ce qui nous permettra de mieux comprendre les raisons pour lesquelles cet insecte présente une performance différente dans ses principaux hôtes. Cette information nous aidera à améliorer les modèles prédictifs et à développer des méthodes visant à réduire l'impact négatif de la TBE.

L'objectif principal de ce projet est de déterminer l'effet de l'éclaircie sur la résistance des arbres hôtes à la TBE. L'hypothèse soulevée dans ce projet est que l'éclaircie augmente la résistance des arbres à la tordeuse de bourgeons de l'épinette, mais que son impact varie avec le temps, la surface terrière prélevée dans le peuplement, la qualité de drainage du site et la diversité des espèces arborescentes présentes sur le terrain.

Objectif principal

Déterminer l'effet de l'éclaircie et de la qualité de drainage du site sur la résistance des arbres hôtes et sur la performance de la TBE.

Objectifs spécifiques

1. Évaluer les effets à court terme de l'éclaircie sur la résistance des arbres hôtes afin de déterminer si cette technique peut être utilisée pour atténuer les dommages causés par la tordeuse.

2. Évaluer les effets à moyen terme de l'éclaircie sur la résistance des arbres hôtes afin de déterminer si cette technique peut être utilisée comme une mesure de lutte préventive.

3. Évaluer les effets à long terme de l'éclaircie sur la résistance des arbres hôtes pour déterminer la durée de la période de résistance accrue.

4. Évaluer l'effet de la qualité nutritionnelle du feuillage des essences hôtes sur l'insecte et sa progéniture.

1.1 Cycle de vie de la tordeuse de bourgeons de l'épinette

La tordeuse des bourgeons de l'épinette est univoltine dans l'est du Canada. L'adulte émerge de la mi-juillet au début du mois d'août. Les femelles pondent leurs œufs sur le feuillage des conifères pendant une période de plusieurs jours. Après l'éclosion, les larves de premier stade se dispersent dans l'arbre hôte ou dans le peuplement, et même au-delà du site selon les courants du vent (Royama 1984). Ces larves de premier stade s'empressent de tisser un cocon de soie appelé hibernaculum, puis elles muent pour passer au deuxième stade larvaire. Elles entrent ensuite dans une période de diapause obligatoire qui dure jusqu'au printemps suivant. Au cours de cette longue période d'hivernage, les larves ne se nourrissent pas. Leur survie dépend exclusivement de la quantité d'énergie, sous forme de réserves, qui leur est fournie par leurs parents (Carisey et Bauce 2002). L'émergence des larves de deuxième stade coïncide généralement avec le gonflement des bourgeons et précède le débourrement de leurs principaux arbres hôtes, à savoir, le sapin baumier et l'épinette blanche (McGugan 1954, Greenbank 1963). Après l'émergence, les larves se dispersent à nouveau pour s'établir dans les sites où elles s'alimenteront sur les arbres hôtes. Elles se nourrissent des aiguilles de 1 à 2 ans ou des graines et des cônes de pollen lorsque ceux-ci deviennent disponibles. Ensuite, elles muent pour passer au troisième stade et continuent à s'alimenter avant que les bourgeons ne se développent (Royama 1984).

Du deuxième au cinquième stade larvaire, les larves restent similaires en apparence, mais leur couleur varie du gris au jaune. Le cinquième stade ne dure que quelques jours, mais il est très important dans le processus d'alimentation de l'insecte. À la fin de ce stade, la TBE modifie ses besoins nutritionnels. Quand elles muent pour passer au sixième stade larvaire, les larves ont besoin d'accumuler des glucides pour augmenter leur poids (Bauce et al. 2001). C'est à ce stade qu'elles consomment avidement le feuillage et sont les plus destructrices. À la fin du mois de juin, les larves cessent de s'alimenter et se transforment en chrysalides, généralement dans le vieux feuillage. Les papillons adultes émergent environ dix jours plus tard, c'est-à-dire de la fin juin à la mi-juillet. Enfin, les papillons s'accouplent et pondent leurs œufs, de préférence sur un arbre sain (Sanders 1991).

1.2 Résistance des plantes

La résistance des plantes aux herbivores comporte deux composantes : la défense et la tolérance (Bauce et al 2001, Haukioja et Koricheva 2001). La défense se réfère aux effets négatifs que la plante peut exercer sur l'insecte, soit en le dissuadant avec un trait de défense (dureté des structures végétales, la présence d'épines, la phénologie) ou en nuisant à sa performance (la croissance, la fécondité ou la survie) grâce à des composés chimiques consommés par l'insecte lorsqu'il dévore les feuilles de la plante (Bauce et al. 2001, Larsson 2002, Boege and Marquis 2005). La tolérance, pour sa part, se réfère à la capacité de la plante à supporter les dégâts engendrés par les insectes sans dommages graves ou réduction du fitness de la plante (Bauce et al. 2001, Haukioja et Koricheva 2001). Cette capacité devrait être un élément très important dans la résistance des plantes ligneuses, car les herbivores les repèrent facilement en raison de leur grande taille et de leur longévité (Feeny 1976). De plus, leurs mécanismes de défense ne peuvent pas empêcher complètement les dommages causés par les herbivores (Bauce et al 2001, Haukioja et Koricheva 2001).

Plusieurs études ont mis en évidence l'importance des composés secondaires dans la défense des plantes. La plupart des terpénoïdes ont des propriétés anti-appétantes et / ou répulsives (Awmack et Leather 2002), tandis que les composés phénoliques comme les tanins ont été reconnus comme des composés dissuasifs pour les herbivores (Feeny 1992). Les monoterpènes sont le groupe le plus abondant et le plus diversifié des métabolites secondaires des plantes (Kogan 1975). Alors que certains insectes sont spécialistes de plantes productrices de monoterpènes et sont capables d’utiliser ces composés pour aider d’autres individus de leur espèce à trouver la plante, la plupart des espèces d'insectes sont disuadées par leur présence (Lerdue et al. 1994). Les monoterpènes sont censés jouer un rôle important dans la résistance des arbres hôtes de la TBE (Mattson et al. 1991, Bauce et al. 1994, Kumbaşlı et al. 2011). Par exemple, certains monoterpènes peuvent affecter négativement la survie, l'ingestion de nourriture, le temps de développement et la masse de la chrysalide de la TBE (Mattson et al. 1991, Bauce et al. 1994, Bauce 1996, Kumbaşlı et al. 2011). Toutefois, certains de ces composés peuvent également avoir des effets positifs sur le comportement des insectes. Par exemple, les monoterpènes des hôtes semblent jouer un rôle dans la préférence des sites de ponte de la TBE (Städler 1974, Grant et al. 2007). Städler (1974) a signalé que la TBE a préféré pondre ses œufs sur des substrats de papier traités avec les terpènes (+)-α-pinène ou (-)-β-pinène, plutôt que sur les contrôles. Par ailleurs, les substrats traités avec (-)-α-pinène, qui est aussi un terpène présent dans le feuillage des essences hôtes, ou avec racémique α-pinène n’ont pas été acceptés.

Les tanins et les composés phénoliques ont longtemps été soupçonnés de jouer un rôle majeur dans la défense chimique des nombreuses essences forestières contre les herbivores. Ils sont connus pour protéger les plantes contre les insectes et les pathogènes (Feeny 1992). Cependant, il n'y a pas de consensus sur l'effet réel des tanins et aucune généralisation ne peut encore être faite. Certaines études soutiennent l'hypothèse que les tanins agissent comme une défense anti-herbivore en réduisant la consommation d'aliments (Reese et al. 1982). D'autres études suggèrent que la toxicité, plutôt que l'inhibition digestive, est le mode d'action (Berenbaum 1983). Enfin, certaines études ont démontré que les tanins n'ont pas d'effets détectables sur les herbivores (Ayres et al. 1997), ou encore qu'ils fonctionnent comme phagostimulants chez certaines autres espèces (Bernays et Woodhead 1982). Ces composés ont été signalés comme toxique pour la TBE. Kumbaşlı et al. (2011) ont constaté que des concentrations élevées de tanins augmentent la mortalité et le temps de développement et réduisent le poids des chrysalides de la TBE à de faibles concentrations d'azote. De leur côté, Delvas et al. (2011) ont rapporté que des phénols tels que le pungenol et le piceol réduisent la survie, retardent le développement et réduisent le poids des chrysalides de la TBE chez des individus résistants de l'épinette blanche. Les composés secondaires, par conséquent, semblent jouer un rôle important dans la défense des arbres hôtes contre ce ravageur forestier.

1.2.1 Résistance des principaux hôtes à l'attaque de la TBE

On a proposé que la TBE ponde ses œufs autant sur l'épinette blanche et l'épinette noire que sur le sapin baumier, et qu'elle complète son cycle vital sur ces trois essences (Nealis et Régnière 2004). Cependant, le degré de résistance de ces essences et les différences au niveau de la performance de la TBE entre ces trois arbres pourraient être influencés par les différences de synchronisation existant entre l'émergence des larves et la phénologie des arbres hôtes (Blais 1957, Mattson et al. 1991, Nealis et Régnière 2004). Le débourrement et l'allongement des pousses se produisent plus tard chez l'épinette noire que chez le sapin baumier et l'épinette blanche, ce qui pourrait la rendre plus résistante à la TBE (Blais 1957). Cette différence en résistance pourrait expliquer la perte de biomasse et la réduction de la croissance plus faibles chez l'épinette noire par rapport au sapin baumier (Henningar et al. 2008, Pothier et al. 2012). On a montré que la phénologie de débourrement affecte la performance des herbivores dans plusieurs systèmes insecte-arbre (Lawrence et al. 1997, Virtanen et Neuvonen 1999, Alfaro et al. 2000, Ostaff et al. 2000, Nealis 2012). Néanmoins, Lawrence et al. (1997) ont montré que le débourrement tardif (i.e., le débourrement se produisant plusieurs semaines après l'émergence des larves) n'affecte pas significativement la survie de la TBE chez l'épinette blanche. Par contre, le débourrement précoce (i.e., le débourrement se produisant avant ou durant l'émergence des larves) a dramatiquement affecté la survie et le poids de la TBE, étant donné que la larve commence à s'alimenter trop tard et ne profite donc pas du haut contenu en azote foliaire qui diminue rapidement durant et immédiatement après le débourrement. Les résultats rapportés par Lawrence et al. (1997) pourraient ainsi être expliqués par la capacité des jeunes larves à miner le feuillage des années passées pour consommer les tissus riches en azote se trouvant sous la couche extérieure de l'aiguille, laquelle présente un niveau bas d'azote, pour ainsi obtenir la quantité d'azote requise pour se développer (Trier et Mattson 1997). L'acquisition d'azote est plus importante que l'acquisition des sucres chez les jeunes larves (Albert et Bauce 1994), ce qui leur permet de survivre jusqu'à 4 semaines avant le débourrement (Trier et Mattson 1997).

La qualité nutritionnelle pourrait aussi jouer un rôle important dans la résistance de l'épinette noire. Par exemple, Thomas (1989) a montré que le feuillage de cette essence comme source de nourriture pour la TBE était moins approprié que celui de l'épinette rouge et de l'épinette blanche, en raison de la concentration élevée de composés secondaires dans son feuillage, ce qui influence de façon négative la performance de l'insecte. De plus, la chimie foliaire change au cours de la saison de croissance, démontrant une baisse graduelle de la qualité nutritionnelle pour la TBE, et ce, de façon variable entre les essences. Notamment la teneur en azote, nutriment limitatif important pour les insectes folivores, diminue plus rapidement au cours de l'été chez l'épinette noire que chez le sapin baumier (Chapitre 4), ce qui pourrait affecter la croissance de la TBE en fin de développement larvaire, selon sa synchronisation avec l'hôte. Alors, les différences au niveau de la qualité de la nourriture fournie par les essences hôtes peuvent affecter la dynamique des populations et les adaptations de la TBE (Carisey et Bauce 2002).

1.3 Facteurs qui affectent la résistance des plantes

1.3.1 L'éclaircie

L'éclaircie a été proposée comme outil sylvicole pour augmenter la croissance en diamètre des arbres résiduels et la disponibilité du bois serré, et pour réduire l'âge de rotation et les coûts de gestion, tout en améliorant la qualité et la valeur du peuplement (Pothier 2002). Par ailleurs, l'éclaircie peut modifier la température du sol et le taux de minéralisation (Thibodeau et al. 2000), la quantité de rayonnement et de précipitations atteignant le sol de la forêt (Pothier et Margolis 1991, Aussenac 2000), et l'activité biologique dans le sol (Piene et van Kleve 1978).

Cette technique sylvicole a également été recommandée pour réduire les dommages causés par les épidémies de TBE (Crook et al. 1979, Bauce 1996, Bauce et al. 2001) et de tordeuse de l’ouest (*Choristoneura occidentalis* Freeman) (Mason et al. 1992). Cependant, des études antérieures ont rapporté des résultats contradictoires. Piene (1989) a trouvé un pourcentage de défoliation et un taux de mortalité plus élevés dans les parcelles éclaircies par rapport aux parcelles non éclaircies. Ces observations pourraient être attribuées à des taux plus élevés de consommation du feuillage plutôt qu’à une augmentation de l'abondance de la TBE dans les parcelles éclaircies. MacLean et Piene (1995) en sont arrivés à la même conclusion, suggérant que l'éclaircie ne devrait pas être utilisée pendant les épidémies. En effet, sa mise en place permettrait à la TBE d'infliger des dommages plus importants sur les peuplements, ce qui se traduirait par une réduction de la croissance et du volume commercialisable dans le peuplement.

L’application combinée de l’éclaircie et des traitements de fertilisation peuvent créer des conditions plus favorables pour le développement de la TBE, bien que les chercheurs n’aient pas été en mesure de séparer la part de chacun sur les dommages provoqués par ce défoliateur (Roberts et Chow 1977). Crook et al. (1979) n'ont pas trouvé d’augmentation de la défoliation dans les peuplements éclaircis, alors que Batzer (1967) a constaté que les peuplements témoins étaient plus fortement défoliés que les peuplements éclaircis. Selon des études menées sur le sapin poussant sur des sites de bonne qualité, Bauce (1996) et Bauce et al. (2001) ont signalé que des changements dans la chimie foliaire un an après l’éclaircie (réduction de 25% de la surface terrière) ont réduit l’antibiose et, par conséquent, la résistance des arbres hôtes à la TBE. Les effets positifs de l'éclaircie sur la production foliaire des arbres hôtes dans les années subséquentes donnent lieu à une tolérance et une résistance accrues contre cet insecte.

Selon Bauce et al. (2001), les résultats contradictoires des différentes études sont dus au fait que les effets de l’éclaircie évoluent dans le temps et varient selon l’âge du peuplement, la qualité de drainage du site et l’évolution épidémique de l’insecte où le traitement est effectué. Ainsi, selon le lieu et le moment (c'est à dire, avant ou pendant une épidémie) où le traitement est appliqué, son efficacité pour réduire les dommages provoqués par la TBE peut varier considérablement. Par exemple, un an après l'éclaircie, les arbres ont montré d'importants changements biochimiques foliaires. Il y a eu une réduction des monoterpènes foliaires dans le cas de l'éclaircie commerciale, alors qu'il y a eu une réduction de la quantité de tannins foliaires après l'éclaircie précommerciale (Bauce 1995). Ces modifications chimiques produisent des effets positifs chez la TBE : une augmentation de la consommation de feuillage dans le cas de l'éclaircie commerciale et une augmentation de la survie des larves dans le cas de l'éclaircie précommerciale), des défoliations massives et une diminution de la résistance des arbres hôtes. Néanmoins, les arbres réagissent à l'éclaircie en augmentant leur production foliaire quelques années après que le traitement ait été appliqué, soit deux ans dans le cas des éclaircies commerciales et trois ans dans le cas de l'éclaircie précommerciale. Cette augmentation de la production foliaire compense les effets positifs du traitement chez l'insecte (qui diminuent progressivement au fil du temps) et augmente la résistance des arbres hôtes à la TBE. Cette résistance dure plusieurs années (Bauce et al. 2001).

1.3.2 Effet de la diversité d'essences présentent dans le peuplement

La modification de la composition des peuplements de sapin baumier pures en les mélangeant avec des feuillus est considérée comme l'une des techniques sylvicoles importantes pour réduire la susceptibilité (probabilité d'être attaqué) et la vulnérabilité (probabilité de subir de dommages une fois attaqué) du sapin à la TBE (Westveld 1946, Blais 1983, Blum et MacLean 1984). Plusieurs études ont constaté que la présence d'essences non hôtes dans les peuplements influence le niveau de défoliation provoquée par la tordeuse (Bergeron et al. 1995, Su et al. 1996, Needham et al. 1999, MacKinnon et MacLean 2003). Afin de réduire la vulnérabilité du peuplement, Croome (1970) a indiqué que sa composition devait comporter entre 30% et 60% d'espèces non hôtes, tandis que van Raalte (1972) a suggéré que 50% du peuplement devait être composé d'espèces non hôtes. Blais (1958) a observé que la défoliation était plus faible dans les peuplements de conifères contenant des feuillus que dans les peuplements purs de conifères. Su et al. (1996) ont trouvé que la défoliation diminuait au fur et à mesure que l'on augmentait le contenu en feuillus. Les peuplements contenant de 0-20 % d'essences feuillues ont subis une défoliation de 58-71% par rapport à la défoliation de 12-15% subie par les peuplements contenant de 81-100% d’essences feuillues. Crook et al. (1979) ont déterminé que la défoliation diminue lorsque la surface terrière des feuillus dans le peuplement est supérieure à 10 m2/ha. Needham et al. (1999) ont constaté que la quantité optimale de feuillus dépend du pourcentage de défoliation. À des niveaux élevés de défoliation, le contenu optimal en feuillus est d'environ 50% du volume sur pied initial. Ces résultats suggèrent que l’utilisation des peuplements mixtes pourrait potentiellement réduire les pertes de volume de sapin baumier dans des zones affectées par des épidémies sévères et fréquentes de la TBE.

Le mécanisme qui permet aux peuplements mixtes de réduire les dommages provoqués par la TBE est à la fois lié à une plus grande diversité et à des densités plus élevés d'ennemis naturels (Kemp et Simmons 1978, Capuccino et al. 1998). En effet, un plus fort contenu en feuillus réduit l'approvisionnement alimentaire et augmente la diversité des plantes, ce qui augmente la quantité d’ennemis naturels de la tordeuse (Capuccino et al. 1998). Par exemple, certains parasitoïdes comme *Meteorus trachynotus*, peuvent hiverner sur les larves de lépidoptères qui se nourrissent de feuillus lorsque la tordeuse n’est pas présente dans le peuplement (Maltais et al. 1989). En outre, les peuplements mixtes ayant une plus grande diversité de plantes à fleurs, qui représentent des sources importantes de nectar pour les parasitoïdes, ont subi moins de dommages causés par la tordeuse (Simmons et al. 1975).

D'autres explications possibles pour l'abondance de la TBE et les dommages qui en résultent dans les peuplements mixtes sont la mortalité provoquée par la dispersion des larves et l'accessibilité à l’hôte. La mortalité liée à la dispersion peut être plus élevée dans les peuplements mixtes, car il y a une plus grande probabilité que les larves en dispersion viennent s’échouer sur des arbres non hôtes (Kemp et Simmons 1979). En plus, il devient plus difficile pour les ravageurs forestiers de trouver un arbre hôte dans les peuplements mixtes parce qu'ils peuvent être physiquement cachés. Finalement, la dispersion des larves de la TBE est perturbée lorsque les arbres hôtes se développent sous un étage supérieur (overstory) dominé par les feuillus (Batzer et al. 1987). Bergeron et al. (1995) ont suggéré qu'un étage supérieur de feuillus dans le peuplement pourrait empêcher les femelles de la tordeuse de trouver et de coloniser les conifères du sous-étage.

1.3.3 Effet de la qualité de drainage du site

Les épidémies d'insectes défoliateurs sont souvent associées à des peuplements forestiers poussant dans des sols bien drainés et de mauvaise qualité (Mason et Tiger 1972, Mattson et Addy 1975, Mattson et Haack 1987). Les conditions du site déterminent le nombre d'espèces hôtes présentes (Mason & Tigner 1972), le type et l'abondance des ravageurs qu'on y trouve (Mason et Tigner 1972, Bevan et Stoakley 1985), et la qualité du feuillage des essences poussant dans le site (Mattson et Haack, 1987). En outre, la qualité de drainage du site a été identifiée comme la variable la plus importante affectant la croissance et la composition de la forêt boréale de l'Est du Canada (Bélanger et al. 1995). Plusieurs auteurs ont examiné la vulnérabilité des arbres hôtes à la tordeuse à l'égard de ce facteur (Hix et al. 1987, MacLean et Ostaff 1989, Archambault et al. 1991, Dupont et al. 1991, Bergeron et al. 1995, MacKinnon et MacLean 2003). Hix et al. (1987) ont constaté que le sapin baumier a subi une mortalité plus élevée sur les sites à drainage imparfait ou mauvais par rapport aux sites bien drainés. En revanche, l'épinette noire a été gravement endommagée sur les sites excessivement drainés. Archambault et al. (1991) ont observé que la mortalité du sapin baumier et de l'épinette blanche était plus élevée sur les sites à drainage imparfait ou mauvais. Dupont et al. (1991) ont constaté que les sites moins productifs (xériques et hydriques) montrent une mortalité plus grande du sapin baumier par rapport aux sites plus productifs (mésiques et subhygriques avec seepage). Cette observation par le fait que les arbres poussant dans les sites moins productifs ont des réserves d'énergie plus faibles, ce qui les rend plus vulnérables aux attaques des insectes (Dupont et al. 1991). En revanche, MacKinnon et MacLean (2003) ont constaté que les sapins poussant dans des sites riches et humides subissent une défoliation de 19% plus élevée que ceux poussant dans des sites pauvres et mal drainés. Enfin, MacLean et Ostaff (1989) et Bergeron et al. (1995) ont signalé qu'il n'existait aucune relation entre la qualité de drainage du site et la mortalité des arbres causée par la tordeuse.

2. Chapitre 1

Site factors and management influence short term host resistance to spruce budworm (*Choristoneura fumiferana* (Clem.)) in a species-specific manner.

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2.1 Résumé

Cette étude a examiné les interactions entre l'éclaircie et la qualité de drainage du site sur la résistance du sapin baumier (*Abies balsamea* (L.) Mill), de l'épinette blanche (*Picea glauca* (Moench) Voss) et de l'épinette noire (*P. mariana* (Mill.) BSP) à la défoliation provoquée par la tordeuse des bourgeons de l'épinette (TBE), *Choristoneura fumiferana* (Clem.) un an après le traitement. Pour estimer la résistance des arbres hôtes, la production foliaire et la consommation de feuillage des larves ont été déterminés afin de générer un indice de résistance visant à quantifier la quantité de feuillage résiduel disponible pour la photosynthèse après la défoliation. L'interaction entre l'éclaircie et la qualité de drainage du site a significativement affecté la résistance des arbres et la chimie foliaire chez le sapin baumier. La qualité de drainage du site a eu un effet significatif sur la performance de la TBE, la chimie foliaire, et la résistance du sapin baumier résistance à ce ravageur forestier, alors qu'aucun effet n'a été observé chez l'épinette blanche. L'éclaircie, pour sa part, a affecté la chimie foliaire du sapin baumier et de l'épinette blanche, mais aucun effet n'a été détecté sur l'épinette noire. Ces résultats montrent que l'éclaircie a réduit la résistance du sapin baumier aux attaques de la TBE un an après l'application du traitement. Cette réponse est liée à des baisses significatives de certains monoterpènes et à une diminution de la production de feuillage chez le sapin baumier, sauf dans le drainage hydrique, ce qui démontre l'importance de la qualité de drainage du site sur la résistance des arbres hôtes à la TBE. Nos résultats suggèrent que l'utilisation de *Bacillus thuringiensis* peut être nécessaire pendant les épidémies de TBE.

Site factors and management influence short term host resistance to spruce budworm (*Choristoneura fumiferana* (Clem.)) in a species-specific manner.

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Running title: Resistance to spruce budworm according to thinning intensity and drainage quality

2.2 Abstract

Background: This study examined the interactions between thinning and soil drainage classes on the resistance of balsam fir (*Abies balsamea* (L.)Mill), white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) BSP) to spruce budworm defoliation, *Choristoneura fumiferana* (Clem.) one year after treatment. To estimate host tree resistance, foliage production and larval foliage consumption were determined to generate an index of resistance quantifying the amount of residual foliage available for photosynthesis after insect defoliation.

Results: Significant interactions on tree resistance and foliage chemistry were detected between thinning and soil drainage in balsam fir. Drainage class affected spruce budworm performance, foliar chemistry, and balsam fir resistance to spruce budworm, whereas no effect was found in white spruce. Thinning had a significant effect on the foliar chemistry of balsam fir and white spruce, but no effect on black spruce.

Conclusion: Thinning reduced balsam fir resistance to spruce budworm defoliation. This response is due to increased defoliation linked to reduction in concentrations of certain monoterpenes, and a decrease in foliage production, except on hydric drainage, demonstrating the importance of drainage class to tree resistance. Our results suggest that the use of *Bacillus thuringiensis* might be required during spruce budworm outbreaks.

Key words: Thinning, drainage quality, spruce budworm, balsam fir, white spruce, black spruce

2.3 Introduction

Stand thinning has been proposed as a silvicultural tool to increase diameter growth of residual trees and saw timber availability, and to shorten rotation age and management costs, while enhancing stand value and quality.[1] At the same time, thinning can alter soil temperature and mineralisation rates,[2] the amount of radiation and precipitation reaching the forest floor,[3,4] and biological activity in the soil.[5]

Thinning has been also recommended for reducing damage caused by outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.))[6-8] and western spruce budworm (*C. occidentalis* Freeman).[9] Previous studies, however, have reported contradictory results. Piene[10] found higher defoliation and mortality rates in thinned plots compared to unthinned plots, which could be attributed to higher feeding rates rather than higher spruce budworm abundances in thinned plots. MacLean and Piene[11] arrived at the same conclusion, further suggesting that thinning should not be used during outbreaks, since its implementation would allow spruce budworm to inflict greater damage on stands, resulting in lower growth rates and merchantable volumes.

Combined thinning and fertilisation treatments can create more favourable conditions for spruce budworm development, but researchers have been unable to separate effects that each treatment exertes on budworm damage (Roberts and Chow, 1977, cited by Crook *et al.*[6]). Crook *et al.*[6] did not find increase in defoliation in thinned stands, whereas Batzer[12] found that control stands were more heavily defoliated than thinned stands. From studies conducted on balsam fir (*Abies balsamea* (L.) Mill)) growing on good quality sites, Bauce[7] and Bauce *et al.*[8] reported that changes in foliar chemistry one year after thinning (25% reduction of basal area) reduced antibiosis and, consequently, host tree resistance against budworm. Positive effects of thinning on host tree foliar production in subsequent years resulted in increased tolerance and resistance against this insect.

Soil drainage class has been reported as the most important variable affecting growth and composition of boreal forest stands in eastern Canada.[13] Several authors have examined host tree vulnerability to spruce budworm with respect to this factor.[14-19] Hix *et al.*[14]

found that balsam fir suffered greater mortality on soils with moderate to poor drainage than on well-drained sites; in contrast, black spruce (*Picea mariana* (Mill.)) was severely damaged on excessively drained sites. Archambault *et al.*[16] observed that mortality of balsam fir and white spruce (*P. glauca* (Moench) Voss) was greater on sites with imperfect or bad drainage. Dupont *et al.*[17] found that less productive (xeric and hydric) sites sustained greater balsam fir mortality than the most productive sites (mesic and subhygric with seepage). This response may be due to trees having lower energy reserves, thereby making them more vulnerable to insect damage.[17] In contrast, MacKinnon and MacLean[19] found that balsam fir on moist-rich sites sustained 19% greater defoliation than on wet-poor sites. Finally, MacLean and Ostaff[15] and Bergeron *et al.*[18] reported no relationship existed between soil drainage and tree mortality caused by spruce budworm.

White and black spruces are less vulnerable to spruce budworm compared to balsam fir. A clear hierarchy of host species susceptibility exists, with balsam fir being the most susceptible, followed by white and black spruce.[20] White spruce shoots grow faster, show greater development, and produce more foliage per unit area relative to those of balsam fir, resulting in reduced defoliation of the former.[21] Late season opening of black spruce buds,[22] together with the inadequacy of its foliage as a food source for young larvae,[21] have been suggested as factors responsible for the relative resistance of this species.

Thinning (25% basal area removed)[7,8] and drainage[14,16,17,19] each affect balsam fir resistance to spruce budworm. The manner in which these variables interact and how they interact with the other principal budworm host species (white spruce and black spruce) remains to be documented. We hypothesised that thinning would increase host tree resistance to spruce budworm, but its impact would vary over time and according to differences in thinning levels, site quality, and host tree species. Our objective was to determine the effects of thinning and site drainage quality on balsam fir, white spruce and black spruce resistance to spruce budworm one year after treatment.

2.4 Methods

2.4.1 Field sites and insect rearing

We conducted our research in the Montmorency experimental forest, 60 km north of Quebec City, Canada. This forest is typical of the Laurentide-Onatcheway region,[23] and most of the stands fitted Grandtner's[24] description of the balsam fir-white birch association. Budworm field-rearing experiments, along with foliar chemical analyses along a gradient of stand thinning density and site drainage quality, were conducted to elucidate the effects of these two variables on host tree resistance and insect performance.

Forty plots (2 ha each) were established to evaluate thinning and drainage class quality effects on spruce budworm and host performance. Field work was conducted along a gradient of stand thinning intensity (0%, 25%, and 40% stand basal area removed) and drainage class (mesic with seepage, class 3; subhygric, class 4; and hydric, class 5). Belanger et al.[25] should be consulted for further details regarding drainage class. Thinning intensities and selected drainage classes were chosen for their feasibility, considering both the risks of windthrow damage when stand openings were too pronounced and operational constraints in terms of slope angle that were too pronounced to allow thinning, i.e., slopes in rapidly drained class 2 sites. We used a completely randomised factorial layout with three levels of soil drainage, three intensities of thinning and four replicates of each treatment combination (36 experimental units, i.e., the 2-ha plots). Four additional experimental units were established in the rapidly drained site to document site effects over the entire range of conditions in which spruce budworm occurs.

In each experimental unit and for each host tree species, two dominant or co-dominant trees were randomly selected (balsam fir: 40 experimental units x 2 = 80; white spruce: 28 experimental units x 2 = 56; black spruce: 12 experimental units x 2 = 24). On each tree, two 75-cm-long branches were selected on the north-northwest side of the tree, at mid-crown level. Each branch was enclosed within a fine-mesh cloth sleeve cage (100 cm x 75 cm), which served as an enclosure for 20 post-diapausing second-instar larvae. Sites were free of local spruce budworm populations. Larvae used in the experiments originated from a colony maintained at Laval University (Laboratory of Forest Entomology) for the last seven years, with introductions from wild populations at three-year intervals. To simulate normal field emergence from winter diapause, the insects were placed in the field cages when 150 degree-days had been attained, i.e., two to three weeks prior to budbreak in the study area (base temperature: 2.7°C). Branches were cut and brought to the laboratory when budworms had pupated. The dry mass of frass produced in each rearing sleeve cage was recorded, larval mortality was determined, pupae were sexed and weighed using an electronic balance (MC 1 Analytic AC 210 S, Sartorius; 10 µg accuracy), and moth emergence was monitored every 8 h. Results from an earlier study on spruce budworm food utilisation that combined laboratory and field-rearing experiments indicates that this approach provides an accurate estimate of frass production.[26]

2.4.2 Defoliation and residual foliage

On each 75-cm-long branch, the total amount of current-year foliage produced, current-year foliage destroyed by larvae, and residual current-year foliage remaining on each branch after budworm defoliation (index of resistance, a net result of antibiosis and tolerance) were assessed by: (1) determining, for each tree, the number of needles cm^{-1} of current-year twigs, and mean needle dry mass; (2) measuring total length of current-year twigs; (3) measuring the length of defoliated twigs; (4) converting cm of twigs to number of needles; and (5) converting needle numbers to foliar mass.[7]

2.4.3 Foliar chemical content

For foliar chemical analysis, we collected branches from each tree that had been selected in field-rearing twice during the growing season. Foliar chemistry was determined on each sample tree using two randomly selected, north-northwest-facing mid-crown branches, which were neither used for field insect rearing nor infested with budworm. The first branch collection was done 15 days after insect installation (21-25 June), and the second when budworm infested-branches were collected (at pupal stage; 16-22 July). Fresh foliage (3 g) was collected on each sample tree (n = 160 samples per collection date), returned to the laboratory on dry ice, flash-frozen in liquid N_2, freeze-dried, ground in a Wiley mill (at -30°C to avoid polyphenolic deterioration), and maintained at -20°C until they were analysed for protein, mineral nutrients (P, K, Ca, Mg), total soluble sugars, total tannins, hydrolysable and condensed tannins, and total phenolic contents. Assays were conducted using methods described by Bauce[7] and Bauce *et al.*[27] Moisture content was determined on two subsamples of 15 current-year twigs. Two additional subsamples of fresh twigs were collected from each tree, placed in crimp seal vials, and kept at -20°C until needle monoterpene concentrations were analysed via gas chromatography, as described by Bauce *et al.*[25] Extracts were injected in a Varian GC3900 gas chromatograph equipped with a flame ionisation detector and a 30m x 0.25mm fused silica capillary column (Supelco SPB-5), and running Galaxy Workstation software (Varian Canada, Mississauga, ON).

2.4.4 Host tree growth and vigour

Host tree growth and vigour were determined one year after treatment on two sample trees in each experimental unit using a Pressler probe (increment borer). The vigour or growth efficiency index was expressed as basal area of current-year wood produced per unit sapwood area. [28]

2.4.5 Winter biology of budworm progeny

Adults obtained from the field-rearing experiment were mated to obtain the F1 generation. In each experimental unit and for each host tree species, 15 individual mating pairs were formed. The number of eggs laid by each female during its lifetime, the number of fertile eggs, first-instar larvae survival, and the subsequent number of second-instar larvae entering diapause were recorded. Larvae were placed in an outdoor insectarium during their winter diapause and winter survival was evaluated the following spring.

2.4.6 Statistical analyses

The experimental design was adapted to separately test the interactions of main effects (drainage, thinning) for each host species. The primary spruce budworm host (balsam fir) was present in all 40 experimental units. White spruce were selected in drainage class 2, 3 and 4, while black spruce, which grows only on drainage class 5 in the ecological domain that we studied, was selected in this drainage class. Statistical analyses were performed for an incomplete split-plot complete randomised factorial design with 4 replicates, with block(drainage) as the error term. Whole plots corresponded to drainage class (4 levels), and sub-plots to thinning treatments (3). Since black spruce could only be found in drainage class 5, it was necessary to replace a main experimental design factor (drainage) with the factor "species." Here, whole plots corresponded to species (black spruce vs. balsam fir), with block(species) as the error term (Table 2.1). The incomplete block structure was due to the inability to thin on drainage class 2.

Table 2.1 ANOVA table for each tree species

Balsam fir		White spruce		Black spruce	
Drainage	3	Drainage	2	Species	1
Bloc(Drainage)	12	Bloc(Drainage)	9	Bloc(Species)	6
Thinning	2	Thinning	2	Thinning	2
Thinning*Drainage	4	Thinning*Drainage	2	Thinning*Species	2
Error	18	Error	12	Error	12
Total	39	Total	27	Total	23

Normality and variance homogeneity tests were performed and the data were subjected to multivariate analysis of variance (MANOVA) on each of the following groups of variables: spruce budworm biological performance (i.e., pupal mass, developmental time, frass production, insect survival); winter biology of budworm progeny (i.e., winter survival, number of eggs laid, mean mass of eggs, number of infertile eggs); host tree monoterpenes, host tree tannins and phenols, and nutrients (i.e., N, P, K, Ca, Mg, and sugar concentrations); and host tree response variables (i.e., vigour index, defoliation, foliage produced, foliage destroyed, residual foliage, diameter at breast height (DBH) and sapwood increment). MANOVA was performed separately for each needle collection of host tree monoterpenes, tannins and phenols, and nutrients. The large number of variables in these groups, compared to the relatively small number of repetitions, did not permit the use of MANOVA on the entire data set. Black spruce monoterpenes were divided into two groups because there were insufficient degrees of freedom (*df*) to perform MANOVA on a single group. The first group corresponded to monoterpenes reported as budworm oviposition stimulants in the literature (group 1: α-pinene, β-pinene, limonene, myrcene, thujone),[29-31] whereas the second group corresponded to monoterpenes reported as being toxic to the insect (group 2: camphene, terpinolene, δ-3-carene, bornyl acetate, borneol).[26,32,33] If MANOVA found a significant effect in a group of variables, data from that group were analysed using Analysis of Variance (ANOVA) to determine which variables were affected by the factors studied (Table 1). Duncan's test was used for comparison of means. Finally, the effect of foliar chemistry on insect performance was analysed using correlation analysis (PROC GLM).[34]

Table 2.2 Multivariate analysis of variance (MANOVA) for A) balsam fir (*A. balsamea*) and B) white spruce (*P. glauca*) groups of variables. P-values and *df* for Wilks' Lambda test (*df* numerator, *df* denominator) from MANOVA with block(drainage) as error term. Numbers in bold indicate statistically significant effects at P=0.05.

A) Balsam fir

	Insect performance[1]		Tree response[2]		Monoterpenes				Tannins and Phenols				Nutrients[3]				Overwintering[4]	
Source					Collection1		Collection2		Collection1		Collection2		Collection1		Collection2			
	P	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*
Drainage	**<0.02**	18,20	**<0.04**	18,20	**<0.01**	30,9	0.9959	30,9	**<0.04**	9,24	**<0.02**	12,24	0.12	18,20	**<0.03**	18,20	0.31	10,16
Thinning	0.82	12,14	0.23	12,14	**<0.01**	20,6	0.6759	20,6	0.31	6,20	0.73	8,18	0.30	12,14	0.19	12,14	0.44	15,22
Drainage*Thinning	0.81	24,25	**<0.03**	24,25	**<0.01**	40,13	0.9934	40,13	0.22	12,26	0.07	16,28	0.66	24,25	0.20	24,25	0.83	20,27

B) White spruce

	Insect performance[1]		Tree response[2]		Monoterpenes				Tannins and Phenols				Nutrients[3]				Overwintering[4]	
Source					Collection1		Collection2		Collection1		Collection2		Collection1		Collection2			
	P	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*
Drainage	0.30	12,8	0.20	12,18	0.44	20,6	0.27	18,2	0.76	6,14	0.23	8,12	0.53	12,8	0.87	12,8	0.16	10,10
Thinning	0.29	12,18	0.42	12,18	0.15	16,4	0.23	18,2	0.61	6,14	0.67	8,12	0.50	12,8	**<0.04**	12,18	0.08	10,10
Drainage*Thinning	0.37	12,8	0.50	12,2	0.20	16,4	0.76	18,2	0.39	6,14	0.15	8,12	0.82	12,8	0.07	12,18	0.05	10,10

[1] Vigour index (basal area of current-year wood produced per unit sapwood area), defoliation (%), foliage produced, foliage destroyed, residual foliage, DBH and sapwood increment.

[2] Pupal mass, developmental time, frass production and survival.

[3] Concentration of N, P, K, Ca, Mg and sugars.

[4] Winter survival, number of eggs laid, mean mass of eggs, number of infertile eggs.

2.5 **Results**

2.5.1 Field-rearing

Drainage class affected the overall suite of performance indicators for insects reared on balsam fir (Table 2.2A); individually, male mass ($F_{(3,12)}$= 5.27, P=<0.02), female mass ($F_{(3,12)}$= 6.67, P=<0.01) and male developmental time ($F_{(3,12)}$= 6.62, P=<0.01) were significantly affected by drainage class. Mean masses for both males and females were higher on drainage class 3 compared to drainage class 5 (Figure 2.1A). Male developmental time was shorter on drainage class 2 and longer on drainage class 4 (Figure 2.1B). However, drainage class did not influence the overall performance of insects reared on white spruce (Table 2.2A).

Unlike drainage class, thinning intensity did not directly affect budworm performance on balsam fir, and white spruce (Table 2.2B) and black spruce (Wilks' Lambda: $F_{\text{thin}(12, 2)}$= 0.25, P=0.9534). Because insect survival was not affected by the treatment, the response regarding foliage destroyed is a good indicator of spruce budworm performance, which indicated that thinning stimulated larval food ingestion in balsam fir, and the response varied by drainage class (Figure 2.2).

Finally, there was a significant correlation between male mass and nitrogen (r=0.49; P=<0.01) and phosphorus (r=0.42; P=<0.01) concentrations on the second collection date. Also, male developmental time and bornyl acetate were significantly correlated (r = -0.38, $P < 0.02$) on the first collection date.

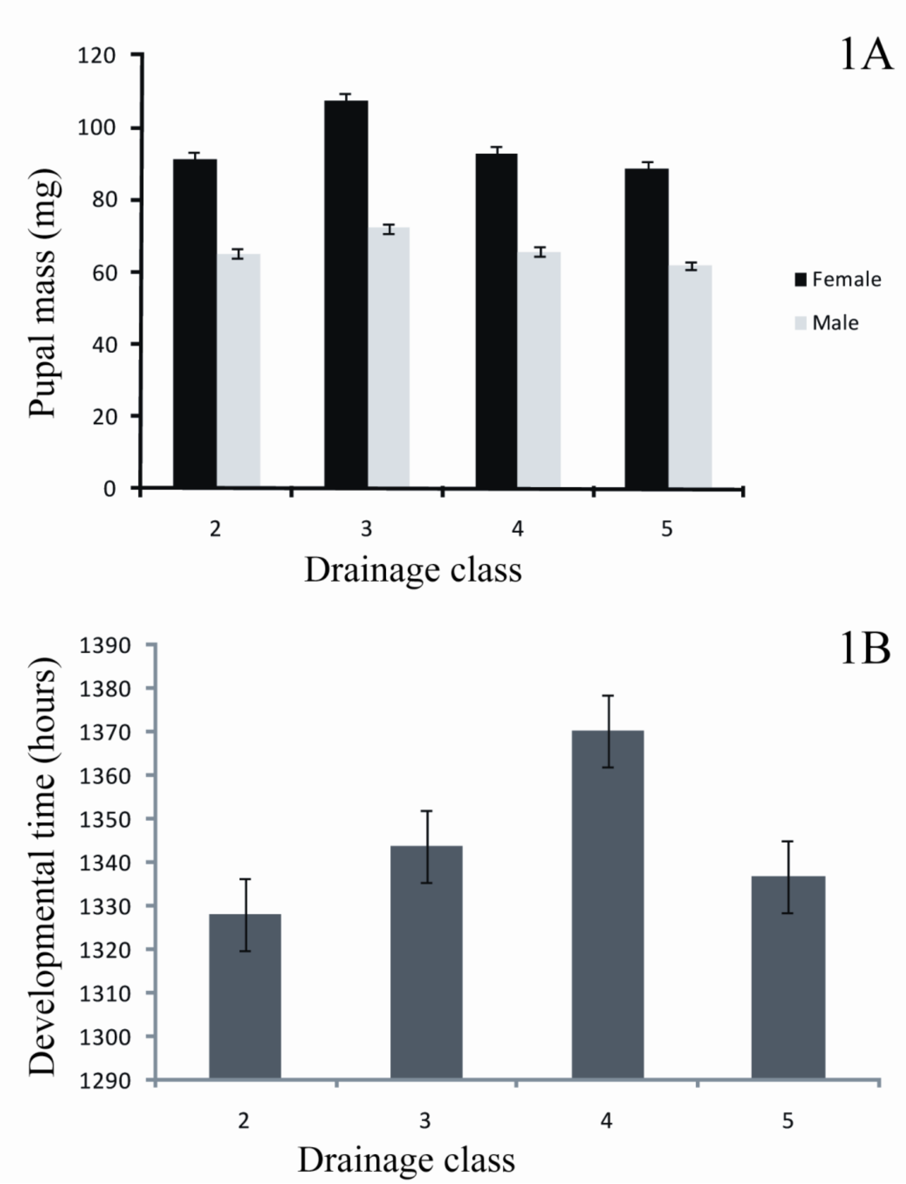

Figure 2.1. Female mass and male mass and male developmental time according to drainage class in balsam fir (*A. balsamea*) (Means ± 2SEM).

2.5.2 Host tree growth and vigour

Effect of thinning intensity on host tree growth and vigour depended upon both drainage class and host tree species, with balsam fir being the most negatively affected. Increased thinning caused the greatest increase in current-year foliage damaged by the budworm in fir, but the magnitude of the response depended on drainage class (thinning*drainage interaction) (Figure 2.2; Table 2.2A). In fact, thinning increased the quantity of foliage

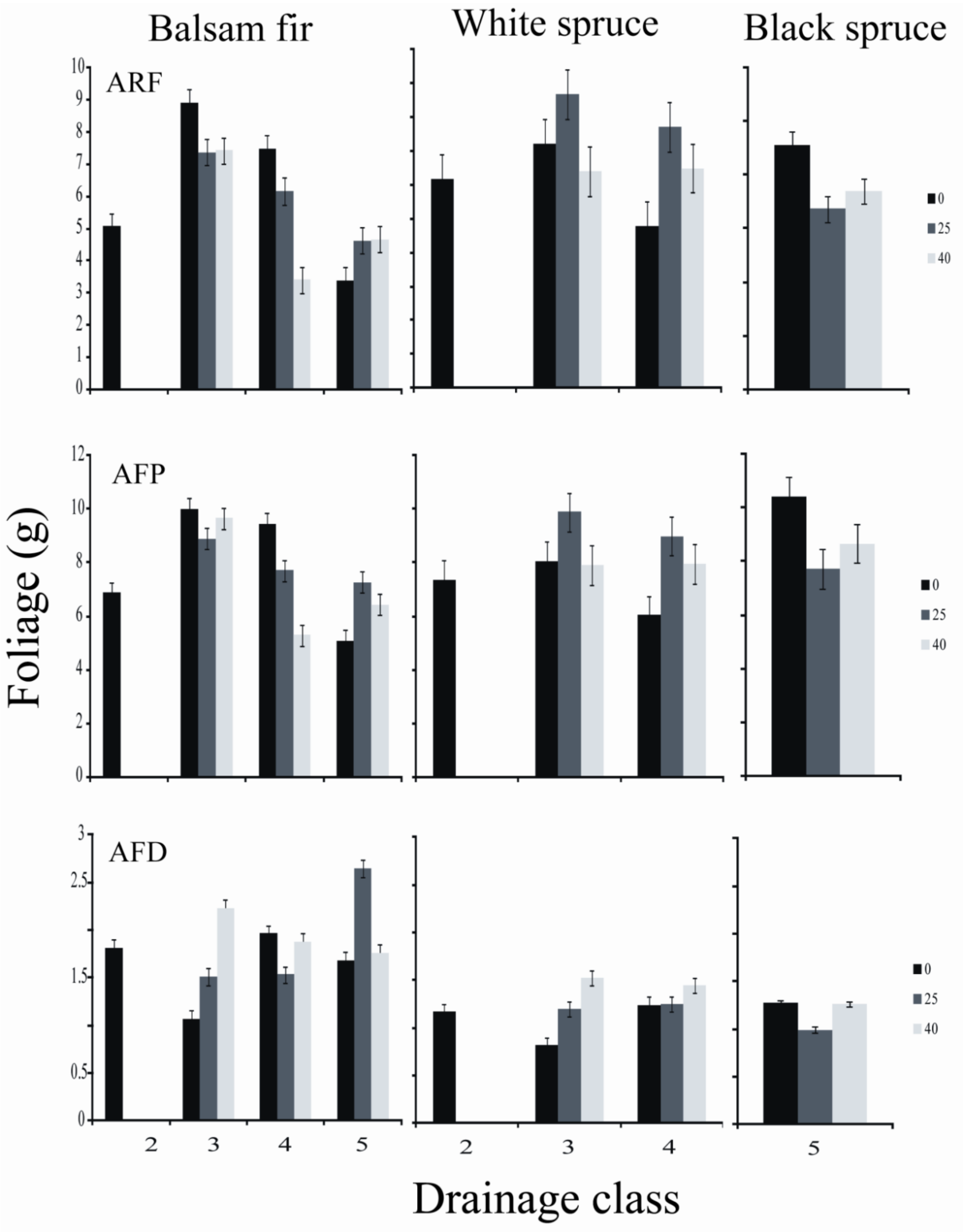

Figure 2.2 Amount of residual current-year foliage remaining (ARF), amount of current-year foliage produced (AFP), and amount of current-year foliage destroyed (AFD) tabulated by thinning intensity (0% unthinned; 25% basal area removed; 40% basal area removed), drainage class and host tree species (mean ± 2SEM).

destroyed ($F_{(4,18)}$= 8.92, P=<0.01) for drainage class 3, whereas foliage destroyed decreased by 21.9% as thinning intensity increased from 0 to 25%, and by 5.1% as thinning increased from 0 to 40% for drainage class 4. The opposite pattern was observed on drainage class 5. Furthermore, the joint action of thinning and drainage class affected defoliation percentage ($F_{(4,18)}$= 5.14, P=<0.01). Defoliation increased as greater thinning was applied, except for drainage class 5, which showed the opposite pattern (Figure 2.3).

Drainage class had a significant overall effect on balsam fir performance based on budworm defoliation effects (Table 2.2A). Trees growing on drainage class 3 had the greatest DBH compared to those growing on the other drainage classes ($F_{(3,12)}$= 12.38, P=<0.01). Both current-year foliage produced ($F_{(3,12)}$= 4.25, P=<0.03) and residual current-year foliage remaining after budworm defoliation ($F_{(3,12)}$= 5.50, P=<0.02) were highest on drainage class 3, decreasing as drainage quality worsened. Furthermore, foliage production decreased on drainage class 3 and 4 as thinning intensity increased, whereas the opposite pattern was observed on class 5. Variation in foliage production affected the amount of residual foliage (Figure 2.2), thereby resulting in a reduction in balsam fir tolerance and resistance to spruce budworm, except on drainage class 5 where the treatment increased resistance of this species. Neither thinning nor drainage class significantly affected white spruce growth and vigour (Table 2.2B), while black spruce was not affected by thinning (Wilks' Lambda: $F_{thin(12,2)}$= 1.34, P=0.50).

Finally, growth and vigour significantly differed between balsam fir and black spruce on drainage class 5 (Wilks' Lambda: $F_{species(6, 1)}$= 353.27, P=<0.05). Vigour index was higher for balsam fir than for black spruce, but the latter experienced significantly lower defoliation, and produced higher quantities of foliage and residual foliage than the former (Table 2.3).

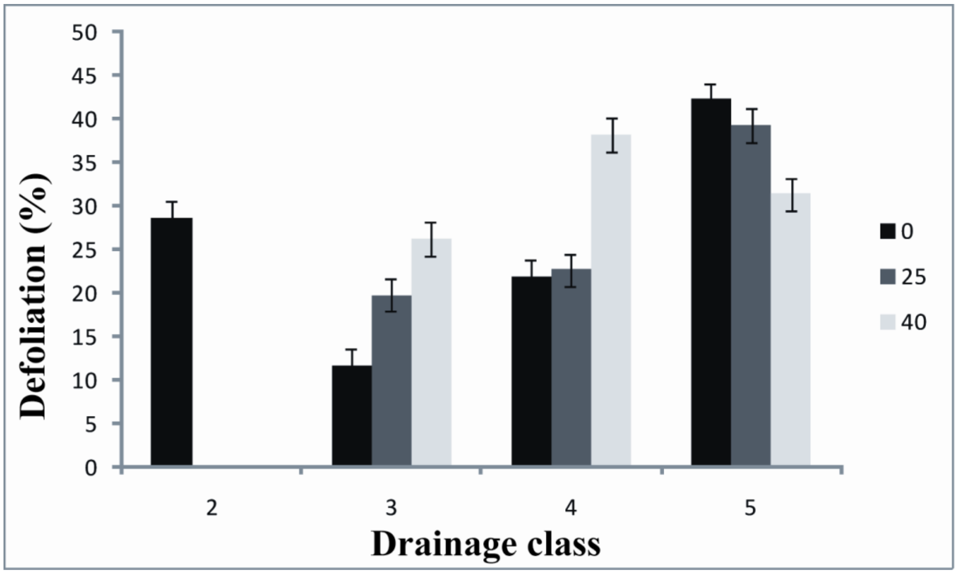

Figure 2.3 Defoliation tabulated by drainage class and thinning intensity (0% unthinned; 25% basal area removed; 40% basal area removed) in balsam fir (A. balsamea) (Means ±2SEM).

2.5.3 Foliar chemical content

Chemical analysis indicated that monoterpene concentrations in the first foliar collection were affected by drainage class, thinning and the interaction between these two factors in balsam fir (Table 2.2A). Concentrations of bornyl acetate ($F_{(4,18)}$= 10.82, P=<0.01) in drainage class 3 decreased as thinning intensity increased, whereas concentrations of this monoterpene in drainage classes 4 and 5 decreased as thinning intensity increased from 0 to 25%, but they increased as thinning intensity increased from 25 to 40% (Figure 2.4A).

Thinning*drainage class interaction was statistically significant for thujone ($F_{(4,18)}$= 3.78, P=<0.03), but there was no consistent pattern in its mean concentrations. Concentrations of thujone in drainage class 3 and 5 decreased as thinning intensity increased from 0 to 25%, but they increased in drainage class 3 as thinning intensity increased from 25 to 40%. Thujone was not detected on drainage class 4 and 5 when 40% of basal area was removed (Figure 4B). Similarly, concentrations of β-pinene and those of camphene were greatest on drainage class 3 and decreased as drainage quality worsened (Table 2.4). In contrast to the first collection, concentrations of monoterpenes were not affected by thinning intensity and drainage class in the second collection (Table 2.2A).

Table 2.3 Tree response for balsam fir (*A. balsamea*) and black spruce (*P. mariana*) on hydric drainage (Means ± SEM).

Parameter	Species				
	Black spruce	Balsam fir	*F*	*df*	*P*
Vigour index	0.06 ± 0.003	0.10 ± 0.012	6.7	1,6	<0.03
Defoliation (%)	18.28 ± 3.54	37.65 ± 2.51	19.65	1,6	<0.01
Foliage produced (g)	10.41 ± 0.73	6.26 ± 0.60	12.46	1,6	<0.01
Residual foliage (g)	9.13 ± 0.47	4.22 ± 0.48	12.46	1,6	<0.01

Concentrations of monoterpenes in white spruce foliage were affected by neither treatment nor drainage class in the first and second collections (Table 2.2B). With black spruce, thinning did not affect the monoterpene concentrations (Wilks' Lambda: $F_{group1(10, 4)}$= 2.99, P=0.15) (Wilk's Lambda: $F_{group2(10, 4)}$= 0.98, P=0.55) in collection one. The same results were observed in collection two (Wilks' Lambda: $F_{group1(10, 4)}$= 2.99, P=0.15) (Wilks' Lambda: $F_{group2(10, 4)}$= 0.98, P=0.55). Monoterpenes that acted as oviposition stimulants differed in their concentrations between black spruce and balsam fir, but only during the first collection (Wilks' Lambda: $F_{species1(5, 2)}$= 324.96, P=<0.01) (Figure 2.5).

Drainage class did not influence foliar nutrient concentrations of balsam fir during the first collection, but foliar nitrogen and phosphorus varied by drainage class in the second collection (Tables 2.2A and 2.4). Thinning did not affect foliar nutrients in fir on either collection date (Table 2A).

Foliar potassium in white spruce was reduced by thinning during the second collection ($F_{2,12}$ = 5.25, P=<0.03), decreasing by 13.23% as thinning intensity increased from 0 to 40%. Foliar concentration of nutrients were not affected by drainage class at either foliage collection for white spruce (Table 2B). Thinning also did not affect black spruce foliar nutrients (Wilks' Lambda: $F_{collection1(12,2)}$= 1.65, P=0.43) (Wilks' Lambda: $F_{collection2(12,2)}$= 11.39, P=0.08). Furthermore, foliar nutrient concentrations did not differ between black spruce and balsam fir (Wilks' Lambda: $F_{species1(6,1)}$= 36.02, P=0.12) (Wilks' Lambda: $F_{species2\ (6,1)}$= 113.12, P=0.07).

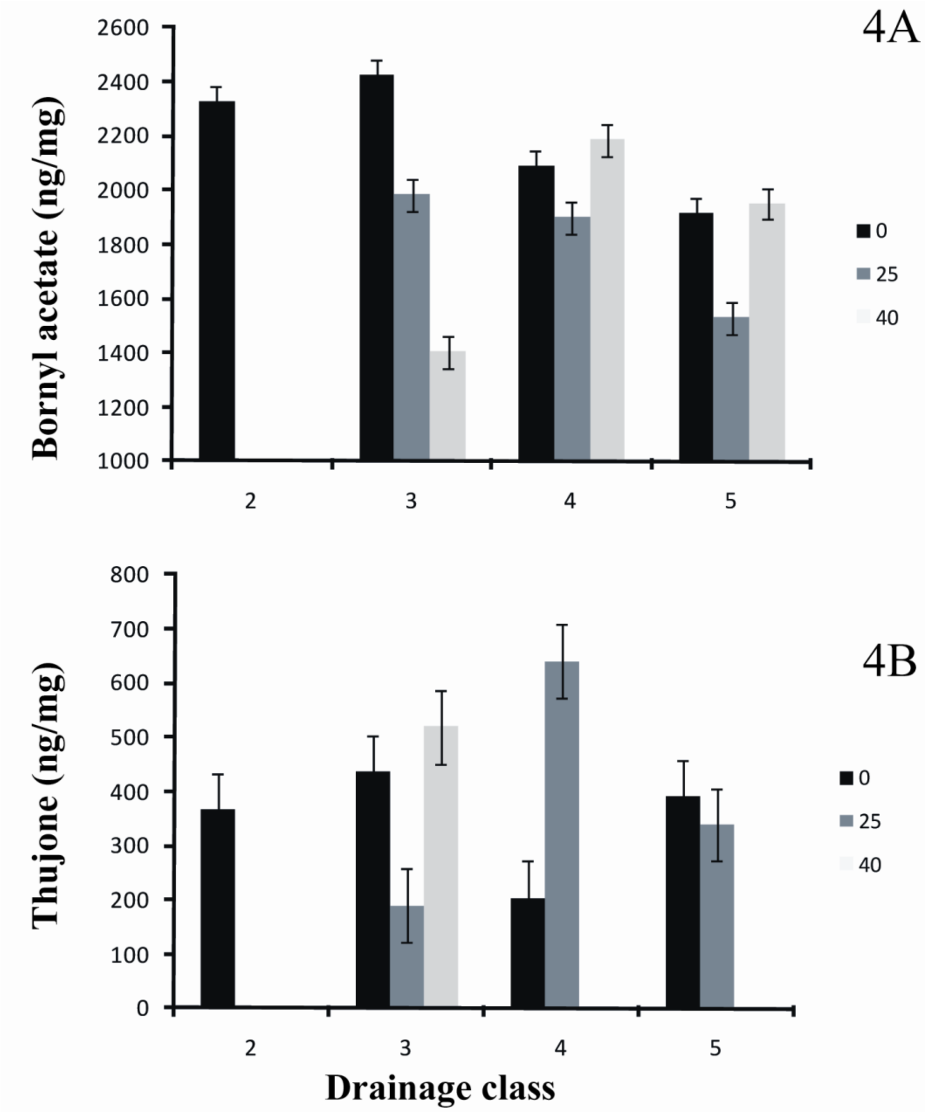

Figure 2.4 Foliar bornyl acetate and thujone concentrations by drainage class and thinning intensity (0% unthinned; 25% basal area removed; 40% basal area removed) (first needle collection) in balsam fir (A. balsamea) (Means ± 2SEM).

Tannin and phenolic concentrations were not affected by thinning in either collection of balsam fir needles, but they were affected by drainage (Table 2A). Total hydrolysed tannins were greater in foliage from fir trees growing in drainage class 5 during collection one, while they were greater on drainage class 4 during collection two. Total tannin concentrations were greatest in fir from drainage class 4 (Table 2.4).

Table 2.4 Nutrient, tannin, phenolic and monoterpene concentrations in balsam fir (*A. balsamea*) needles by drainage class (Means ± SEM).

Parameter	Drainage[1]							
	2	3	4	5	*F*	*df*	*P*	Collection
β-pinene (ng/mg)	5616 ± 483ab	6787 ± 437a	5886 ± 331ab	4487 ± 441b	5.94	3,12	<0.01	1
Camphene (ng/mg)	907.66 ± 41.99a	945.70 ± 61.72a	859.24±51.43ab	706.08 ± 38.19b	3.9	3,12	<0.03	1
N (μg/g)	1.527 ± 0.048b	1.761 ± 0.049a	1.524 ± 0.037b	1.395 ± 0.036b	14.69	3,12	<0.01	2
P (μg/g)	2165 ± 50a	2199 ± 92a	2022 ± 60a	1748 ± 61b	13.93	3,12	<0.01	2
Total hydrolysed tannins (cm2)	0.390 ± 0.004b	0.420 ± 0.019b	0.430 ± 0.009b	0.537 ± 0.023a	20.37	3,12	<0.01	1
Total phenolics (% dry mass)	0.596 ± 0.022b	0.590 ± 0.021b	0.590 ± 0.017b	15.354 ± 1.663a	15.5	3,12	<0.01	1
Total tannins (cm2)	16.32 ± 0.219a	14.87 ± 1.33a	17.03 ± 0.276a	0.418 ± 0.008b	136.24	3,12	<0.01	2
Total hydrolysed tannins (cm2)	13.70 ± 0.107a	12.98 ± 1.17a	14.43 ± 0.165a	0.63 ± 0.019b	78.44	3,12	<0.01	2
Total phenolics (% dry mass)	9.720 ± 0.657c	11.44 ± 0.361b	11.02 ± 0.376b	13.77 ± 0.269a	19.71	3,12	<0.01	2

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan multiple range test.

[1] Rapid drained soil (class 2), mesic with seepage (class 3), subhygric (class 4), hydric (class 5).

Tannins and phenolics were not altered by drainage class in either collection of white spruce needles. Moreover, their overall concentrations were not affected by thinning intensity in white (Table 2B) or black spruce (Wilks' Lambda: $F_{thin1(6,8)}$= 0.49, P=0.79) (Wilks' Lambda: $F_{thin2(8,6)}$=2.51, P=0.13). Finally, tannin and phenolic concentrations of black spruce and fir were similar (Wilks' Lambda: $F_{species1(3,4)}$= 5.27, P=0.07) (Wilks' Lambda: $F_{species2(4,3)}$= 0.99, P=0.52).

2.5.4 Winter biology of budworm progeny

Winter biology of budworm progeny was affected neither by thinning intensity nor by drainage class in balsam fir (Table 2.2A). A similar response was observed in both white (Table 2.2B) and black spruce (Wilk's Lambda: $F_{trait(10,4)}$= 1.12, P=0.49). Furthermore, the winter biology of budworm progeny was similar between black spruce and balsam fir (Wilk's Lambda: $F_{spe1(5,2)}$= 0.39, P=0.83) (Wilk's Lambda: $F_{spe2(4,3)}$= 0.99, P=0.52).

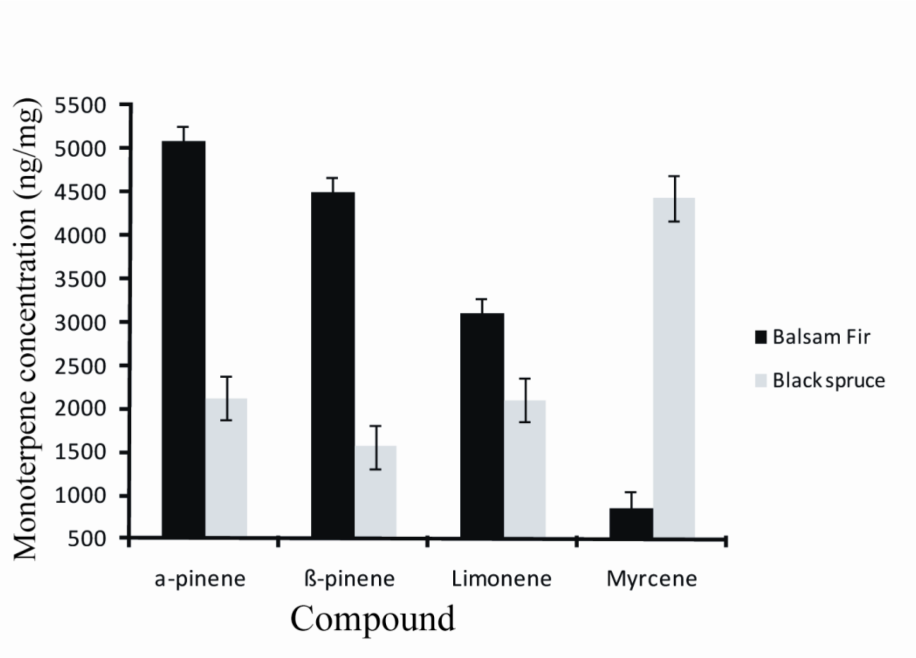

Figure 2.5 Oviposition stimulants foliar monoterpene concentrations (by tree species) occurring on drainage class 5 (first needle collection) (Means ± 2SEM).

2.6 Discussion

Previous studies have shown that host tree resistance to spruce budworm increases,[7,8,12] decreases[10,11] or remains unchanged after thinning.[6] We found that variation in bornyl acetate was associated with thinning, which could account for increased defoliation and the amount of current-year foliage destroyed. Our finding is consistent with previous studies, which have indicated that thinning altered monoterpene concentrations in balsam fir one year after its application.[7,8] This response may decrease balsam fir resistance to spruce budworm because monoterpenes negatively affect insect performance. For example, Mattson *et al.*[32] showed that spruce budworm larvae survival declined linearly with increasing log-dosages of camphor and bornyl acetate, while Bauce *et al.*[26] reported that high levels of monoterpenes accounted for low feeding rates of sixth-instar budworm fed foliage of young trees, compared with those fed foliage of old trees. Despland et al.[35] reported that spruce budworm larvae fed on foliage containing high level of monoterpenes exhibit longer intervals between meals, suggesting a toxic effect of these compounds. Furthermore, balsam fir was more vulnerable to spruce budworm one year after treatment because the former exhibited no increment in the quantity of foliage produced (Figure 2), consistent with a previous report by Bauce.[7] Nevertheless, we expected host chemistry to stabilise and foliage production to increase and, therefore, balsam fir resistance to increase from the third year post-treatment application.[8]

Increases in defoliation and the quantity of foliage destroyed can greatly affect balsam fir productivity[36] and survival[10,11] by reducing a tree's photosynthetic base. However, this response varied with drainage class (Fig. 2.2). Defoliation was higher on poorly-drained sites, and decreased as drainage improved (Fig. 2.3). This response is consistent with previous work,[14,15,17] which reported greater damage and mortality in balsam fir growing in poorly-drained soils than those growing in well-drained sites. Balsam fir is better adapted to grow in the latter sites,[14] which provide good oxygenation and additional water for the roots, thereby allowing trees to obtain the necessary nutrients to continue healthy development.[13] This ability decreases in poorly-drained soils. Adaptations of balsam fir may also explain the reduced defoliation percentage observed in hydric sites caused by thinning. The sylvicultural prescription reduced the number of trees competing for limited nutrients in these sites, thereby increasing foliage production and, therefore, balsam fir tolerance (Figure 2). This response shows that balsam fir positively reacted to thinning in hydric soil over the short-term, suggesting that the technique might be used to reduce budworm damage in these kinds of sites.

Foliar production was greatest in drainage class 3, resulting in a lower degree of defoliation and greater amount of residual foliage. Soil drainage quality has been positively related to foliar nitrogen, phosphorus and potassium levels;[37] therefore, sites with good drainage should allow trees to take up greater quantities of N and P than sites with poor drainage (Table 2.4). Because tree tolerance is related to the amount of residual foliage,[8] the highest foliar production in well-drained sites should increase balsam fir tolerance against spruce budworm in these sites. These results highlight the importance of considering drainage quality in planning thinning operations that reduce the economic impact of this insect because drainage can influence the effectiveness of the treatment.

Thinning did not directly affect spruce budworm performance, but it stimulated larval food ingestion in balsam fir. Piene[10] and Bauce[7] reported a similar response and concluded that thinning should be avoided during spruce budworm outbreaks because tree stress provoked by the treatment might render them more vulnerable to the insect. By contrast, drainage class directly affected pupal mass and male budworm developmental time. Higher masses were found in well-drained sites (Figure 2.1A), whereas faster development of males was found in poorly-drained sites (Figure 2.1B). Male pupal mass was positively correlated to nitrogen and phosphorus concentration, whereas male development time was negatively correlated to bornyl acetate concentration. The highest concentration of these nutrients was found on well-drained sites (Table 2.4). Nitrogen is growth-limiting nutrient; budworm pupal mass is reduced and development time is increased when the diet of this insect contains low N concentrations,[38,39] and phosphorus is positively correlated with increase in pupal mass,[40] while monoterpenes can negatively affect insect mass, developmental time and survival.[26,32,33] Kumbaşlı *et al.*[33] reported that monoterpenes had a negative effect on budworm performance and concluded that reduction in spruce budworm growth was due in great part to diversion of metabolic energy to reducing toxic effects of monoterpenes instead of using it to further insect development.

White and black spruces were not affected by the treatments tested in this study, but we did observe an interesting trend. White spruce produced more foliage in thinned stands than in unthinned stands, increasing residual foliage and, therefore, white spruce tolerance. By contrast, black spruce showed the opposite response (Fig. 2.2). One possible explanation to the lack of significant effect in these species is that thinning intensities used in this study were not heavy enough to rapidly enhance tree growth and vigour. Previous studies that reported considerably positive responses of white[41,42] and black spruce[43] used heavier thinning intensities, which may be responsible for rapid short-term responses, but lighter thinning intensities have been recommended over the longer term. The latter result in greater merchantable volume,[42] while avoiding risks that excessive removals may result in wind damage.[44] Consequently, we expect increased in resistance of these two species over the medium- to long-term, but the use of *Bacillus thuringiensis* Berliner ssp. *Kurstaki* (Btk) would be necessary to protect these species against spruce budworm in the short-term.

2.7 Conclusion

This study has demonstrated that resistance of balsam fir to spruce budworm, unlike white and black spruce, is significantly reduced one year after thinning (Fig. 2.2). This phenomenon is produced by increased defoliation linked to reduction in concentrations of certain monoterpenes and to decreased foliage production, except on drainage class 5, where the treatment increased fir resistance. Higher defoliations in thinned stands were not only due to concentration of budworm populations on fewer trees, but density-independent changes in interactions between spruce budworm and balsam fir. Therefore, it would not be advisable to conduct a thinning one year before or during a spruce budworm outbreak, unless this treatment is accompanied by aerial sprays of the microbial insecticide Btk. This insecticide can protect trees during this period of low resistance to the insect, since it prevents substantial balsam fir mortality and growth losses[45]. The effect caused by thinning is consistent with the findings of Piene[10], MacLean and Piene[11] and Bauce.[7] Furthermore, drainage class proved to be an important factor in balsam fir resistance to spruce budworm, because trees growing in well-drained sites produced more foliage and had greater concentrations of monoterpenes than those growing in sites with moderate to poor drainage, which allowed trees to cope better with attacks of this defoliator. Although white and black spruce were not significantly affected by the treatment, it would be convenient to conduct thinning after female moths finish laying eggs to avoid an excessive pressure of insects on the remaining trees. Finally, these results can aid forest manager in the planning of thinning and Btk aerial spray operations to reduce the economic impact of this insect. Further research is necessary to determine the medium-term effects of thinning and drainage class on host tree resistance to evaluate whether this silvicultural tool can be used as preventive control measure during the endemic phase of the budworm population.

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3. Chapitre 2

Soil drainage class, host tree species and thinning influence host tree resistance to the spruce budworm.

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3.1 Résumé

L’éclaircie a été souvent recommandée pour réduire les dommages causés par la tordeuse des bourgeons de l’épinette (*Choristoneura fumiferana* (Clemens)). On croit que cette technique améliore les mécanismes de résistance des arbres (antibiose et tolérance) à la tordeuse des bourgeons de l’épinette. Cependant, les résultats rapportés par les nombreuses études effectuées sur le sujet sont contradictoires. Une meilleure compréhension de l’effet de l’éclaircie sur la résistance des arbres et la performance de la tordeuse des bourgeons de l’épinette peut nous aider à réduire l’impact de ce ravageur tout en respectant l’intégrité écologique de la forêt. Cette étude se penche sur l’effet de l’éclaircie commerciale et de la classe de drainage de la station sur la résistance du sapin baumier (*Abies balsamea* (L.) Mill.), de l’épinette blanche (*Picea glauca* (Moench) Voss) et de l’épinette noire (Picea mariana (Mill.) Britton, Sterns & Poggenb.) à la tordeuse des bourgeons de l’épinette trois ans après l’application de l’éclaircie pour déterminer si l’on peut utiliser cet outil sylvicole comme mesure préventive. Des élevages de tordeuse des bourgeons de l’épinette sur le terrain et des analyses chimiques foliaires des essences hôtes ont été effectués en fonction d’un gradient d’éclaircie (0% (témoin), 25% (légère) et 40% (forte)) et de classe de drainage de la station (drainage rapide, classe 2; mésique avec drainage latéral, classe 3; subhygrique, classe 4; et hydrique, classe 5) dans la sapinière à bouleau blanc. L’éclaircie forte a amélioré la performance (poids des chrysalides) et la survie hivernale de la tordeuse des bourgeons de l’épinette. Par contre l’éclaircie forte a accru la tolérance (quantité de feuillage résiduel) du sapin baumier et de l’épinette blanche assez pour entraîner une augmentation de la résistance globale à l’insecte. Cette augmentation de résistance résulte d’une forte production de feuillage en réaction au traitement effectué trois ans auparavant. L’éclaircie légère n’a pas accru la résistance des arbres hôtes, sauf chez les tiges de sapin baumier et d’épinette blanche croissant respectivement dans les stations hydriques et subhygriques, démontrant ainsi l’importance de l’effet de cette variable sur la résistance des arbres hôtes. Ces résultats indiquent que l’éclaircie forte pourrait être utilisée comme mesure de lutte préventive pendant la phase endémique des populations de tordeuse des bourgeons de l’épinette car ce traitement a augmenté la production de feuillage chez le sapin baumier et l’épinette blanche, ce qui les rend plus résistants aux attaques de ce ravageur.

Soil drainage class, host tree species and thinning influence host tree resistance to the spruce budworm.

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3.2 Abstract

Thinning has frequently been recommended for reducing damage caused by spruce budworm (*Choristoneura fumiferana* (Clem.)). It is believed that this technique enhances the mechanisms of resistance of trees (antibiosis and tolerance) to this insect. However, various research projects that have focused upon effects of this silvicultural tool on host tree resistance have yielded equivocal results. A better understanding of the effects of this technique on host tree resistance and budworm performance can help us to reduce the impact of this insect while respecting the ecological integrity of the forests. We examined the effects of stand commercial thinning and drainage class on balsam fir (*Abies balsamea* (L.) Mill.)), white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) BSP) resistance to spruce budworm, *Choristoneura fumiferana* (Clem.), three years after thinning. We wanted to determine if this technique could be used as preventive tool against insect defoliators. Field-rearing experiments of spruce budworm were conducted, together with foliar chemical analyses, along a gradient of stand thinning intensity (0% (control), 25% (light), 40% (heavy)) and drainage class (rapidly drained, class 2; mesic with seepage, class 3; subhygric, class 4; and hydric, class 5). Despite having favoured budworm performance (high pupal mass) and winter survival, heavy thinning increased balsam fir and white spruce tolerance (amount of current-year foliage remaining) to a level that resulted in overall increased host tree resistance to the insect. This response was caused by strong foliage production in reaction to the thinning treatment. Light thinning did not increase host tolerance, except in balsam fir and white spruce that were growing on hydric and subhygric sites, respectively, demonstrating the importance of this variable in determining host tree resistance. These results suggest that heavy thinning may be used as a preventive measure during the low density phase of budworm populations, since this technique increased foliar production in balsam fir and white spruce, rendering them more resistant to attack by this insect.

Key words: Thinning, drainage quality, spruce budworm, balsam fir, white spruce, black spruce

3.3 Introduction

Outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) occur throughout North America's maritime and boreal forests, and usually last 5 and 20 years at the local and regional scale, respectively. Such outbreaks lead to a substantial decline in vigour and increased mortality of affected trees. During its last outbreak in the Province of Quebec (Canada), this insect caused about 500 million m^3 of wood fiber losses through mortality and growth reduction (Coulombe et al. 2004). Infestations of this irruptive forest defoliator occur periodically, with the last three outbreaks in the province being separated by intervals of about 30 years. A new outbreak is currently developing in various regions of Quebec affecting over 1.6 million hectares in 2011 (MRNF, 2011), thereby compromising the wood supply for the province's forest industry.

Forest manipulations using silvicultural prescriptions represent an attractive approach to forest pest management because they may be less expensive than pesticide treatments, effective, long-lasting, and have low environmental impact (Muzika and Liebhold 2000). Thinning has been recommended to reduce damage caused by spruce budworm (Crook et al. 1979, Bauce 1996, Bauce et al. 2001) and western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks (Mason et al. 1992). However, various research projects that have focused upon effects of this silvicultural tool on host tree resistance have yielded equivocal results. Previous studies have demonstrated that resistance to spruce budworm may increase (Batzer 1967, Bauce 1996, Bauce et al. 2001, D'Amato et al. 2011), decrease (Piene 1989, MacLean and Piene 1995), or remain unchanged (Crook et al. 1979) after thinning. According to Bauce et al. (2001), these contradictory results could result from variation in the treatment effect over time and be due to differences in stand age, soil drainage, host tree species, and site quality. Thus, depending upon where and when (i.e., prior to or during an outbreak) the treatment is being implemented, its effectiveness in limiting spruce budworm damage could be quite different.

From a study conducted in balsam fir (*Abies balsamea* (L.) Mill.)) stands growing on good quality sites, Bauce (1996) and Bauce et al. (2001) reported that changes in foliar chemistry one year after thinning (25% stand basal area removal) reduced antibiosis and, consequently, host tree resistance against spruce budworm. The authors observed reductions in the concentrations of certain monoterpenes, which have been reported as toxic to spruce budworm (Mattson et al. 1991, Bauce et al. 1994, Kumbaşli et al. 2011). This variation in foliar chemical content was related to positive effects on insect performance, such as shorter developmental times and faster foliage consumption rates (Bauce 1996).

The earlier results concur with those reported by Fuentealba and Bauce (2012a). These authors evaluated the short-term effects of thinning and drainage class on balsam fir, white spruce, and black spruce resistance to spruce budworm. They found that, unlike white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) BSP), balsam fir resistance to spruce budworm was significantly reduced by thinning one year after treatment was carried out. This phenomenon resulted from an increase in defoliation that was linked to reduction in certain monoterpene concentrations and to a decrease in foliage production, except on hydric drainage sites where the treatment increased the resistance of this species. The decrease in monoterpenes resulted in shorter male developmental times and greater pupal mass. They concluded that thinning one year before or during a spruce budworm outbreak was not advisable, unless this treatment was accompanied by aerial spraying with the microbial insecticide *Bacillus thuringiensis* Berliner ssp. *kurstaki* (Btk) to protect trees during this period of low resistance to the insect. These results confirm that thinning cannot be used to mitigate damage during an outbreak. However, we hypothesize that thinning increases host tree resistance to spruce budworm by enhancing its capacity to tolerate budworm defoliation, but its impact will vary over time and according to differences in thinning levels, site quality, and host tree species. Consequently, an increase in tolerance and, therefore, resistance of host tree species can be expected over the medium- to long-term because the positive effect of this silvicultural treatment on residual trees should allow them to start producing more foliage three years following the treatment. Further, antibiosis should return to its pre-treatment level.

In this paper, we evaluated the effects of commercial thinning (hereafter called thinning) and site drainage quality on balsam fir, white spruce, and black spruce resistance to spruce budworm three years after the treatment was conducted to determine whether or not this technique can be used as preventive control measure to reduce damage caused by spruce budworm infestation.

3.4 Methods

3.4.1 Field insect rearing

We conducted our research in Laval University's Montmorency Experimental Forest, which is located 60 km north of Quebec City, QC, Canada. The forest cover is typical of the Laurentide-Onatcheway region (Rowe 1972), and most of the stands fit Grandtner's (1966) description of the balsam fir-white birch association. Budworm field-rearing experiments, together with foliar chemical analyses along a gradient of stand thinning intensity and site drainage quality, were conducted to elucidate the effects of these two variables on host tree resistance and insect performance.

Forty plots (2 ha each) were established to evaluate thinning and drainage class quality effects on spruce budworm and host performance (Figure 3.1). Field work was conducted along a gradient of stand thinning intensity (0%, 25%, and 40% of stand basal area removed) and drainage class (mesic with seepage, class 3; subhygric, class 4; and hydric, class 5). Belanger et al. (1995) should be consulted for further details regarding drainage class. Thinning intensities and selected drainage classes were chosen for their feasibility, considering both the risks of windthrow damage when stand openings were too pronounced and operational constraints in terms of slope angles that were too pronounced to allow thinning, i.e., slopes in rapidly drained class 2 sites. Stands selected were 50-years-old and basal area ranged between 27 and 44 m^2/ha. Drainage class 2, 3 and 4 sites supported balsam fir (65%), white spruce (22-30%) and hardwood species (5-13%), whereas drainage class 5 sites supported balsam fir (65%) and black spruce (35%). Stand composition was the same after thinning treatments. We used a split-plot design with

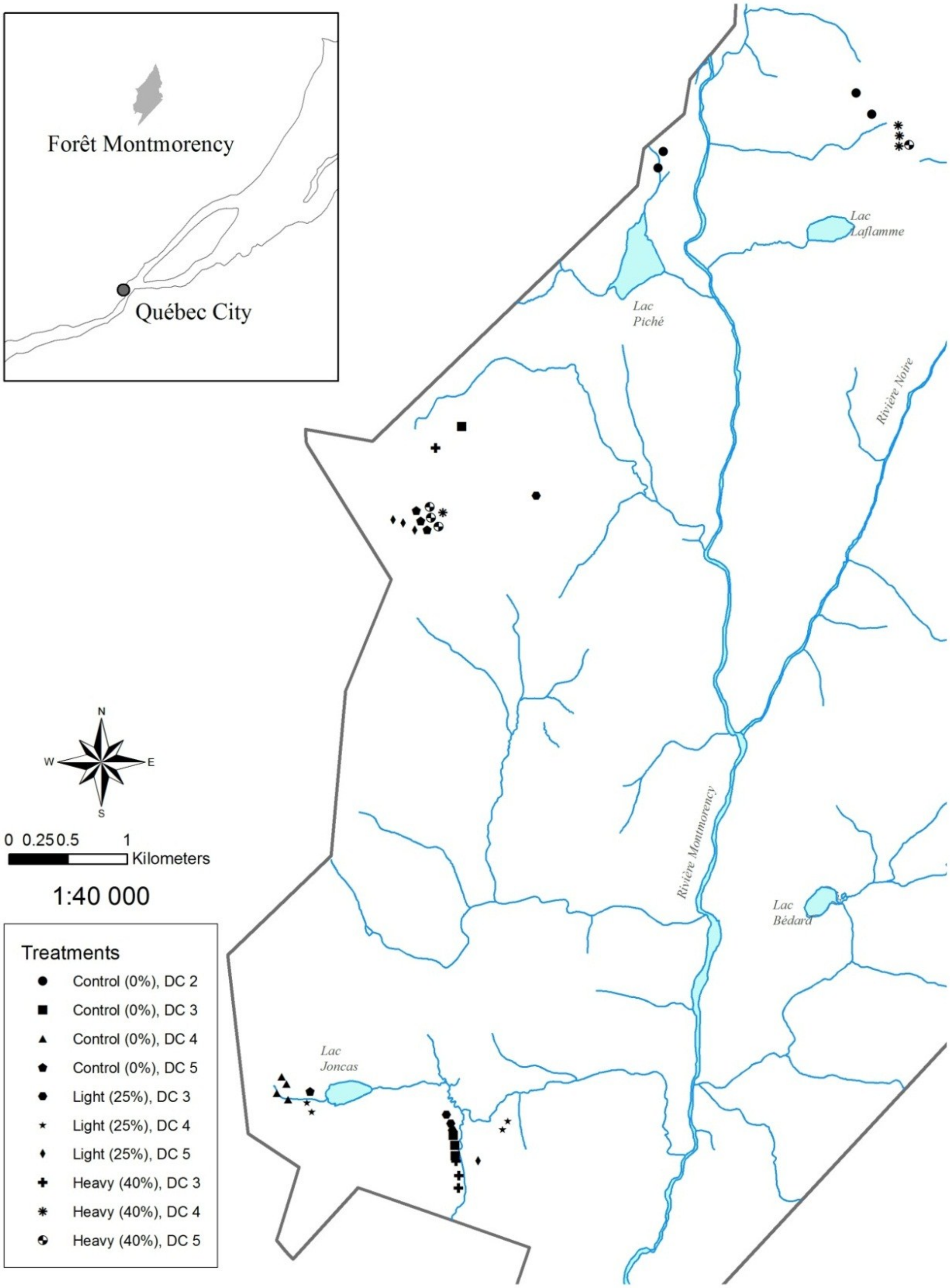

Figure 3.1 Distribution of plots in the study area (Forêt Montmorency) according to thinning intensity and drainage class (DC).

three levels of soil drainage, three intensities of thinning, and four replicates of each treatment combination (36 experimental units of 2-ha each). Four additional experimental units were established on the rapidly drained site to document site effects over the entire range of conditions in which spruce budworm occurs.

In each experimental unit and for each host tree species, two dominant or co-dominant trees were randomly selected (balsam fir: 40 experimental units x 2 = 80; white spruce: 28 experimental units x 2 = 56; black spruce: 12 experimental units x 2 = 24). The selection of trees was intended to avoid edge effects. All trees were selected in the centre part of the plot. On each tree, two 75-cm-long branches were selected on the north-northwest side of the tree, at mid-crown level. Each branch was enclosed within a fine-mesh cloth sleeve cage (100 cm x 75 cm), which served as an enclosure for 20 post-diapause second-instar larvae. Sites were free of local spruce budworm populations. Larvae that were used in the experiments originated from a colony maintained at Laval University (Laboratory of Forest Entomology) for the last seven years, with introductions from wild populations at three-year intervals. To simulate normal field emergence from winter diapause, the insects were placed in the field cages when 150 degree-days had been accumulated, i.e., two to three weeks prior to budbreak in the study area (base temperature: 2.7°C). Branches were cut and brought to the laboratory when budworms had pupated. The dry mass of frass produced in each rearing cage was recorded, larval mortality was determined, pupae were sexed and weighed using an electronic balance (MC 1 Analytic AC 210 S, Sartorius; 10 μg accuracy), and moth emergence was monitored every 8 h. Results from an earlier study on spruce budworm food utilization, which combined laboratory and field-rearing experiments, indicates that this approach provides an accurate estimate of frass production (Bauce et al. 1994).

3.4.2 Defoliation and residual foliage

On each 75-cm-long branch, the total amount of current-year foliage produced, current-year foliage destroyed by larvae, and residual current-year foliage remaining on each branch after budworm defoliation (i.e., an index of resistance, a net result of antibiosis and tolerance) were assessed by: (1) determining, for each tree, the number of needles

cm^{-1} of current-year twigs and mean needle dry mass; (2) measuring total length of current-year twigs (cm); (3) measuring the length of defoliated twigs (cm); (4) converting cm of twigs to number of needles; and (5) converting needle numbers to foliar mass (Bauce 1996).

3.4.3 Foliar chemical content

For foliar chemical analysis, we collected branches twice during the growing season from each tree that had been selected for field-rearing. Foliar chemistry was determined on each sample tree using two randomly selected, north-northwest-facing mid-crown branches, which had been neither used for field insect rearing nor infested with budworm. The first branch collection was done 15 days after insect installation (21-25 June), and the second when budworm infested-branches were collected (at pupal stage; 16-22 July). Branches used for chemical analysis were not enclosed within fine-mesh cloth sleeve cages. This means that we assumed that sleeve cages did not alter foliage chemistry and quality for spruce budworm. The same methodology has been used in a number of studies in which field insect rearing within cages has been conducted (Mattson et al. 1991, Hanhimäki and Senn 1992, Lawrence et al. 1997, Johns et al. 2010). Furthermore, enclosing branches in mesh bags for several weeks has not been found to affect foliage quality of a deciduous tree for *Epirrita autumnata* larvae (Hanhimäki and Senn 1992). Fresh foliage (3 g) was collected on each sample tree (n = 160 samples per collection date), returned to the laboratory on dry ice, flash-frozen in liquid N_2, freeze-dried, ground in a Wiley mill (at -30°C to avoid polyphenolic deterioration), and maintained at -20°C until they were analyzed for protein, mineral nutrients (P, K, Ca, Mg), total soluble sugars, total tannins, hydrolyzable and condensed tannins, and total phenolic contents. Assays were conducted using methods described by Bauce (1996) and Bauce et al. (2006) Moisture content was determined on two subsamples of 15 current-year twigs. Two additional subsamples of fresh twigs were collected from each tree, placed in crimp seal vials, and kept at -20°C until needle monoterpene concentrations were analyzed via gas chromatography, as described by Bauce et al. (1994). Extracts were injected into a Varian GC3900 gas chromatograph that was equipped with a flame ionization detector and a 30 m x 0.25 mm fused silica capillary column (Supelco SPB-5), and which was running Galaxy Workstation software (Varian Canada, Mississauga, ON).

3.4.4 Host tree growth and vigour

Host tree growth and vigor were determined one year after treatment on two sample trees in each experimental unit using a Pressler probe (increment borer). The vigour or growth efficiency index was expressed as basal area of current-year wood produced per unit sapwood area (Waring et al. 1980).

3.4.5 Winter biology and performance of budworm progeny

Adults that had been collected from the field-rearing experiment were mated to obtain the F1 generation. We formed 15 individual mating pairs in each experimental unit and for each host tree species. The number of eggs laid by each female during its lifetime, the number of fertile eggs, first-instar larval survival (%), and the subsequent number of second-instar larvae entering diapause were recorded. Larvae were placed in an outdoor insectarium during their winter diapause and overwinter survival was evaluated the following spring.

3.4.6 Statistical analyses

The experimental design was adapted to separately test the interactions of main effects (drainage, thinning) for each host species. The primary spruce budworm host (balsam fir) was present in all 40 experimental units. White spruce were selected in drainage class 2, 3 and 4, while black spruce, which grows only on drainage class 5 in the ecological domain that we studied, was selected in this drainage class. Statistical analyses were performed for an incomplete split-plot factorial design with 4 replicates, with block(drainage) as the error term. Whole plots corresponded to drainage class (4 levels), and sub-plots to thinning treatments (3). Since black spruce could only be found in drainage class 5, it was necessary to replace a main experimental design factor (drainage) with the factor “species.” Here, whole plots corresponded to species (black spruce vs balsam fir), with block(species) as the error term (Table 3.1). The incomplete block structure was due to our inability to thin on drainage class 2 sites.

Table 3.1 ANOVA table of split-plot design used to test the impact of thinning intensity[1] and soil drainage quality[2] on the resistance of three host trees species[3] against spruce budworm.

Balsam fir		White spruce		Black spruce	
Source of variation	*df*	Source of variation	*df*	Source of variation	*df*
Drainage	3	Drainage	2	Species	1
Bloc(Drainage)	12	Bloc(Drainage)	9	Bloc(Species)	6
Thinning	2	Thinning	2	Thinning	2
Thinning*Drainage	4	Thinning*Drainage	2	Thinning*Species	2
Error	18	Error	12	Error	12
Total	39	Total	27	Total	23

[1] Control (0%), Light (25%) and Heavy (40%) thinning intensity.

[2] (Rapid drained soil (class 2), mesic with seepage (class 3), subhygric (class 4), hydric (class 5).)

[3] Balsam fir (*A. balsamea*), White spruce (*P. glauca*), Black spruce (*P. mariana*).

Normality and homogeneity of variance tests were performed, after which the data were subjected to multivariate analysis of variance (MANOVA) on each of the following groups of variables: spruce budworm biological performance (i.e., pupal mass, developmental time, frass production, insect survival); winter biology of budworm progeny (i.e., winter survival, number of eggs laid, mean mass of eggs, number of infertile eggs); host tree monoterpenes, host tree tannins and phenols, and nutrients (i.e., N, P, K, Ca, Mg, and sugar concentrations); and host tree response variables (i.e., vigour index, defoliation, foliage produced, foliage destroyed, residual foliage, diameter at breast height (DBH), and sapwood increment). MANOVA was performed separately for each needle collection of host tree monoterpenes, tannins and phenols, and nutrients. The large number of variables in these groups, compared to the relatively small number of replicates, did not permit the use of MANOVA on the entire data set. Black spruce monoterpenes were divided into two groups because there were insufficient degrees of freedom (df) to perform MANOVA on a single group. The first group corresponded to monoterpenes that have been reported as budworm oviposition stimulants in the literature (group 1: α-pinene, β-pinene, limonene, myrcene, thujone) (Städler 1974, Chen et al. 2002, Grant et al. 2007), whereas the second group corresponded to monoterpenes reported as being toxic to the insect (group 2: camphene, terpinolene, δ-3-carene, bornyl acetate, borneol) (Mattson et al. 1991, Bauce et al. 1994, Kumbaşli et al. 2011). Partial correlation coefficients (r) between the variables were calculated to assess the power of MANOVAs (Table 3.8 and 3.9). In case of high correlations between the dependent variables, the power of MANOVA decreases (Tabachnick and Fidell 2007). We found that nitrogen and phosphorous ($r = 0.8$), bornyl acetate and camphene ($r = 0.9$), and female pupal mass and number of eggs laid ($r = 0.7$) were the only dependent variables that were highly correlated (≥ 0.7). Although inclusion of these variables may decrease the power of MANOVA, we retained them because of their important effect on spruce budworm performance. To be sure that these highly correlated variables did not affect the results of MANOVAs, we excluded one of the dependent variable in each pair of correlated variables (phosphorous, camphene and number of eggs laid). The analysis yielded the same results. If MANOVA found a significant treatment effect in a group of variables, data from that group were analyzed using Analysis of Variance (ANOVA) to determine which variables were affected by the factors studied (Table 3.1). Duncan's test was used for comparison of means (PROC GLM, SAS Institute 2003).

3.5 Results

3.5.1 Field-rearing

Thinning intensity affected the overall suite of performance indicators for insects reared on balsam fir (Table 3.2A); individually, male mass ($F = 26.87$; df = 2,18; $P < 0.0001$) and female mass ($F = 44.33$; df = 2,18; $P < 0.0001$) were significantly affected by thinning intensity. Mean masses for both males and females were higher when 40% of stand basal area was removed compared with the other treatments (Figure 3.2). Insect survival ($F = 2.49$; df = 2,18; $P = 0.111$) and frass production ($F = 1.05$; df = 2,18; $P = 0.372$) were not affected by the treatment. Insect survival was relatively high (9 to 11 larvae per branch). In contrast, thinning intensity did not influence the overall performance of insects reared on white spruce (Table 3.2B) and black spruce (Wilks' Lambda: $F_{\text{thinning}} = 3.10$; df = 12,2; $P = 0.270$). In contrast to thinning intensity, drainage class did not directly affect spruce budworm performance on balsam fir and white spruce

Table 3.2 Multivariate analysis of variance (MANOVA) for balsam fir and white spruce groups of variables and biological performance of spruce budworm larvae reared on the aforementioned host tree species. *P*-values and *F*- approximation of Wilks' Lambda (df numerator, df denominator) from MANOVA with block(drainage) as error term. Numbers in bold indicate statistically significant effects at *P* = 0.05.

A) Balsam fir

	Field-reared larval performance[a]		Adult & progeny performance[b]		Tree response[c]		Monoterpenes				Tannins and Phenols				Nutrients[d]			
Source							Collection1[e]		Collection2[f]		Collection1		Collection2		Collection1		Collection2	
	P	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df
Drainage	0.133	18,20	0.733	15,22	**0.002**	18,17	**0.048**	30,6	0.789	33,6	0.733	9,24	0.408	9,24	**0.033**	18,20	**0.015**	18,20
Thinning	**0.011**	12,14	**0.047**	10,16	**0.001**	12,12	0.686	20,4	0.766	22,4	0.634	6,20	0.147	6,20	**0.003**	12,14	0.141	12,14
Drainage*Thinning	0.236	24,25	0.277	20,27	0.083	24,22	0.166	40,9	0.993	44,9	0.128	12,26	0.492	12,26	0.292	24,25	0.132	24,25

B) White spruce

	Field-reared larval performance[a]		Adult & progeny performance[b]		Tree response[c]		Monoterpenes				Tannins and Phenols				Nutrients[d]			
Source							Collection1[e]		Collection2[f]		Collection1		Collection2		Collection1		Collection2	
	P	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*	df
Drainage	0.714	12,8	0.641	10,10	**0.043**	8,12	0.688	12,4	0.105	18,2	0.688	8,10	0.173	8,8	0.056	12,8	0.634	12,8
Thinning	0.762	12,8	0.528	10,10	**0.033**	8,12	0.643	12,4	0.116	18,2	0.753	8,10	0.317	8,8	**0.023**	12,8	0.317	12,8
Drainage*Thinning	0.394	12,8	0.964	10,10	0.155	8,12	0.361	12,4	0.604	18,2	0.843	8,10	0.087	8,8	**0.006**	12,8	0.918	12,8

[a] Pupal mass, developmental time, frass production and survival.

[b] Winter survival, number of eggs laid, mean mass of eggs, number of infertile eggs.

[c] Vigor index (basal area of current-year wood produced per unit sapwood area), defoliation (%), foliage produced, foliage destroyed, residual foliage, DBH and sapwood increment.

[d] Concentration of N, P, K, Ca, Mg and sugars.

[e] First foliage collection (21-25 June).

[f] Second foliage collection (16-22 July).

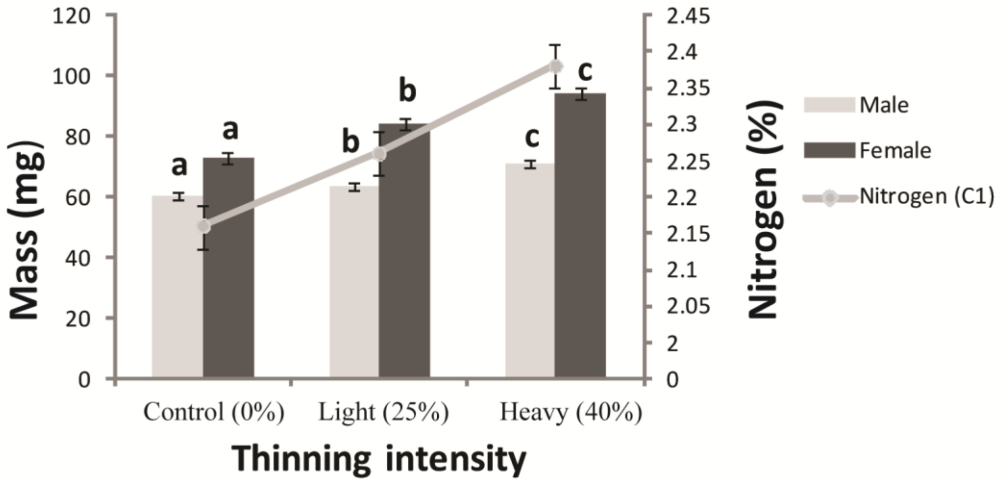

Figure 3.2 Mean (±2SEM) masses of female and male spruce budworm (*C. fumiferana*) pupae according to thinning intensity in balsam fir (*A. balsamea*). Nitrogen (C1) corresponds to balsam fir foliar nitrogen concentrations in the first collection. Columns followed by the same letter do not differ significantly at $P<0.05$ according Duncan multiple range test.

(Table 3.2). Finally, there were no differences in budworm performance between insects reared on balsam fir and black spruce on hydric sites (Wilks' Lambda: $F_{thinning} = 1.23$; df = 12,2; $P = 0.532$).

3.5.2 Host tree growth and vigour

MANOVA of data for balsam fir and white spruce showed that drainage class and thinning intensity had a significant effect on host tree growth and vigour (Table 3.2). In contrast, growth and vigour were not affected by thinning intensity in black spruce (Wilks' Lambda: $F_{\text{thinning}} = 7.60$; df = 12, 2; $P = 0.122$). Furthermore, there were no significant differences in growth and vigour between balsam fir and black spruce on hydric sites (Wilks' Lambda: $F_{\text{species}} = 17.55$; df = 6,1; $P = 0.181$).

Balsam fir growing on thinned stands exhibited higher quantities of total current-year foliage produced (AFP) ($F = 4.77$; df = 2,16; $P = 0.024$) and current-year foliage remaining (ARF) ($F = 15.40$; df = 2,16; $P = 0.0002$) than those growing on unthinned stands after budworm defoliation. The same response was observed on white spruce for AFP ($F = 7.09$; df = 2,9; $P = 0.014$) and ARF ($F = 12.82$; df = 2,9; $P = 0.002$) (Figure 4). Likewise, balsam fir ($F = 11.98$; df = 2,16; $P = 0.0007$) and white spruce ($F = 7.06$; df = 2,9; $P = 0.014$) individuals growing in heavily thinned stands (40% of stand basal area removed) exhibited the lowest defoliation percentage (Figure 3.3).

Drainage class had a significant overall effect on balsam fir performance based on the amount of current-year foliage that had been destroyed (AFD) (Figure 3.4), and on defoliation effects caused by budworm (Figure 3.3). Trees growing on drainage class 3 had the greatest DBH ($F = 34.63$; df = 3,11; $P < 0.0001$) and AFD ($F = 5.11$; df = 3,11; $P = 0.017$), compared with those growing on the other drainage classes. As for white spruce, drainage class had a significant effect on DBH ($F = 6.98$; df = 2,9; $P = 0.015$) and foliage destroyed ($F = 15.11$; df = 2,9; $P = 0.001$). White spruce individuals coming from drainage class 3 showed greater DBH and amount of foliage destroyed than individuals coming from the other drainage classes.

3.5.3 Foliar chemical content

Chemical analysis indicated that balsam fir monoterpene concentrations in the first foliar collection were affected by drainage class three years after the treatment had been conducted (Table 3.2A), more specifically bornyl acetate, camphene and α-pinene (Table

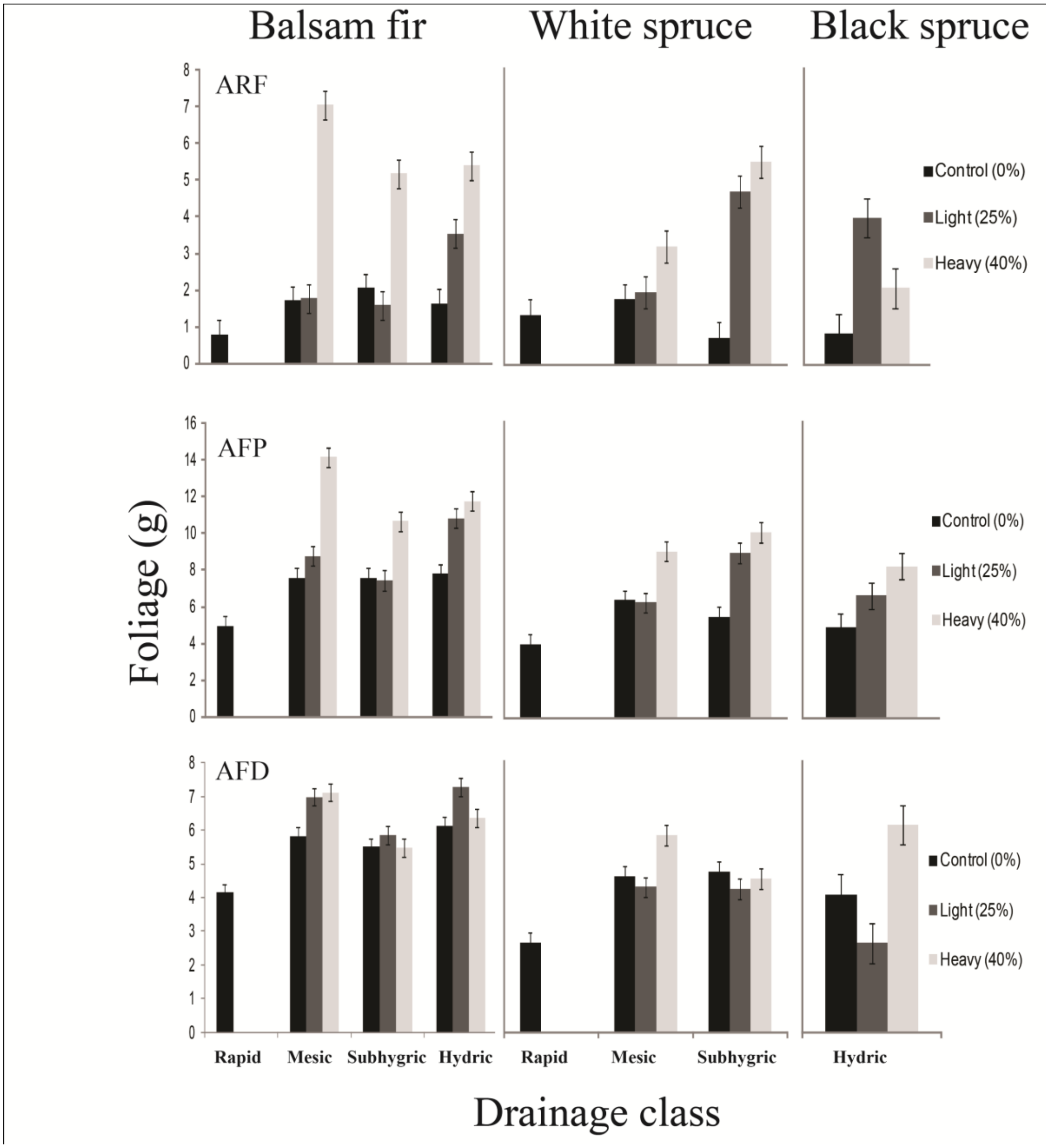

Figure 3.3 Amount of residual current-year foliage remaining (ARF), amount of current-year foliage produced (AFP), and amount of current-year foliage destroyed (AFD) tabulated by thinning intensity, drainage class and host tree species (mean ± 2SEM).

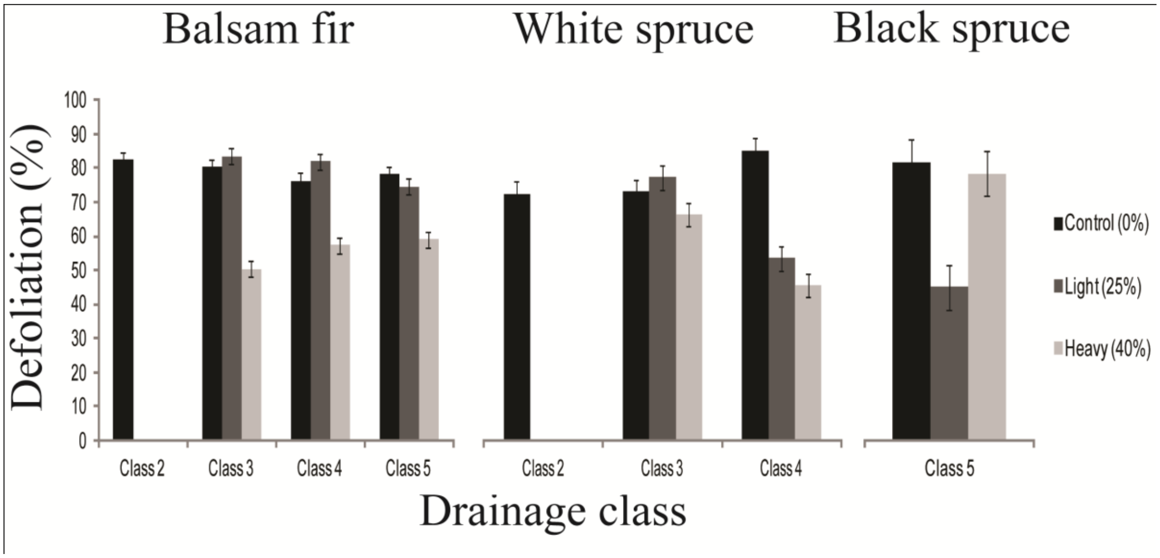

Figure 3.4. Defoliation by spruce budworm (*C. fumiferana*) larvae reared in sleeve cages on foliage of *Abies balsamea*, *Picea glauca*, and *P. mariana* tabulated by thinning intensity, drainage class and host tree species (mean ± 2SEM).

3.3). Concentrations of bornyl acetate and camphene were higher on drainage class 5, whereas the concentration of α-pinene was higher on drainage class 3 (Table 3.3). In contrast to the first collection, concentrations of monoterpenes in the second collection were not affected by thinning or drainage (Table 3.2A). Although thinning did not significantly affect total monoterpene concentrations in balsam fir, we observed that trees from thinned stands had 15% less bornyl acetate and 16 % less camphene than trees from unthinned stands in the first foliage collection.

Concentrations of monoterpenes in white spruce foliage were affected by neither treatment nor drainage class in both collections (Table 3.2B). As for black spruce, thinning did not significantly affect monoterpene concentrations in the first collection on hydric sites (Wilks' Lambda: $F_{\text{thinning effect on monoterpenes stimulants (G1)}} = 2.99$; df = 10,4; $P = 0.151$; $F_{\text{thinning effect on toxic monoterpenes (G2)}} = 0.98$; df = 10, 4; $P = 0.560$). The same result was observed in the second collection (Wilks' Lambda: $F_{\text{thinning effect on stimulant monoterpenes (G1)}} = 2.99$; df = 10,4; $P = 0.151$; $F_{\text{thinning effect on toxic monoterpenes (G2)}} = 0.98$; df = 10,4; $P = 0.560$), but there were significant differences between black spruce and balsam fir in terms of monoterpene concentrations that had been classed in the oviposition stimulant group for both collections on drainage class 5. (Wilks' Lambda: $F_{\text{species effect on stimulant monoterpenes collection 1 (C1)}}$ = 41.11; df = 5,2; P = 0.024; $F_{\text{species effect on stimulant monoterpenes collection 2 (C2)}}$ = 106.98; df = 5,2; P = 0.009) (Figure 3.5).

Table 3.3 Nutrient and monoterpene concentrations (first needle collection) in balsam fir (*A. balsamea*) needles by drainage class[1] (Means ± SEM).

Parameter	Drainage						
	Rapid	Mesic	Subhydric	Hydric	*F*	df	*P*
α-pinene (ng/mg)	5887.24 ± 718.93b	7535.17 ± 416.45a	5874.48 ± 241.51b	6788.44 ± 348.34ab	5.4	3,18	0.014
Camphene (ng/mg)	1269.67 ± 101.04b	1794.73 ± 115.85a	1798.19 ± 110.15a	1897.27 ± 155.46a	7.27	3,18	0.005
Bornyl acetate (ng/mg)	3005.94 ± 285.94b	3971.50 ± 200.32a	3971.60 ± 234.01a	4178.90 ± 327.17a	6.83	3,18	0.006
N (% dry mass)	2.33 ± 0.05a	2.39 ± 0.05a	2.27 ± 0.06ab	2.10 ± 0.06b	5.65	3,18	0.012
P (μg/g)	2542.08 ± 98.58a	2494.69 ± 64.39a	2440.17 ± 82.40ab	2321.38 ± 78.68b	3.81	3,18	0.039
Ca (μg/g)	644.50 ± 59.00b	844.57 ± 70.48ab	1080.87 ± 105.82a	1078.91 ± 94.50a	14.06	3,18	0.0003

Values in each row followed by the same letter do not differ significantly at $P = 0.05$ according to Duncan multiple range test.

[1] Rapid drained soil (class 2), mesic with seepage (class 3), subhygric (class 4), hydric (class 5).

Drainage class influenced foliar nutrient concentrations of balsam fir during the first and second collections (Table 3.2A). Concentrations of foliar nitrogen and phosphorus in the first collection (Table 3.3), and concentrations of P in the second collection increased as drainage quality improved (Table 3.4), whereas the opposite pattern was observed for calcium in the first collection (Table 3.3). Thinning also increased foliar N and P, and decreased Ca in the first collection (Table 3.4), whereas no effect was detected in the second collection (Table 3.2A).

Significant effects of thinning and significant interaction between thinning and drainage classes were detected on foliar nutrient concentrations of white spruce in the first collection only (Table 2B). Individuals growing on thinned stands (40% stand basal area reduction) had the greatest foliar P concentrations (F_{thinning} = 15.95; df = 2,10; P = 0.0008). Furthermore, thinning increased foliar phosphorus on drainage classes 3 and 4 ($F_{\text{interaction}}$ = 10.55; df = 2,10; P = 0.004). In contrast, foliar nutrients were not affected by thinning intensity in black spruce on drainage class 5 (Wilks' Lambda: $F_{\text{thinning collection 1}}$

$_{\text{(C1)}}$ = 1.51; df = 12,2; *P* = 0.467; $F_{\text{thinning collection 2 (C2)}}$ = 9.89; df = 12,2; *P* = 0.095). However, there were significant differences in foliar nutrient concentrations between black spruce and balsam fir on hydric sites, but only in the second collection (Wilks' Lambda: $F_{\text{species collection 2 (C2)}}$ = 593.51; df = 6,1; P = 0.031; Table 3.5).

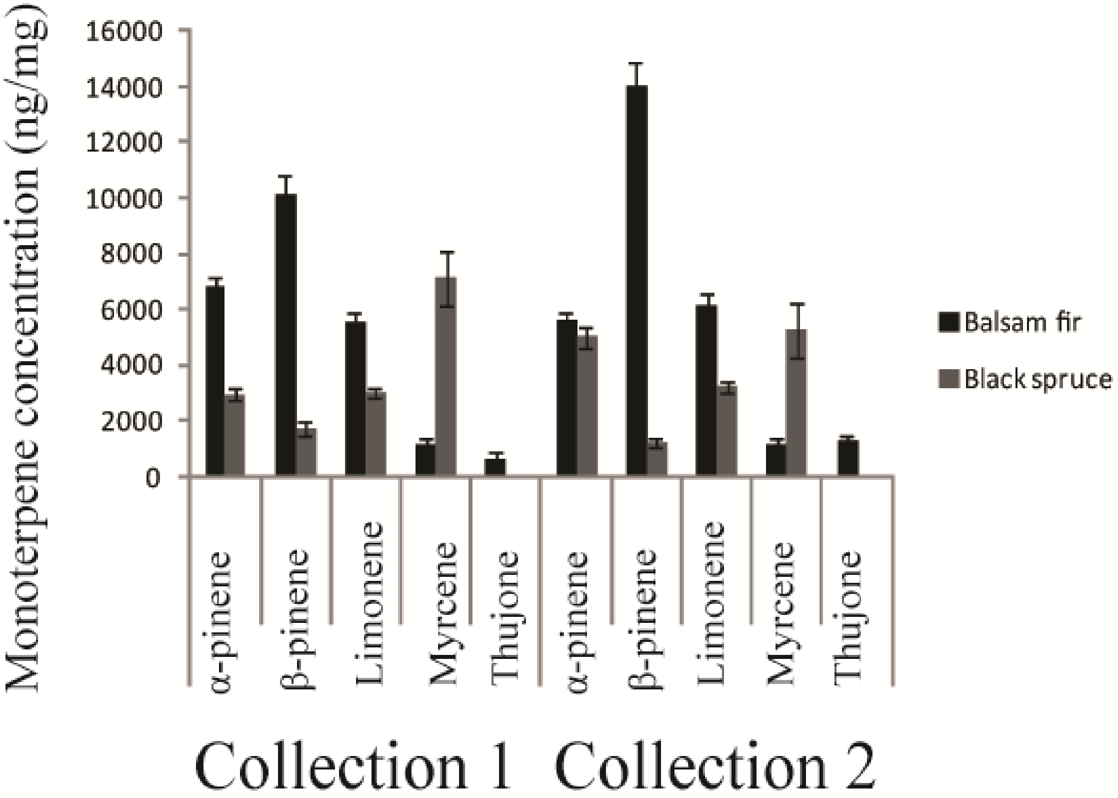

Figure 3.5. Foliar monoterpene concentrations occurring on drainage class 5 (Hydric sites) tabulated by host tree species (Balsam fir and Black spruce) (mean ± 2SEM). The first branch collection was done 15 days after insect installation (21-25 June), and the second when budworm infested-branches were collected (at pupal stage; 16-22 July).

Thinning and drainage class did not affect tannin and phenol concentrations in either foliage collection for balsam fir and white spruce (Table 3.2). Furthermore, concentrations of tannins and phenols in black spruce were not affected by thinning intensity at either needle collection on hydric sites (Wilks' Lambda: $F_{\text{thinning collection 1 (C1)}}$ =

0.49; df = 6,8; P = 0.799; $F_{\text{thinning collection 2 (C2)}}$ = 2.51; df = 8,6; P = 0.139). Finally, there were no significant differences in concentrations of tannins and phenols between black spruce and balsam fir at either needle collection on drainage class 5 (Wilks' Lambda: $F_{\text{species collection 1 (C1)}}$ = 5.27; df = 3,4; P = 0.071; $F_{\text{species collection 2 (C2)}}$ = 0.99; df = 4,3; P = 0.526).

Table 3.4 Nutrient concentrations (first needle collection) in balsam fir (*A. balsamea*) needles by thinning intensity (Means ± SEM).

Parameter	Thinning intensity (%)					
	0	25	40	*F*	*df*	*P*
N (% dry mass)	2.16 ± 0.04b	2.27 ± 0.06ab	2.38 ± 0.07a	8.29	2,18	0.003
P (µg/g)	2311.49 ± 55.05b	2450.99 ± 49.82ab	2570.63 ± 91.22a	6.15	2,18	0.009
Ca (µg/g)	1102.05 ± 92.97a	847.37 ± 81.81b	902.40 ± 77.09ab	7.64	2,18	0.004

Values in each row followed by the same letter do not differ significantly at P<0.05 according to Duncan multiple range test.

Table 3.5 Nutrient concentrations (by tree species) occurring on drainage class 5 (second needle collection) (Means ± SEM).

Parameter	Host tree species				
	Balsam fir	Black spruce	*F*	*df*	*P*
N (% dry mass)	1.59 ± 0.02a	1.36 ± 0.05b	35.64	1,12	0.001
Ca (µg/g)	2163.58 ± 128.17a	901.71 ± 61.27b	206.42	1,12	<0.0001
Mg (µg/g)	554.89 ± 55.05b	695.32 ± 45.48a	8.86	1,12	0.025

Values in each row followed by the same letter do not differ significantly at P<0.05 according to Duncan multiple range test.

3.5.4 Winter biology and performance of budworm progeny

The winter biology of budworm progeny was affected by thinning intensity on balsam fir (Table 3.2A). The treatment affected the overall suite of winter biology indicators; individually, these included egg mass, average number of eggs laid by females, female mass, and overwintering larval survival (Table 3.6). In contrast, thinning intensity did not affect winter biology of insects reared on white spruce (Table 3.2B) and black spruce (Wilks' Lambda: F_{thinning} = 2.81; df = 10,4; P = 0.165). Furthermore, drainage class did not have a significant effect on winter biology of budworm progeny that had been reared on balsam fir and white spruce (Table 3.2), and there were no significant differences in winter biology of budworm progeny between black spruce and balsam fir on hydric sites (Wilks' Lambda: $F_{species} = 1.07$; df = 5,2; $P = 0.548$).

Table 3.6 Winter biology indicators of spruce budworm progeny of parents reared on balsam fir (*A. balsamea*) needles by thinning intensity (Means ± SEM).

Parameter	Thinning intensity (%)					
	0	25	40	*F*	*df*	*P*
Egg mass (mg)	299 ± 10b	281 ± 10b	358 ± 10a	8.91	2,18	0.002
N° egg by female	74.03 ± 6.07a	81.14 ± 4.05a	58.71 ± 3.22b	6.45	2,18	0.008
Female mass (mg)	76.96 ± 2.22c	82.79 ± 1.65b	88.95 ± 2.27a	10.2	2,18	0.001
Overwintering survival (%)	46.67 ± 5.30b	49.59 ± 4.83b	64.77 ± 2.66a	5.36	2,18	0.015

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan multiple range test.

3.6 Discussion

Heavy thinning (40% of stand basal area removed) increased the amount of current-year foliage produced and the amount of current-year foliage remaining in balsam fir and white spruce after defoliation (Figure 3.4). This pattern shows that heavy thinning (40%) increased host tree tolerance compared with light thinning (25% of stand basal area removed) and the unthinned controls three years after treatment. These results confirm, in part, findings reported by Bauce (1996) and Bauce et al. (2001), who found that thinning (25%) increased balsam fir resistance on well-drained sites by increasing foliar production and foliar concentrations of certain chemical compounds toxic to the budworm. In the current study, however, tree tolerance was increased in all drainage classes by using heavy thinning (40%), suggesting that heavy intensities (40%) are more appropriate for reducing budworm damage than were light intensities (25%). In fact, balsam fir and white spruce trees coming from heavily thinned stands had 73.6% and 70.7% more residual foliage (Figure 3.4), respectively, available for photosynthesis (photosynthetic capacity) than those trees coming from control stands, even when insect population levels at the end of the development were relatively high (9 to 11 larvae per branch). Furthermore, lightly thinned (25%) and control stands exhibited severe defoliation (>75% of current-year foliage destroyed; Figure 3.3). This level of damage can result in reduction of volume growth by up to 20% after one year (Piene 1980) and greater tree mortality after 4-5 consecutive years of severe defoliation (Batzer 1973, Blais 1979). Heavily thinned stands (40%), in contrast, showed moderate levels of defoliation (<53%). Because volume growth is positively correlated with tree photosynthetic capacity, heavy thinning (40%) may attenuate wood losses attributed to tree mortality and volume growth reductions by diminishing defoliation (Figure 3.3) and increasing the amount of foliage produced (Figure 3.4).

The lack of effectiveness of light thinning in increasing host tree tolerance may be explained by the high overall survival rate of spruce budworm (51.11%) found in this study compared with that reported (26.25%) by Bauce (1996) two years after treatment. Although the amount of current-year foliage destroyed can be affected by several factors, insect population levels are the most important (Blais 1979). Given that neither thinning nor drainage quality affected insect survival; it is difficult to explain the increase of this parameter. Climatic conditions may provide some clue to understanding the high survival rate of spruce budworm. It has been suggested that feeding rate and larval activity decrease with low temperatures and wet conditions (Greenbank 1956, Blais 1958), but the opposite conditions, such as those found in 2006 (Table 3.7), may stimulate insect feeding (Rouault et al., 2006) and reduce natural enemy performance (Gray 2008). According to Mattson et al. (1991), high temperatures can increase spruce budworm developmental rates and survival of large larvae. Consequently, climatic conditions may have increased spruce budworm survival and, therefore, the amount of foliage destroyed.
Light thinning (25%) was capable of increasing balsam fir tolerance on hydric sites and white spruce tolerance on subhygric sites (Figure 3.4), which demonstrates the importance of this variable in determining host tree resistance. Balsam fir (Hix et al. 1987) and white spruce (Wang and Klinka 1995) are best-adapted to grow in well-drained sites, which provide adequate nutrients and moisture to support vigorous tree growth. This enhances the ability of these species to withstand and recover from defoliation

(Belanger et al. 1995). This adaptation of balsam fir and white spruce may explain the respective increases in foliage produced in hydric and subhygric sites that are caused by thinning, since this technique reduced the number of trees competing for limited nutrients in poorly-drained sites, increasing foliage produced and, therefore, balsam fir tolerance (Figure 3.4).

Table 3.7 Mean temperature (°C) and mean precipitation (mm) from May to August for La Forêt Montmorency.

	Mean temperature (°C)				Mean precipitation (mm)			
Year	May	June	July	August	May	June	July	August
2005	5.7	13.6	14.5	13.5	61.8	132.4	170.6	127.4
2006	13.1	13.1	16.1	12.0	122.0	122.0	177.4	68.4
2007	7.0	12.6	13.4	11.8	34.0	73.2	144.0	132.8
2008	5.1	13.2	14.4	13.5	78.2	196.4	176.6	73.8
2009	5.2	11.5	13.6	13.5	89.2	77.2	165.6	113.4

Source: http://climat.meteo.gc.ca/climateData/canada_f.html

The results also show that thinning increased budworm performance. Pupal mass was favoured by the treatments in balsam fir. In fact, pupae reared on trees coming from heavily thinned stands (40%) exhibited the greatest mass (Figure 3.2). These results could be explained by the high content in foliar N and P found in balsam fir growing in thinned stands (Figure 2, Table 4). Nitrogen is very important for budworm performance, since larvae fed on a food source with sufficient nitrogen have higher growth rates and shorter developmental times (Bidon 1993, Carisey and Bauce 1997, Mattson et al. 1991), while phosphorus has been positively correlated with increased pupal mass (Schmitt et al. 1983, Fuentealba and Bauce 2012a). Furthermore, mean egg mass, winter survival and female mass were also favoured by thinning (40%) (Table 3.6). Spruce budworm overwintering survival relies on the nutritional reserves provided by the female parent (Carisey and Bauce 2002); therefore, the increase of foliar nutrients produced by thinning may have increased the quantity or quality of these reserves, which are very important because they represent the sole energy available to the progeny for embryogenesis and maintenance prior to hatching (Rossiter 1991) and can affect larval survival, development, and behaviour (Rossiter 1991, Carisey and Bauce 2002, Fuentealba and Bauce 2012b). Nevertheless, the positive effect of thinning on insect performance did not result in increased defoliation because the treatment also increased foliar production, offsetting the augmentation in foliage destroyed. This contrasting effect of thinning has also been reported by Bauce et al. (2001) in a balsam fir-spruce budworm system and by Moreau and Quiring (2011) in a balsam fir-*Neodiprion abietis* system. The former authors found that the positive effect of thinning on budworm performance disappeared with the passage of time, resulting in increased tree resistance to the insect for up to 8 years (Bauce et al 2001). We may expect, therefore, host chemistry to stabilize in subsequent years, thereby ceasing favourable conditions to insect performance and increasing tree resistance.

Finally, the lack of significant differences between balsam fir and black spruce growth and vigour on drainage class 5 confirms that thinning can be used to increase balsam fir resistance on hydric sites. One year after treatment, black spruce exhibited greater current-year foliar production and residual foliage than balsam fir on drainage class 5 (Fuentealba and Bauce 2012a), but this pattern is reversed three years after treatment. As for insect performance, there were no significant differences between insects reared on these species, but insects reared on balsam fir destroyed 35.1% more current-year foliage than those reared on black spruce. This result suggests that foliage of balsam fir growing on hydric sites is not an optimal source of food for spruce budworm, compelling the insect to increase its consumption rate. The high concentration of Ca in balsam fir foliage (Table 4) might have interfered with the uptake of micronutrients (Mattson et al. 1991), such as iron and zinc, which are known to be important catalysts of several enzyme reactions (Mattson and Scriber 1987), forcing the insect to consume more food to meet its nutritional requirements. Furthermore, high concentrations of monoterpenes such as α-pinene and β-pinene in balsam fir foliage (Figure 3.5) did not affect insect performance, implying that increases in total monoterpene concentrations do not necessarily render trees more resistant to budworm attack; rather, the augmentation of specific monoterpene concentrations increases tree resistance. Monoterpenes such as α-pinene and β-pinene are well-known oviposition stimulants for spruce budworm and do not cause toxic effects on the larvae (Städler 1974, Chen et al. 2002, Grant et al. 2007).

Table 3.8 Partial correlations among dependent variables reported in Tables 3.3 and 3.4.

	Dependent variables					
	α-pinene	Camphene	Bornyl acetate	N collection 1	P collection 1	Ca collection 1
α-pinene	.	0.13	0.13	.	.	.
Camphene	0.13	.	0.96	.	.	.
Bornyl acetate	0.13	0.96	.	.	.	.
N collection 1	.	.	.	.	0.85	-0.22
P collection 1	.	.	.	0.85	.	-0.33
Ca collection 1	.	.	.	-0.22	-0.33	.

Table 3.9 Partial correlation among dependent variables reported in Tables 3.5 and 3.6.

	Dependent variables						
	N collection 2	Ca collection 2	Mg collection 2	Egg mass	N° egg by female	Female mass	Overwintering survival
N collection 2	.	0.11	0.63	.	.	.	.
Ca collection 2	0.11	.	0.23	.	.	.	.
Mg collection 2	0.63	0.23	.	.	.	.	.
Egg mass	.	.	.	.	-0.68	-0.53	0.24
N° egg by female	.	.	.	-0.68	.	0.76	-0.37
Female mass	.	.	.	-0.53	0.76	.	-0.25
Overwintering survival	.	.	.	0.24	-0.37	-0.25	.

3.7 Conclusion

Thinning (40%) increased balsam fir and white spruce tolerance to spruce budworm three years after the treatment was conducted by increasing foliar production and, therefore, tree resistance. This response occurred despite the fact that the treatment favoured the performance of spruce budworms that were reared on balsam fir by allowing insects to access to a richer source of food. The effect of thinning intensity on tree tolerance and insect performance varied according to drainage quality, with the effect being more positive on well-drained sites because trees growing in these sites produced more foliage, thereby allowing them to cope more effectively with attacks by this defoliator. These results suggest that thinning (40%) may be used as preventive control measure during the low density phase of the budworm population. However, the number of years that the effectiveness of this measure lasts remains to be documented.

Black spruce was not significantly affected by thinning, but individuals of this species that were growing in thinned stands started to exhibit, three years after treatment, a trend towards producing more foliage than those growing in unthinned stands. This response suggested that the species has started to positively react to thinning. Consequently, we may expect a significant increase in black spruce resistance in the future. Finally, forest managers can use these results as guidelines for planning thinning and Btk aerial spray campaigns to reduce the economic impact of this insect. Further research is necessary to determine the long-term effects of thinning and drainage class on host tree resistance to determine the duration of increment in tree tolerance.

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4. Chapitre 3

Interactions between stand thinning, site quality and host tree species on spruce budworm biological performances and host tree resistance over a six year period after thinning.

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4.1 Résumé

Des activités d'aménagement forestier telles que l'éclaircie ont été proposées pour réduire l'impact de la défoliation de la tordeuse des bourgeons d'épinette (TBE) (Choristoneura fumiferana (Clem.)). Toutefois, les informations sur l'impact de l'éclaircie sur la vulnérabilité des arbres et des peuplements à la TBE sont ambiguës. Une meilleure compréhension des effets de l'éclaircie sur la résistance des arbres hôtes et sur la performance de la TBE pourrait être utile pour réduire l'impact de cet insecte tout en respectant l'intégrité écologique des forêts. Les objectifs de cette étude étaient (1) d'évaluer les effets de l'éclaircie et de la qualité de drainage du site sur la résistance du sapin baumier (Abies balsamea (L.) Mill.)), de l'épinette blanche (Picea glauca (Moench) Voss) et de l'épinette noire (P. mariana (Mill.) BSP) à la TBE dans le temps (six ans) et (2) de produire un modèle de classification de la résistance pouvant être utilisé par les gestionnaires forestiers dans le processus de prise de décision leur permettant de déterminer le moment et le lieu adéquats pour effectuer ce traitement. Des élevages de la TBE sur le terrain, ainsi que des analyses chimiques foliaires ont été réalisés le long d'un gradient d'intensité d'éclaircie (0% (témoin), 25% (légère), 40% (forte)) et de classe de drainage (drainage rapide, classe 2; mésique, classe 3; subhygrique, classe 4 et hydrique, classe 5). La performance biologique des insectes a été suivie tout au long de leur cycle de vie, y compris leur biologie hivernale. La résistance du sapin baumier, contrairement à celle de l'épinette blanche et noire, a été significativement réduite un an après l'éclaircie. Cette réponse des sapins se rapportait à la défoliation accrue liée à la réduction des concentrations de monoterpènes dans les sites mésiques et à la réduction de la production foliaire dans les sites subhygriques. Dans les sites hydriques, le traitement a accru la résistance du sapin baumier en augmentant sa production foliaire. Trois ans après le traitement, on a observé une réponse opposée. L'éclaircie de forte intensité (40%) a eu un impact positif sur la tolérance du sapin baumier et de l'épinette blanche et, par conséquent, sur la résistance des arbres en augmentant la production foliaire et la quantité de feuillage résiduel sur les arbres après le passage de la TBE, pour toute la période d'étude, sauf chez les individus de l'épinette blanche poussant sur les sites mésiques, six

ans après l’éclaircie. À partir de la quatrième année, la résistance de l’épinette noire a été positivement affectée par l'éclaircie. Cette réponse a été observée malgré le fait que l'éclaircie ait également favorisé la performance de l’insecte (poids élevé des chrysalides femelles), ce qui s’est traduit par une plus grande quantité de feuillage détruit par l’insecte dans les peuplements éclaircis. L’ensemble de ces résultats suggèrent que l'éclaircie peut être utilisée pour augmenter la résistance des arbres et des peuplements à la TBE. Notre système de classification de résistance peut être utile pour les aménagistes forestiers afin de planifier l’éclaircie leur permettant de réduire l'impact de la TBE au niveau du peuplement.

Interactions between stand thinning, site quality and host tree species on spruce budworm biological performances and host tree resistance over a six year period after thinning.

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4.2 Abstract

Forest management activities such as thinning have been proposed to reduce defoliation damage incurred by spruce budworm (Choristoneura fumiferana (Clem.)). Yet, information regarding thinning effects on tree and stand vulnerability to spruce budworm is equivocal. A better understanding of thinning with respect to host tree resistance and budworm performance could be useful to reduce its impacts while respecting forest ecological integrity. Our objectives were (1) to evaluate the effects of thinning and site drainage quality on balsam fir (Abies balsamea (L.) Mill.), white spruce (Picea glauca (Moench) Voss) and black spruce (P. mariana (Mill.) BSP) resistance to spruce budworm through time (six years) and (2) to produce a resistance classification model that could be used by forest managers to determine when and where to apply this treatment. Field-rearing experiments of spruce budworm were conducted, together with foliar chemical analyses, along a gradient of stand thinning intensity (0%, control; 25%, light; 40%, heavy) and drainage class (rapidly drained, class 2; mesic with seepage, class 3; subhygric, class 4; hydric, class 5). Budworm performance was followed throughout the insect's life cycle, including its winter biology. Balsam fir resistance, unlike that of white and black spruce, was significantly reduced one year after thinning. Fir response was related to increased defoliation linked to reduction of certain monoterpenes on mesic sites and to decreased foliage production on subhygric sites. On hydric sites, thinning increased fir resistance by increasing foliage production. We observed an opposite response three years after treatment. Heavy thinning (40%) positively affected balsam fir and white spruce tolerance and, therefore, tree resistance, by increasing foliage production and the amount remaining after budworm feeding throughout the study, except six years after thinning in white spruce growing on mesic sites. From the fourth year onward, black spruce resistance was positively affected by thinning. This response was observed despite thinning also having favoured insect performance (high female pupal mass), which resulted in greater foliage destruction in thinned stands. These findings suggest that thinning may be used to increase tree and stand resistance to spruce budworm. Our resistance classification system could be useful to forest managers in planning thinning that would reduce budworm impacts at the stand level.

4.3 Introduction

Spruce budworm (Choristoneura fumiferana (Clemens); Lepidoptera: Tortricidae), is the most destructive insect pest in the maritime and boreal forests of North America. For centuries, the North American boreal forest has experienced natural periodic budworm outbreaks that led to a substantial decline in vigour and increased mortality of affected trees. Aerial application of insecticides has been used routinely in the past to protect current foliage and to prevent tree mortality that is incurred during spruce budworm outbreaks (Kettela, 1975). Forest protection against spruce budworm in the Province of Quebec (Canada) currently relies upon Bacillus thuringiensis Berliner ssp. kurstaki (Btk). This microbial insecticide can protect trees during the period of low tree resistance to the insect, since the bacterium prevents substantial host tree mortality and growth losses (Fournier et al., 2010). Yet, results of previous studies (Bauce et al., 2002; Carisey et al., 2004) have shown that host tree foliar chemical composition can reduce the effectiveness of Btk applications. For example, Carisey et al. (2004) showed that, as foliar tannin content of host trees increased, the efficacy of Btk formulations decreased against spruce budworm. Reduced efficacy has necessitated the use of formulations with higher Btk concentrations, which is both expensive and less socially acceptable from an environmental standpoint. It is therefore necessary to develop alternative or complementary methods for reducing spruce budworm damage.

Forest management activities such as reducing the rotation age of balsam fir (*Abies balsamea* (L.) Miller)) to 50 years or less, breaking up the continuity of extensive areas of spruce-fir forest, and maintaining mixed-species stands wherever possible have been proposed to reduce the effects of spruce budworm defoliation (Mattson et al., 1988). Thinning also has been recommended to reduce damage caused by spruce budworm defoliation (Crook et al., 1979; Bauce, 1996; Bauce et al., 2001). However, various research projects focussing on the effects of this silvicultural tool on host tree resistance have yielded equivocal results. Previous studies have demonstrated that resistance to spruce budworm may increase (Batzer, 1967; Bauce, 1996; Bauce et al., 2001; D'Amato et al., 2011), decrease (Piene, 1989; MacLean and Piene, 1995), or remain unchanged (Crook et al., 1979) after thinning. According to Bauce et al. (2001), these contradictory results could result from variation in the treatment effect over time and attributable to differences in stand age, soil drainage, host tree species, and site quality. Depending where and when (i.e., prior to or during an outbreak) the treatment is being implemented, its effectiveness in limiting spruce budworm damage could thus be quite different.

Indeed, thinning is known to reduce host tree resistance one year after treatment when it is conducted during periods of high budworm infestation, by diminishing the quantity of secondary compounds (Bauce, 1996; Bauce et al., 2001, Fuentealba and Bauce, 2012a). This change in foliar chemical content have been manifested in positive effects on insect performance, such as shorter developmental times, greater pupal mass, and greater foliage consumption (Bauce, 1996; Fuentealba and Bauce, 2012a). However, positive effects of thinning on host tree foliar production in subsequent years resulted in increased tolerance and resistance against budworm (Bauce, 1996; Bauce et al., 2001; Fuentealba and Bauce, 2012b).

An understanding of plant resistance and how it is affected by silvicultural treatments such as thinning can help us to develop better control methods that would reduce the damage caused by insects and the losses that are incurred to the forest products industry. Plant **resistance** to herbivores has two components: defense and tolerance (Haukioja and Koricheva, 2000; Bauce et al., 2001). Defense refers to negative effects that plants exert upon insects, either by deterring them with some defensive trait (toughness of plant structures, thorns, phenology), or by harming insect performance (growth, fecundity or survival) with chemical compounds (**antibiosis**) that are consumed as the insects feed upon the plants (Bauce et al., 2001; Larsson, 2002). **Tolerance**, in turn, refers to the capacity of the plant to endure insect damage without serious damage or marked decreases in plant fitness (Haukioja and Koricheva, 2000; Bauce et al., 2001).

Here, we have reported on the continuation of an experiment dealing with thinning effects on balsam fir, white spruce and black spruce resistance to spruce budworm that had been initially reported after 1 (Fuentealba and Bauce, 2012a) and 3 (Fuentealba and Bauce, 2012b) years following treatment. The objectives of this paper were (1) to evaluate the effects of thinning and site drainage quality on resistance (antibiosis: variation in foliar chemistry; tolerance: amount of current-year foliage remaining) the aforementioned tree species to spruce budworm during a six years period after the treatment was conducted to determine the number of years that the increased host tree resistance lasts and (2) to produce a resistance classification system that can be used by forest managers to decide when and where conduct this silvicultural treatment and to select the best thinning intensity to obtain the intended increase in resistance. This experiment has allowed us to evaluate thinning effects on host tree resistance over a period equivalent to a local-scale spruce budworm outbreak.

4.4 Methods

4.4.1 Field insect rearing

We conducted our research in Montmorency Experimental Forest, which is located 60 km north of Quebec City (QC, Canada) and administered by Laval University. Fuentealba and Bauce (2012a,b) have provided detailed information on the forest in the study area, stand characteristics, defoliation and residual foliage, and chemical analysis methods, so only an overview will be given here.

In 2003, forty plots (2 ha each) were established to evaluate thinning and drainage class quality effects on spruce budworm and host performance. Field work was conducted along a gradient of stand thinning intensity (0%, 25%, and 40% of stand basal area removed) and drainage class (rapid drained, class 2; mesic with seepage, class 3; subhygric, class 4; and hydric, class 5). Bélanger et al. (1995) should be consulted for further details regarding drainage class. Thinning could not be conducted on rapidly drained class 2 sites because slope angles were too pronounced. Stands that had been selected were 45- to 50-years-old and basal area ranged between 27 and 44 m^2/ha. Drainage class 2, 3 and 4 sites supported balsam fir (65%), white spruce (22-30%) and hardwood species (5-13%), whereas drainage class 5 sites supported balsam fir (65%) and black spruce (35%). Stand composition remained the same after thinning treatments. We used a split-split-plot design with three levels of soil drainage (whole plot), three intensities of thinning (sub-plot), four replicates of each treatment combination (36 experimental units, i.e., the 2-ha plots), and conducted in four different years (sub-sub-plot). Four additional experimental units were established on the rapidly drained site to document site effects over the entire range of conditions in which spruce budworm occurs. Initially, it was planned to measure the plots every two years starting from 2004, but trees produced staminate flowers in 2007, which may influence spruce budworm performance (Bauce and Carisey, 1996). Therefore, we had decided to conduct measurements in this particular year to evaluate the effects of staminate flowers on insect performance. However, no interaction between thinning and staminate flower production was detected on host tree resistance and, therefore, we did not include this factor in the study.

The experiment was conducted in 2004, 2006, 2007 and 2009. In each experimental unit and for each host tree species, two dominant or co-dominant trees were randomly selected (balsam fir: 40 experimental units x 2 = 80; white spruce: 28 experimental units x 2 = 56; black spruce: 12 experimental units x 2 = 24). For each tree, two 75-cm-long branches were selected on the north-northwest side of the tree, at mid-crown level. Each branch was enclosed within a fine-mesh cloth sleeve cage (100 cm x 75 cm), which served as an enclosure for 20 post-diapause second-instar budworm larvae. To simulate normal field emergence from winter diapause, the insects were placed in the field cages when 150 degree-days had been accumulated, i.e., two to three weeks prior to budbreak in the study area (base temperature: 2.7°C). Branches were cut and brought to the laboratory when budworms had pupated. The dry mass of frass produced in each rearing cage was recorded, larval mortality was determined, pupae were sexed and weighed using an electronic balance (MC 1 Analytic AC 210 S, Sartorius; 10 µg accuracy), and moth emergence was monitored every 8 h.

4.4.2 Defoliation and residual foliage

On each 75-cm-long branch, the total amount of current-year foliage that was produced, current-year foliage that was destroyed by larvae, and residual current-year foliage that remained on each branch after budworm defoliation (i.e., an index of resistance, a net result of antibiosis and tolerance) was assessed, as described by Bauce (1996).

4.4.3 Foliar chemical content

For foliar chemical analysis, we collected branches once during the growing season from each tree that had been selected for field-rearing. Foliar chemistry was determined on each sample tree using two randomly selected, north-northwest-facing, mid-crown branches. These had been neither used for field insect rearing nor infested with budworm. This branch collection was done when the budworm-infested branches were collected (at the pupal stage; 16-22 July). Branches that were used for chemical analysis had not been enclosed within fine-mesh cloth sleeve cages; we assumed that sleeve cages did not alter foliage chemistry and quality for spruce budworm. Fresh foliage (3 g) was collected on each sample tree (n = 160 samples), returned to the laboratory on dry ice, and maintained at -20°C until it could be analysed for protein, mineral nutrients (P, K, Ca, Mg), total soluble sugars, total tannins, hydrolysable and condensed tannins, and total phenolic content. Assays were conducted using methods that were described by Bauce (1996) and Bauce et al. (2006). Moisture content was determined on two subsamples of 15 current-year twigs. Two additional subsamples of fresh twigs were collected from each tree, placed in crimp seal vials, and kept at -20°C until needle monoterpene concentrations could be analysed by gas chromatography, as described by Bauce et al. (1994).

4.4.4 Winter biology and performance of budworm progeny

Adults that had been collected from the field-rearing experiment were mated to obtain the F1 generation. We formed 15 individual mating pairs in each experimental unit and for each host tree species. The number of eggs laid by each female during its lifetime, the number of fertile eggs, first-instar larvae survival (%), and the subsequent number of second-instar larvae entering diapause were recorded. Larvae were placed in an outdoor insectarium during their winter diapause and winter survival was evaluated the following spring.

4.4.5 Statistical analyses

The experimental design was adapted to separately test the interactions of main effects (drainage, thinning, time) for each host species. The primary spruce budworm host (balsam fir) was present in all 40 experimental units. White spruce were selected in drainage class 2, 3 and 4, while black spruce, which grows only on drainage class 5 in the ecological domain that we studied, was selected in this drainage class. Statistical analyses were performed for an incomplete split-split-plot factorial design with 4 replicates, with block(drainage) as the main error term. Whole plots corresponded to drainage class (4 levels), sub-plots to thinning treatments (3), and sub-sub-plots to time (4 years). Since black spruce could only be found in drainage class 5, it was necessary to replace a main experimental design factor (drainage) with the factor "species." Here, whole plots corresponded to species (black spruce vs. balsam fir), with block(species) as the error term (Table 4.1). The incomplete block structure was due to the inability to thin on drainage class 2.

Table 4.1 ANOVA table of split-plot design used to test the impact of thinning intensity[1], soil drainage quality[2] and time[3] on the resistance of three host trees species[4] against spruce budworm.

Balsam fir		White spruce		Black spruce	
Source of variation		Source of variation		Source of variation	
Drainage	3	Drainage	2	Species	1
Block(Drainage)	9	Block(Drainage)	6	Block(Species)	3
Thinning	2	Thinning	2	Thinning	2
Drainage*Thinning	4	Drainage*Thinning	2	Thinning*Species	2
Block(Drainage*Thinning)	18	Block(Drainage*Thinning)	12	Block(Species*Thinning)	12
Years	3	Years	3	Years	3
Years*Drainage	9	Years*Drainage	6	Years*Species	3
Years*Thinning	6	Years*Thinning	6	Years*Thinning	6
Years*Drainage*Thinning	12	Years*Drainage*Thinning	6	Years*Species*Thinning	6
Error	93	Error	66	Error	57
Total	159	Total	111	Total	95

[1] Control (0%), Light (25%) and Heavy (40%) thinning intensity.

[2] (Rapid drained soil (class 2), mesic with seepage (class 3), subhygric (class 4), hydric (class 5).)

[3] Four years (2004, 2006, 2007, 2009).

[4] Balsam fir (*A. balsamea*), White spruce (*P. glauca*), Black spruce (*P. mariana*).

Normality and homogeneity of variance tests were performed, after which the data were subjected to multivariate analysis of variance (MANOVA) on each of the following groups of variables: spruce budworm biological performance (i.e., pupal mass, developmental time, frass production, insect survival); winter biology of budworm progeny (i.e., winter survival, number of eggs laid, number of infertile eggs); host tree monoterpenes, host tree tannins and phenols, and nutrients (i.e., N, P, K, Ca, Mg, and sugar concentrations); and host tree response variables (i.e., defoliation, foliage produced, foliage destroyed, residual foliage, diameter at breast height (DBH)). Black spruce monoterpenes were divided into those that have been reported in the literature as oviposition stimulants and those reported as toxic to the insect (For details, see Fuentealba and Bauce 2012a, b). If MANOVA found a significant treatment effect in a group of variables, data from that group were analyzed using Analysis of Variance (ANOVA) to determine which variables were affected by the factors studied (Table 4.1). Duncan's test was used for comparison of means (PROC GLM: SAS Institute 2003).

Canonical correlation analysis (CCorA) was used to examine the degree to which components of insect performance were correlated with each foliar chemistry group of variables (PROC CANCORR, SAS Institute, 2003). Finally, the variable developmental time (DT), was transformed into developmental rate (DR) by using the following formula: DR= 1/DT.

4.5 Results

4.5.1 Field-rearing

Thinning intensity affected the adult performance of budworm individuals reared on balsam fir (Table 4.2A); specifically, female mass ($F_{2,18}$ = 7.61, P = 0.004). Mean masses for females were higher in thinned stands compared with control treatment (Figure 4.1). In contrast, thinning intensity did not influence the performance of budworm individuals reared on white spruce (Table 4.2B) and black spruce (Wilks' Lambda: $F_{6,20\ \text{thinning}} =$ 1.21, P = 0.3411). In contrast to thinning intensity, drainage class did not directly affect spruce budworm performance on balsam fir and white spruce (Table 4.2). Finally, there were no significant differences between performances of insects reared on balsam fir and black spruce (Wilks' Lambda: $F_{3,1\ \text{species}} =$ 0.361, P = 0.8048).

Canonical correlation analysis (CCorA) revealed a significant correlation between spruce budworm performance and the nutrient data ($R_c^2 = 0.66$, Wilks' Lambda: $F_{30,870} = 7.18$, $P=<0.0001$). Only the first canonical variate for insect performance was significant. The canonical structure coefficients showed that female and male developmental rates were positively associated with the first canonical variate of insect performance ($r>|0.45|$). Nitrogen and potassium coefficients on the first canonical variate of insect performance suggested that these nutrients have a positive effect on female and male developmental rate (Table 4.3). Furthermore, spruce budworm performance and monoterpene data were significantly correlated, according to CCorA ($R_c^2 = 0.61$, Wilks' Lambda: $F_{60,1529} = 7.18$, $P=<0.0001$). Again, only the first canonical variate for insect performance was significant. In this analysis, the canonical structure coefficients showed that female mass and frass production were negatively associated with the first canonical variate of insect performance ($r > |0.45|$). Coefficients for bornyl acetate, α-pinene and limonene-β-phellandren indicated that these monoterpenes negatively affected female mass and frass production (Table 4.3). According to CCorA, spruce budworm performance and the tannin and phenolics data set were significantly correlated ($R_c^2 = 0.61$, Wilks' Lambda: $F_{18,730}=9.71$,$P=<0.0001$).

Table 4.2 Multivariate analysis of variance (MANOVA) for balsam fir and white spruce groups of variables and biological performance of spruce budworm larvae reared on the aforementioned host tree species. P-values and F- approximation of Wilks' Lambda (df numerator, df denominator) from MANOVA with block(drainage) and block(drainage*treatment) as error terms. Numbers in bold indicate statistically significant effects at *P* = 0.05.

A) Balsam fir

	Adult performance[a]		Progeny performance[d]		Tree response[b]		Monoterpenes		Tannins and Phenols		Nutrients[c]	
Source	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*
Drainage	0.0692	18,11	0.082	9,17	**0.0022**	12,16	0.1020	27,3	0.6224	9,17	0.1652	18,11
Thinning	**0.0042**	12,26	**0.0042**	6,32	**0.001**	8,30	**0.0444**	18,20	0.1264	6,32	**0.033**	12,26
Drainage*Thinning	0.6399	24,46	0.1128	12,42	0.7976	16,46	0.3869	36,39	0.4714	12,42	0.3986	24,46
Years	**<.0001**	18,37	**<.0001**	9,39	**<.0001**	12,39	**<.0001**	27,29	**<.0001**	9,39	**<.0001**	12,26
Years*Drainage	0.1524	54,70	0.1259	27,47	0.5058	36,57	0.6749	81,73	**<.0001**	27,47	**0.0401**	36,59
Years*Thinning	0.1259	36,59	0.1089	18,45	**0.0256**	24,53	0.0604	54,55	0.37	18,45	0.6318	24,46
Years*Drainage*Thinning	0.0955	72,76	0.2341	36,48	0.9375	48,59	0.9819	108,85	0.1165	36,48	0.7625	48,68

B) White spruce

	Adult performance[a]		Progeny performance[d]		Tree response[b]		Monoterpenes		Tannins and Phenols		Nutrients[c]	
Source	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*	*P*	*df*
Drainage	0.24	12,2	0.4889	6,8	0.1073	8,6	0.0723	15,5	0.1031	6,8	0.4297	12,2
Thinning	0.1115	12,14	0.2416	6,20	**0.0448**	8,18	0.1594	18,8	0.6627	6,20	0.4116	12,14
Drainage*Thinning	0.3382	12,14	0.2233	6,20	0.241	8,18	0.143	18,8	0.137	6,20	0.4017	12,14
Years	**<.0001**	18,20	**<.0001**	9,24	**0.0003**	12,24	0.4549	9,4	**<.0001**	9,24	**<.0001**	12,14
Years*Drainage	0.5946	36,33	0.8888	18,28	0.5529	24,32	0.3592	18,8	0.2077	18,28	0.1209	24,25
Years*Thinning	0.2176	36,33	0.5064	18,28	0.361	24,32	0.2783	18,8	0.849	18,28	0.1849	24,25
Years*Drainage*Thinning	0.1612	36,33	0.7959	18,28	0.998	24,32	0.39	18,8	0.1047	15,28	0.2301	24,25

[a] Pupal mass, developmental time, frass production and survival.

[b] Winter survival, number of eggs laid, number of infertile eggs.

[c] Defoliation (%), foliage produced, foliage destroyed, residual foliage, DBH.

[d] Concentration of N, P, K, Ca, Mg and sugars.

The canonical structure coefficients showed that insect survival, frass production, and female and male developmental rate were positively associated with the first canonical variate of insect performance ($r > |0.45|$), but these aforementioned insect performance variables were negatively correlated, in turn, with the coefficients for total tannins and total hydrolysable tannins (Table 4.3).

4.5.2 Host tree growth and vigor

For balsam fir, MANOVA showed that drainage class, thinning intensity, time and the interaction between thinning and time had significant effect on host tree growth and vigour (Table 4.2A). Thinning intensity and time also had a significant effect on white spruce (Table 4.2B) and black spruce (Wilks' Lambda: $F_{8,18\ \text{thinning}} = 3.34$, $P = 0.0161$) growth and vigour.

Thinning intensity affected balsam fir growth, but this effect varied with time, particularly for foliar production (AFP) ($F_{6,88} = 4.53$, $P = 0.0005$), and foliage remaining (ARF) ($F_{6,88} = 6.47$; df =; $P = <.0001$) following budworm defoliation, but the effect varied according to drainage quality. In mesic sites, fir that was growing in thinned stands exhibited both lower foliage production (Figure 4.2a) and a lower quantity of foliage remaining (Figure 4.2g) than those individuals growing in control stands one year post-treatment. From 2006 onwards, we observed that, in contrast to previous years, fir growing in heavily thinned stands (40%) had the greatest foliar production and quantity of foliage remaining. Lightly thinned stands (25%), in turn, exhibited greater production of foliage (Figure 4.2a) and that which remained (Figure 4.2g) than in control stands from 2007. Further, we observed a response in subhygric sites similar to that found in mesic sites. However, lightly thinned stands produced more foliage than heavily thinned stands over the long-term; in the medium-term, it was the heavy thinning intensity that produced the greatest quantity of foliage (Figure 4.2b) and that which remained (Figure 4.2h).

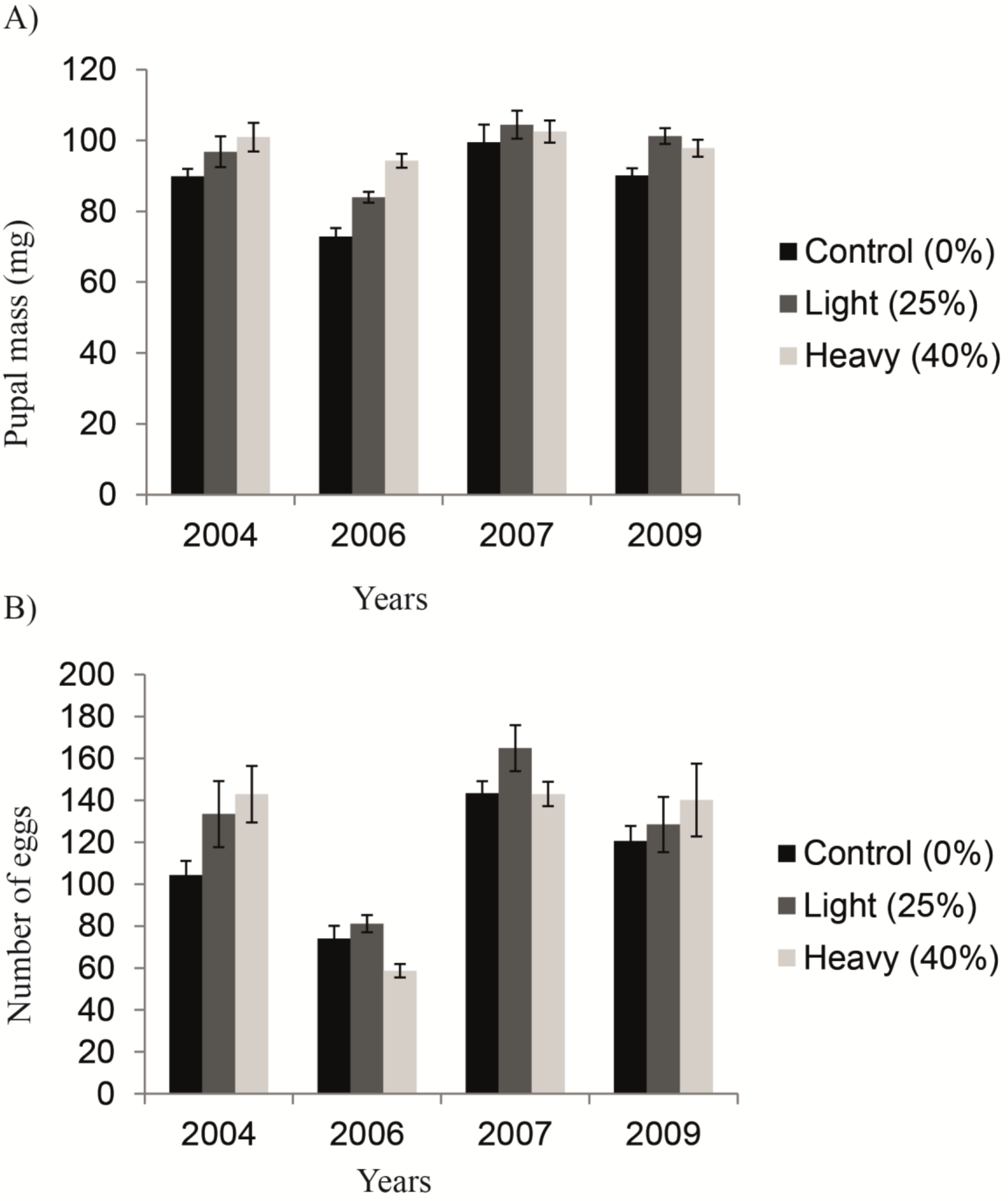


Figure 4.1 Mean (±2SEM) masses of female pupae and number of eggs laid by female spruce budworm (*C. Fumiferana*) tabulated by year in balsam fir (*A. balsamea*).

Table 4.3 Canonical structure coefficients

		Canonical structure coefficients			
a) Insect variables	C1*	a) Insect variables	C1*	a) Insect variables	C1*
Female mass	-0.2842	Female mass	-0.5590	Female mass	-0.0285
Male mass	-0.0411	Male mass	-0.2100	Male mass	0.0975
Female developmental rate	0.8541	Female developmental rate	0.0909	Female developmental rate	0.6052
Male developmental rate	0.8039	Male developmental rate	0.0419	Male developmental rate	0.7127
Insect survival	0.3722	Insect survival	0.1014	Insect survival	0.9069
Frass	-0.2807	Frass	-0.6438	Frass	0.7813
b) Nutritive elements		b) Monoterpenes		b) Tannins and phenols	
Nitrogen	0.5119	α-pinene	0.4892	Total tannins	-0.6633
Phosphorus	-0.0648	Camphene	0.4128	Total hydrolisables tannins	-0.6631
Potassium	0.6173	β-pinene	0.2927	Total phenols	0.0447
Calcium	0.2697	Myrcene	0.2471		
Sugars	-0.0098	δ-3-carene	0.2105		
		Limonene-β-phellandren	0.5188		
		Terpinolene	-0.3512		
		Thujone	0.2366		
		Borneol	0.1361		
		Bornyl acetate	0.4560		

*First canonical variate for insect performance

Lastly, thinned stands in hydric sites exhibited greater production of foliage (and that which remained) than comparable control stands from 2004 (Figure 4.2c,i). Likewise, defoliation percentage ($F_{6,88} = 7.99$, $P = <.0001$) in balsam fir exhibited a similar pattern to the amount of foliage produced and destroyed in the different drainage classes (Figure 4.3).

Drainage class had a significant overall effect on balsam fir resistance, based on the quantity of current-year foliage that had been destroyed (AFD). Foliar destruction was lowest in drainage class 2 (3.4037g), and increased monotonically as drainage quality worsened (Drainage class 3, 3.8776g; Drainage class 4, 3.9408g; Drainage class 5, 4.4837g). Duncan's test showed that only AFD on drainage class 2 and 5 were significantly different. Trees growing on drainage class 3 had the greatest mean DBH ($F_{3,9} = 31.70$, $P <0.0001$) compared with those individuals growing on sites with the other drainage classes.

Thinning intensity also had a significant effect on white spruce foliar production (AFP) ($F_{2,12} = 4.59$, $P = 0.0081$), foliage remaining (ARF) ($F_{2,12} = 7.57$, $P = 0.0024$) after budworm defoliation and defoliation percentage ($F_{2,12} = 3.82$, $P = 0.0103$). However, the thinning effect varied with drainage quality. In mesic sites, thinning intensity did not significantly affect white spruce foliar production one year post-treatment (Figure 4.4a). Nevertheless, in 2006 and 2007, heavily thinned stands produced the greatest quantity of foliage (Figure 4.4a) and left the greatest quantity remaining (Figure 4.4e) after budworm defoliation, thereby rendering the remaining individuals more resistant to insect attack. Increased resistance produced by heavily thinning intensity seemed to decrease from 2007onward, since the amount of foliage (Figure 4.4a) and remaining (Figure 4.4e) decreased considerably in 2009 (Figure 4.4). In contrast, individual white spruce in subhygric sites continued to react positively from the onset of thinning, increasing the production foliage (Figure 4.4b) and that which remained (Figure 4.4f) after budworm defoliation and, therefore, tree tolerance. This tolerance lasted at least until 2009. Likewise, thinning intensity affected the overall suite of growth and vigour indicators for black spruce (Wilks' Lambda: $F_{4,22\ \text{thinning}} = 4.19$, $P = 0.0113$). Individually, black spruce foliar production (AFP) ($F_{2,12} = 8.20$, $P = 0.0057$) and foliage remaining (ARF) ($F_{2,12} =$

5.95, *P* = 0.0161) after budworm defoliation. Thinning increased the amount of foliage that was produced and that which remained and, therefore, tree tolerance from 2007 to 2009 (Fig. 5).

Drainage class had a significant overall effect on balsam fir performance based on amount of current-year foliage destroyed (AFD). The amount of foliage destroyed was lowest on drainage class 3, increasing as drainage quality worsened (Figure 4.2). Trees growing on drainage class 3 had the greatest DBH (*F* = 31.70; df = 3,9; *P* <0.0001) compared with those growing on the other drainage classes.

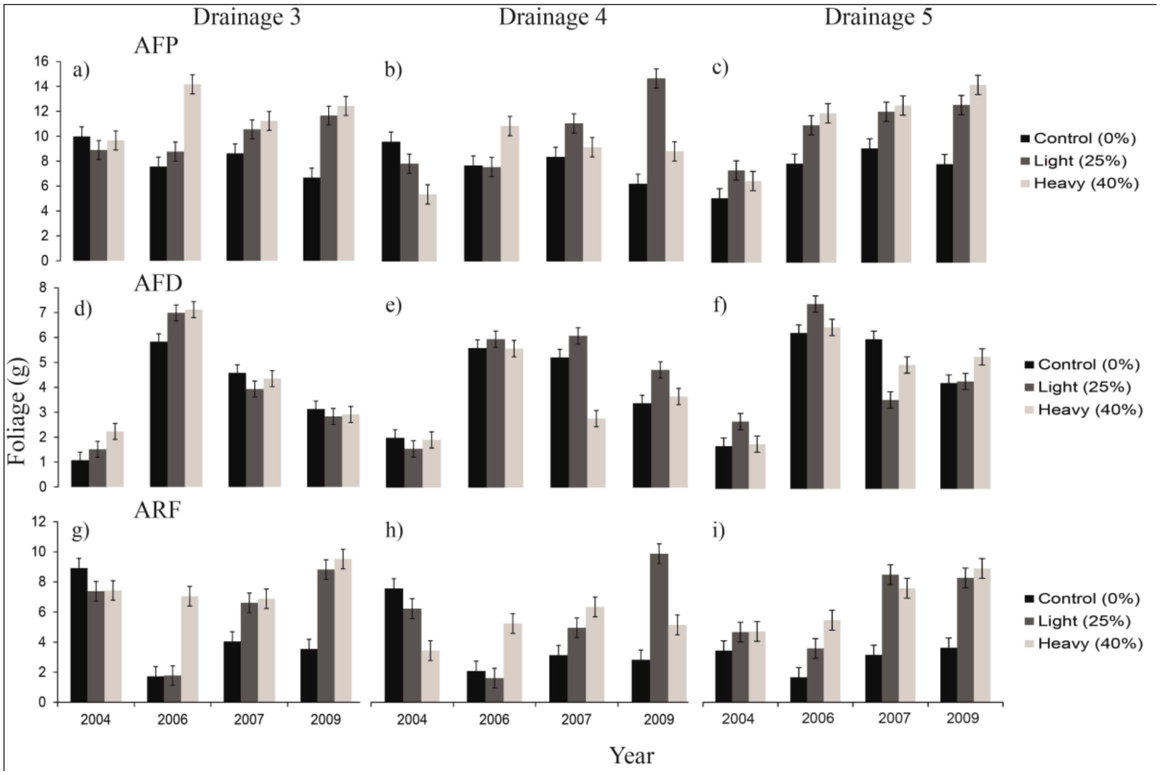


Figure 4.2 Amount of residual current-year foliage remaining (ARF), amount of current-year foliage produced (AFP), and amount of current-year foliage destroyed (AFD) in balasam fir (*A. balsamea*) tabulated by thinning intensity, drainage class, and year (mean ± 2SEM).

4.5.3 Foliar chemical content

Chemical analysis indicated that balsam fir monoterpene concentrations were affected by thinning and time (Table 4.2A), more specifically camphene, δ-3-carene and terpilonene (Table 4.4). Concentration of camphene was higher on control stands, except in 2009 (Table 4.4). Concentration of δ-3-carene was higher on control stands throughout the study period, whereas the concentration of terpilonene was higher on thinned stands, except in 2007 (Table 4.4). Concentrations of monoterpenes in white spruce foliage were affected neither by treatment nor drainage class (Table 4.2B). As for black spruce, thinning did not significantly affect monoterpene concentrations (Wilks' Lambda: $F_{\text{thinningG1}} = 0.41$; df = 10,16; $P = 0.9224$; $F_{\text{thinningG2}} = 1.09$; df = 10, 16; $P = 0.4418$).

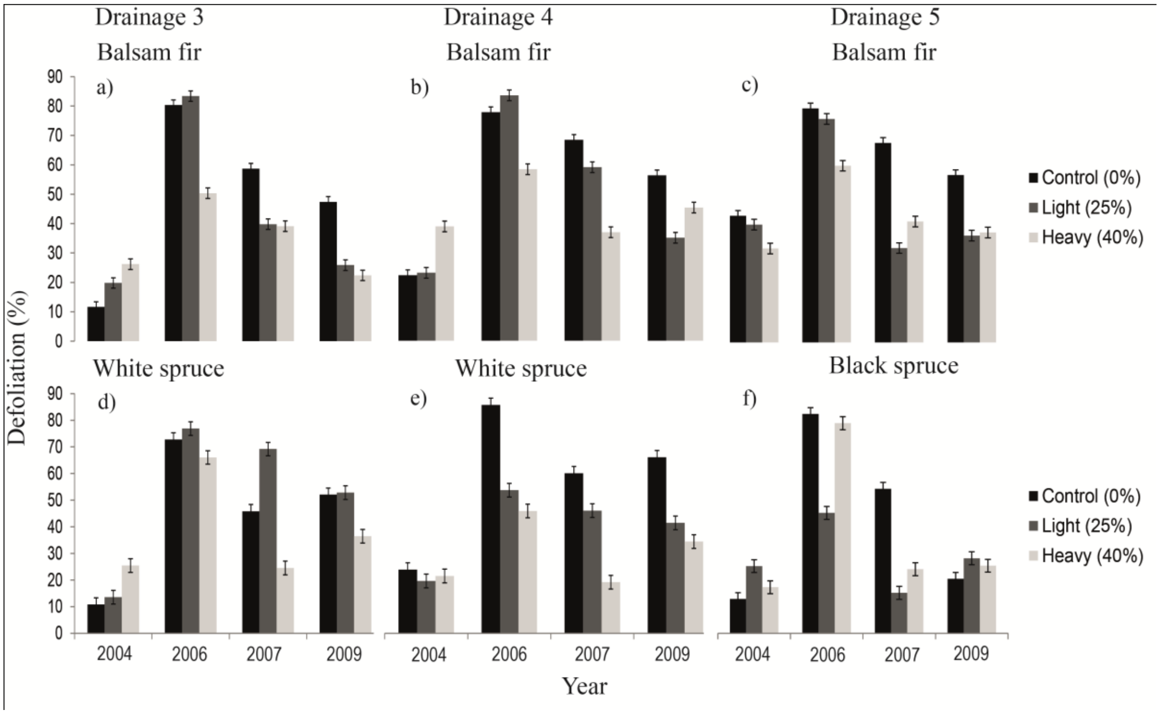


Figure 4.3 Defoliation by spruce budworm (*C. Fumiferana*) larvae reared in sleeve cages on foliage of *Abies balsamea*, *Picea glauca*, and *P. mariana* tabulated by thinning intensity, year and host tree species (mean ± 2SEM).

Foliar nutrient concentrations of balsam fir were influenced by thinning, time and time x drainage class interaction (Table 4.2A). Individuals growing on control stands had the greatest foliar K concentrations (Table 4.4). Concentrations of foliar nitrogen increased as drainage quality improved. This phenomenon was observed to a greater or lesser extent during the whole study period. In contrast, thinning and drainage class did not affect nutrient concentrations in white spruce (Table 4.2B) and black spruce (Wilks' Lambda: $F_{\text{thinning}} = 0.98$; df = 6,20; P= 0.4653).

Thinning and drainage class did not affect tannin and phenol concentrations in balsam fir and white spruce (Table 4.2). Furthermore, concentrations of tannins and phenols in black spruce were not affected by thinning intensity (Wilks' Lambda: $F_{\text{thinning}} = 0.53$; df = 6,20; $P = 0.7795$). Finally, there were no significant differences in concentrations of tannins and phenols between black spruce and balsam fir (Wilks' Lambda: $F_{\text{species}} = 6.05$; df = 3,1; $P = 0.2884$).

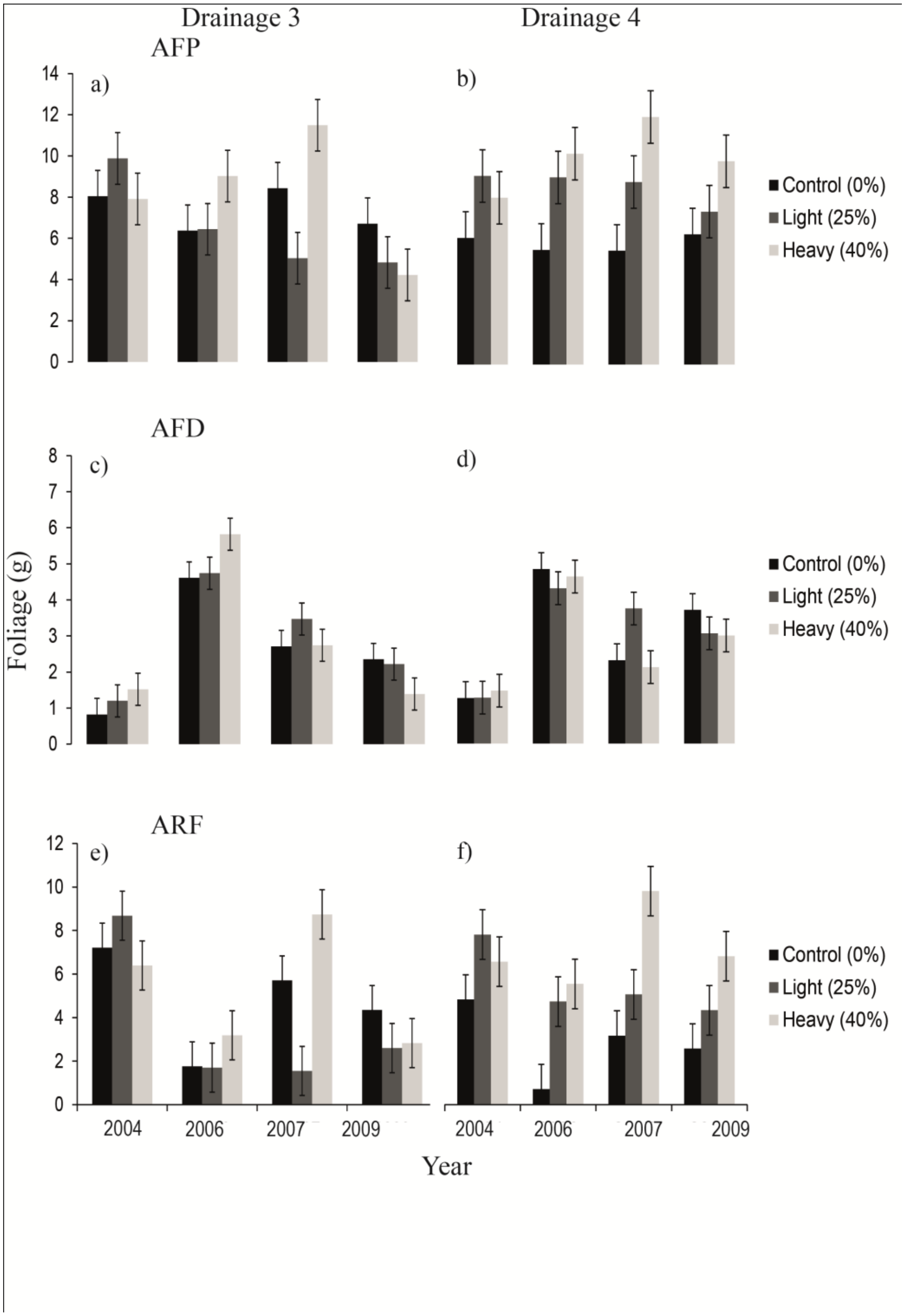


Figure 4.4 Amount of residual current-year foliage remaining (ARF), amount of current-year foliage produced (AFP), and amount of current-year foliage destroyed (AFD) in White spruce (*P. glauca*) tabulated by thinning intensity, drainage class, and year (mean ± 2SEM).

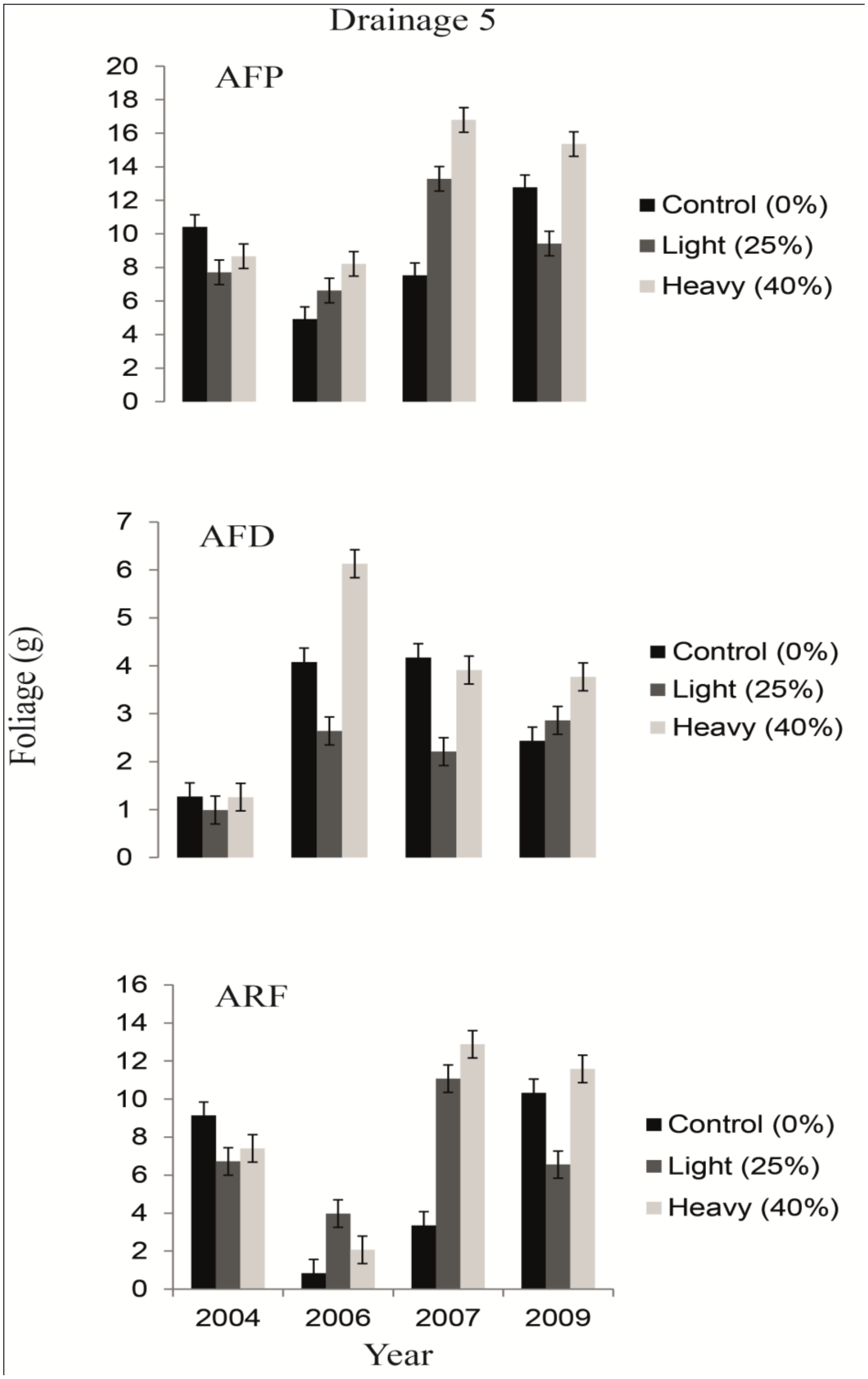


Figure 4.5 Amount of residual current-year foliage remaining (ARF), amount of current-year foliage produced (AFP), and amount of current-year foliage destroyed (AFD) in Black spruce (*P. mariana*) tabulated by thinning intensity and year (mean ± 2SEM).

Table 4.4 Monoterpene and Nutrient concentrations in balsam fir (*A. balsamea*) needles by thinning intensity[1] (Means ± SEM).

Parameter	Thinning intensity (%)					
	0	25	40	*F*	*df*	*P*
Camphene (ng/mg)	1190.70 ± 131.15a	1048.89 ± 125.36b	1138.16 ± 146.13ab	4.01	2,18	0.0362
δ-3-carene (ng/mg)	718.52 ± 149.40a	326.68 ± 81.53b	685.28 ±124.99a	4.12	2,18	0.0336
Terpilonene (ng/mg)	48.95 ±4.88a	36.17 ±5.60b	48.72 ± 4.87a	4.15	2,18	0.033
K (µg/g)	5861.10 ± 400.60a	5659.57 ±435.60b	5576.31 ± 437.24b	6.24	2,18	0.0087

Values in each row followed by the same letter do not differ significantly at *P* = 0.05 according to Duncan multiple range test.

4.5.4 Winter biology and performance of budworm progeny

The winter biology of budworm progeny reared on balsam fir was only affected by thinning intensity (Table 4.2A). The treatment affected average number of eggs laid by females (Figure 4.1). In contrast, thinning intensity did not affect winter biology of budworm progeny reared on white spruce (Table 4.2B) and black spruce (Wilks' Lambda: F_{thinning} = 0.64; df = 6,20; *P* = 0.6997). Furthermore, drainage class did not have a significant effect on winter biology of budworm progeny that had been reared on balsam fir and white spruce (Table 4.2), and there were no significant differences in winter biology of budworm progeny between black spruce and balsam fir on hydric sites (Wilks' Lambda: F_{species} = 0.28; df = 3,1; *P* = 0.8467).

4.6 Discussion

Our results, together with those reported by Fuentealba and Bauce (2012a,b), allow us to understand why previous works yielded equivocal results regarding thinning effect on host tree resistance to spruce budworm. We observed that balsam fir antibiosis was affected by this sylvicultural tool one year after treatment application. Indeed, foliar concentration of certain monoterpenes such as bornyl acetate and camphene decreased as a result of thinning (Fuentealba and Bauce 2012a). Some monoterpenes, such as bornyl acetate, and camphene, have been found to be toxic to budworm larvae because they affect survival, growth, development and food utilization (Bauce et al. 1994, Kumbaşli et al. 2011, Mattson et al. 1991); therefore, the reduction in monoterpene concentration may have favoured insect performance and increased the amount of foliage destroyed which rendered the remaining trees more susceptible to spruce budworm damage. However, this effect varied according drainage class quality. Balsam fir individual growing on hydric sites showed a positive response from the first year after the treatment (Figure 4.2) probably because this species is ill-adapted to grow on wet sites (Hix et al. 1987); therefore, thinning produced a positive effect on remaining trees by reducing tree competition for the scarce resources available.

Three years after the treatment, the conditions were still excellent for spruce budworm because of the high concentration of foliar N and P found in balsam fir growing in heavy thinned stands (Fuentealba and Bauce 2012b). Both nutrients are very important for spruce budworm growth, development and survival (Bidon 1993, Carisey and Bauce 1997, Fuentealba and Bauce 2012a, Mattson et al. 1983, 1991, Schmitt et al. 1983). The importance of these nutrients is confirmed by CCA (Table 4.3). Nevertheless, remaining individuals of balsam fir (Figure 4.2) and white spruce (Figure 4.4) growing in heavy thinned stands were capable of increasing their foliar production, resulting in an increase capacity to tolerate spruce budworm defoliation. It is noteworthy that lighter thinning intensities could only increased balsam fir tolerance on hydric sites (Figure 4.2) and white spruce tolerance on subhygric sites (Figure 4.4) probably because these species are not well-adapted to grow in poorly-drained sites (Hix et al. 1987, Wang and Klinka 1995). Consequently, the reduction of the number of trees competing for the limited resources in this kind of sites produced by thinning may allow the remaining trees to increase foliage production and, therefore, tree tolerance. Although black spruce was not significantly affected by thinning, this species produced more foliage in thinned stands than in unthinned stands, increasing residual foliage and, therefore, black spruce tolerance (Figure 4.5) (Fuentealba and Bauce 2012b).

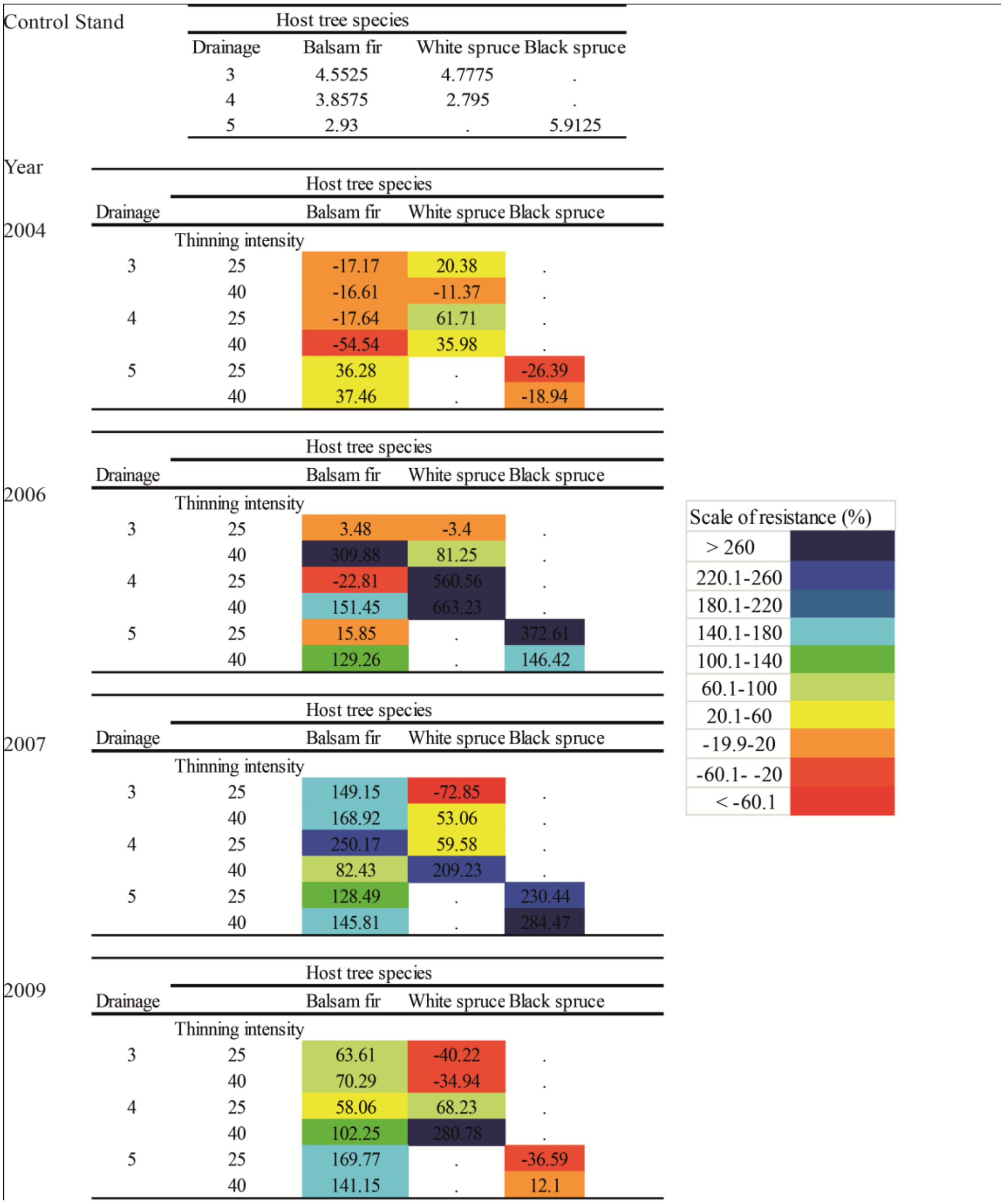
Four years after the treatment, however, black spruce started to show a positive significant response to the treatment by increasing its foliar production as compared with trees coming from control stands on hydric sites (Figure 4.5). This late response of this species as compared with that of balsam fir and white spruce could be explained either by the greater shade tolerance of black spruce ((Lamhamedi and Bernier 1994) in relation to the other tree species studied, which may results in a lower capacity to enhance its efficiency in light utilization (Goudiaby et al. 2011), by the number of samples used in this study, or by the fact that black is well-adapted to grow in poorly-drained sites (Hix et al. 1987), which may produce a delayed response to the better conditions provided by the treatment. For example, Goudiaby et al. (2012) observed significant positive stem volume increments four years after thinning was conducted. Hillman and Takyi (1998) reported that thinning increased total volume growth of black spruce trees two times after six growing seasons and Vincent et al. (2009), using heavier thinning intensities, reported that positive effect of this treatment on black spruce became apparent from the second year. What is clear now, however, is that black spruce foliage production offset the amount of foliage destroyed by spruce budworm which in turn increased its tolerance to this insect for at least 2 years (Figure 4.5). A similar response was observed in balsam fir individuals growing on light and heavy thinned stands in all drainage classes (Figure 4.2). This increased tolerance persisted until the end of the study period. In contrast, remaining white spruce individuals growing only on drainage class 4 showed a positive response to thinning from 2007 to the end of the study (Figure 4.3). The increased tolerance is lost in white spruce six years after the treatment on mesic sites. This response was unexpected because this species is well-adapted to grow on well-drained sites (Wang and Klinka 1995) and respond positively to thinning on these good quality sites (Stiell 1980). Unfortunately, the parameters measured in the current study do not allow us to explain the cause of this pattern. Examination of the tree root system and nutrient uptake may help us to explain the reduction of white spruce tolerance in thinned stands occurring on mesic sites reported in this study.

The results reported here suggest that tolerance is more important than defense in the resistance of host tree species studied to spruce budworm. Concentrations of secondary compounds such as monoterpenes and tannins started to stabilize three years after the treatment but insect performance was not affected (Fuentealba and Bauce 2012b) perhaps because negative effects of increased secondary compound concentrations on host quality were offset by positive effects of increased foliar nutrients such as nitrogen and phosphorous. On the other hand, it has been suggested that tolerance plays a role more important than generally acknowledge in tree resistance because of their large size and long lifespan make them more apparent than herbaceous plants to herbivores (Feeny 1976), increasing the risk of losing some of their biomass to herbivores (Haukioja and Koricheva 2000). Furthermore, their defense mechanisms do not completely exclude damage (Haukioja and Koricheva 2000, Bauce et al. 2001); therefore, the capacity to tolerate and recover from defoliation becomes very important for trees. Given the importance of tolerance as mechanism of resistance, treatments designed to increase it (like thinning) should be successful in decreasing tree vulnerability to spruce budworm. Consequently, the use of this kind of treatments should be encouraged to reduce the losses produced by this insect.

As for the insect performance, it seems that the positive effects of thinning start to gradually disappear with the passage of time. Thinning favoured only female pupal mass throughout the study period (Figure 4.1). Although reductions in certain monoterpene concentrations (Bauce 1996, Fuentealba and Bauce 2012a) and increases in foliar nitrogen and phosphorus (Fuentealba and Bauce 2012b) produced by thinning have resulted in increased pupal mass on the short and medium term respectively, these phenomena cannot explain the persistence of high female pupal mass on the long term. The reduction in foliar potassium caused by thinning on the long term may provide some clue to understanding the best performance of females on heavy thinned stands (Table 4.4). CCA found that there is a weak negative correlation between this nutrient and female pupal mass (Table 4.3). It has been suggested that decreases in foliar potassium may have negative effects over trees such as a decrease in volume growth and basal area (Truong and Gagnon 1975), photosynthesis and the size and number of resin ducts (Jokela et al. 1997), which may compromise the accumulation of monoterpenes, and thus the tree capacity to defend itself against the spruce budworm and other pathogens agents (Burr and Clancy 1993). Mattson et al. (1991) found that budworm growth was negatively correlated with potassium foliar content. The authors assumed that potassium was highly correlated with some tree defensive trait that caused the effect; therefore, the slightly higher foliar potassium concentration found in control stands could explain the differences in female pupal mass. These results show that, despite having favoured parental and progeny performance of spruce budworm (Figure 4.1), thinning intensity increased host tree tolerance to a level that resulted in overall increased host tree resistance to the insect on medium to long term.

4.7 Management implications

Forest managers have to choose the best management options that would optimise forest functions and maximise forest values, while reducing insect damage. These decisions can subsequently influence forest susceptibility to insect pest damage. However, information regarding the effects of silvicultural practices such as thinning on tree and stand susceptibility to spruce budworm is equivocal. Our results have suggested that thinning can be used as a preventive measure by increasing overall host tree resistance and, therefore, decreased tree and stand susceptibility. Figure 4.6 has provided a summary of mean residual foliage mass in control stands and the responses of the three host tree species that were used in this study to the treatments, according to drainage class and thinning intensity by year. Variation in stand resistance can be obtained by comparing the quantities of residual foliage present in thinned stands versus control stands. The results (expressed as a percentage) are then classified according to a scale of resistance. This classification system would allow the forest managers to determine whether the thinning effect on the remaining trees is positive or negative, and how this effect may develop over time in the different drainage classes. These responses could facilitate the decision-making process, as to when and where to conduct this silvicultural treatment and what is the best intensity to obtain the intended increase in resistance. For example, let us assume that a forest manager has a stand composed of balsam fir and black spruce individuals growing on hydric sites and that he or she wishes to determine the effect of thinning on stand resistance to spruce budworm. By checking the resistance classification system (Figure 4.6), we can observe that thinning would increase balsam fir resistance from the first year onward, but a heavy thinning intensity would produce the greatest increases throughout the six-year period. In the case of black spruce, thinning would produce little reduction in its resistance during the first year after treatment, but three years after thinning, black spruce resistance would increase until the positive effect of the treatment starts to disappear by the sixth year. Consequently, the forest manager could apply thinning to increase stand resistance without resorting to complementary treatments that would protect black spruce against spruce budworm, given that this tree species is less prone to being defoliated by spruce budworm because of late budbreak (Blais, 1957; Greenbank, 1963) and given that its foliage is rich in toxic compounds detrimental to insect performance (Thomas, 1989; Fuentealba and Bauce, 2012c). These traits have rendered black spruce less susceptible, resulting in lower defoliation and growth reduction when compared with balsam fir (Henningar et al., 2008; Pothier et al., 2012). If thinning were to be applied in pure balsam fir stands that were growing on mesic or subhygric sites, it would be advisable to conduct this treatment in tandem with aerial *Btk* sprays to protect the remaining trees during the period of low resistance to the insect (See Figure 4.6).



Control Stand

	Host tree species		
Drainage	Balsam fir	White spruce	Black spruce
3	4.5525	4.7775	.
4	3.8575	2.795	.
5	2.93	.	5.9125

Year

2004

Drainage	Thinning intensity	Balsam fir	White spruce	Black spruce
3	25	-17.17	20.38	.
	40	-16.61	-11.37	.
4	25	-17.64	61.71	.
	40	-54.54	35.98	.
5	25	36.28	.	-26.39
	40	37.46	.	-18.94

2006

Drainage	Thinning intensity	Balsam fir	White spruce	Black spruce
3	25	3.48	-3.4	.
	40	309.88	81.25	.
4	25	-22.81	560.56	.
	40	151.45	663.23	.
5	25	15.85	.	372.61
	40	129.26	.	146.42

2007

Drainage	Thinning intensity	Balsam fir	White spruce	Black spruce
3	25	149.15	-72.85	.
	40	168.92	53.06	.
4	25	250.17	59.58	.
	40	82.43	209.23	.
5	25	128.49	.	230.44
	40	145.81	.	284.47

2009

Drainage	Thinning intensity	Balsam fir	White spruce	Black spruce
3	25	63.61	-40.22	.
	40	70.29	-34.94	.
4	25	58.06	68.23	.
	40	102.25	280.78	.
5	25	169.77	.	-36.59
	40	141.15	.	12.1

Scale of resistance (%)	
> 260	⬛
220.1-260	🟦
180.1-220	🟦
140.1-180	🟦
100.1-140	🟩
60.1-100	🟩
20.1-60	🟨
-19.9-20	🟧
-60.1- -20	🟥
< -60.1	🟥

Figure 4.6 Classification of resistance of thinned stands as compared with control stands. The mean amount of residual foliage (g) on control stands and the variation in residual foliage (%) in the three host tree species used in this study to the treatment is reported according to drainage class and thinning intensity by year. The variation in stand resistance is obtained by comparing the amount of residual foliage of thinned stands to that of control stands. The results (expressed in percentage) are then classified according to a scale of resistance.

The effectiveness of thinning, however, would be quite different, depending on where and when (i.e., prior to or during an outbreak) the treatment was being implemented. Thinning should be more effective in reducing budworm damage if it is conducted during the low density phase of budworm populations; otherwise, such a course of action could increase tree vulnerability to the insect (Piene, 1989; MacLean and Piene, 1995; Bauce, 1996; Fuentealba and Bauce, 2012a). This silvicultural practice has been proven effective in increasing resistance at the tree and stand level, but we do not know what is the impact of this technique at the landscape level or if it can alter budworm outbreaks. It is unlikely that budworm outbreaks could be eliminated using current forest management practices. However, these practices may influence the scale, periodicity, or duration of the outbreaks (Robert et al., 2012). Silvicultural treatments at the stand-level by themselves cannot influence defoliator outbreaks (Muzika and Liebhold, 2000), but their cumulative effects at the landscape-level may affect budworm outbreaks (Robert et al. 2012) and, therefore, reduce their impacts. For example, Campbell et al. (2008) found that the hardwood content of forests surrounding mature balsam fir-spruce stands can significantly reduce growth reductions elicited by spruce budworm, suggesting that increasing hardwood content of forest landscapes could be useful in reducing the effects of budworm outbreaks on timber supplies. Furthermore, fragmentation of the landscape that is created by forest management may delay the response of natural enemies to increases in budworm populations (Capuccino et al., 1998), thereby affecting the intensity and duration of its outbreaks (Robert et al., 2012). Appropriate selection of practices, and the timing and scales at which they are applied are key to achieving reductions in wood losses and tree mortality. Consequently, forest management plans that aim to reduce damages incurred by this defoliator should consider applying suites of different silvicultural techniques, such as thinning, increasing non-host tree species and aerial spray applications of *Btk*, to successfully reduce landscape susceptibility to the insect.

4.8 Conclusions

Our findings have lent support to the notion that thinning treatments can be used to increase tree and stand resistance to low population levels of spruce budworm. Thinning not only increased balsam fir and black spruce resistance to spruce budworm but this increased resistance lasted several years in balsam fir and black spruce. The same response was observed in white spruce individuals that were growing on subhygric sites. The increase in host tree resistance is important because it would allow decreasing host tree and stand susceptibility to spruce budworm. Increased resistance would enable trees to withstand and recover from defoliation, while attenuating stand wood losses attributed to tree mortality and volume growth reductions. These results have reinforced the conclusions of Fuentealba and Bauce (2012b), viz., thinning may be used to reduce the damage produced by spruce budworm because host trees increased their resistance for a period sufficiently long enough (6 years) to withstand spruce budworm defoliation. Attacks by this insect can lead tree death after 4-5 years of severe defoliation (Blais, 1979), which correspond to a local-scale spruce budworm outbreak. Our resistance classification system would be useful to forest managers in plannning thinning and aerial sprays of *Btk* schedules to reduce spruce budworm effects at the stand level. However, thinning should be accompanied by other silvicultural practices that would reduce the impact of this defoliator at the landscape level; otherwise, the implementation of thinning alone could produce the opposite outcome. Finally, it should be kept in mind that our results apply to a moderate-sized spruce budworm population (20 larvae per branch). A degree of uncertainty still exists as to whether this additional resistance will be sufficient on withstanding budworm defoliation in case host trees face higher densities of this insect or if all trees within the stand will respond in the same manner to the treatment. The ongoing outbreak in eastern Quebec provides a good opportunity to test our findings.

4.9 Acknowledgements

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5. Chapitre 4

Carry-over effect of host nutritional quality on performance of spruce budworm progeny

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5.1 Résumé

L'effet de la qualité nutritionnelle sur la performance d'une génération parentale de la tordeuse des bourgeons de l'épinette (TBE) (*Choristoneura fumiferana* (Clemens)) et de sa progéniture a été étudié à l'aide des élevages de l'insecte dans le terrain et en laboratoire et des analyses chimiques foliaires. Du feuillage du sapin baumier (*Abies balsamea* (L.) Mill.), de l'épinette blanche (*Picea glauca* (Moench) Voss) et de l'épinette noire (*P. mariana* (Mill.) BSP) a été utilisé pour élever la génération parentale dans le terrain, alors qu'une diète artificielle a été utilisée pour élever la progéniture en conditions de laboratoire. Des différences importantes dans la qualité de la nourriture fournis par les trois essences hôtes ont été détectés. Le feuillage de l'épinette noire avait des concentrations plus élevées de certains monoterpènes dissuasifs et de composés phénoliques totaux, avec fortes baisses saisonnières des éléments nutritifs tels que N, P et Mg, par rapport aux autres essences hôtes. Nous formulons l'hypothèse que cette tendance pourrait être liée à une mauvaise performance et à une basse de la survie de la progéniture. L'élevage en laboratoire a montré que les descendants des parents qui se sont nourrit du feuillage de l'épinette noire ont présenté un temps de développement plus long, une plus grande mortalité, une plus faible masse de chrysalides par rapport aux descendants de parents qui se sont nourrit du feuillage d'autres essences hôtes utilisées dans cette étude. En outre, la progéniture des insectes élevés sur feuillage de l'épinette noire a atteint le sixième stade larvaire plus tard, avec moins de masse, et a montré un taux de croissance relative (RGR) plus haut par rapport à la progéniture des insectes élevés sur feuillage d'autres essences hôtes utilisées dans cette étude. Ces résultats suggèrent l'existence des effets parentaux liés à la qualité nutritionnelle de la nourriture. Ces résultats ont également confirmé que la qualité de la nourriture consommée par les parents peut influencer le fitness de la prochaine génération.

Carry-over effect of host nutritional quality on performance of spruce budworm progeny

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Running title: Host nutritional quality and spruce budworm performance

5.2 Abstract

The effect of host nutritional quality on spruce budworm (*Choristoneura fumiferana* (Clemens)) parental and offspring performance was studied using field and laboratory rearing experiments, and foliar chemical analyses. Foliage of balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*P. mariana* (Mill.) BSP) was used to rear the parental generation in the field, whereas an artificial diet was used to rear the progeny under laboratory conditions. Important differences in the food quality were provided by the three hosts. Black spruce foliage had higher concentrations of certain monoterpene deterrents and total phenolics, together with stronger seasonal declines in nutrients such as N, P and Mg, compared with the other hosts. We hypothesise that this trend may be related to poor performance and survival of the progeny. Laboratory rearing showed that progeny fed on artifitial diet and from parents that fed on black spruce exhibited longer developmental times and greater mortality, and had lower pupal mass than progeny of parents fed on the other hosts. Further, artificial food-fed progeny of insects reared on black spruce reached sixth-instar later, with lower mass, and exhibited higher relative growth rate (RGR) than progeny of parents fed on the other hosts. These results suggest nutritionally-based parental effects. These results also confirmed that the quality of food consumed by the parents can influence the fitness of the next generation.

5.3 Introduction

The eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), is the most destructive insect pest in the maritime and boreal forests of North America. Populations of this forest defoliator have reached outbreak densities over extensive forested areas on a fairly regular basis for the past three centuries, at the very least (Blais, 1965). Losses to the forest products industry that could be attributed to spruce budworm during its last outbreak amounted to 44 million m^3 of wood per year (Sterner & Davidson 1982). Budworm feeds on several conifer hosts, most preferably on balsam fir (*Abies balsamea* (L.) Mill.), followed by white spruce (*Picea glauca* (Moench) Voss), red spruce (*P. rubens* Sarg.), and black spruce (*P. mariana* (Mill.) BSP) (Hennigar et al., 2008).

This univoltine insect emerges as an adult from its pupa in mid-summer to mate and lay its eggs. Immediately after egg hatch, first-instar larvae spin hibernacula, moult to the second-instar, and enter into an obligatory diapause until the following spring (Han & Bauce, 2000). During this long overwintering period, the larvae do not feed. Their survival depends exclusively on the reserves provided by the female parent (Han & Bauce, 2000). While the quality of these reserves may be affected by the quality of food which had been consumed by the mother, the quality and quantity of food that is subsequently consumed by a larva influences its overall fitness and performance, thereby affecting growth rate, developmental time, final body mass, dispersal ability, and probability of survival (Slansky & Scriber, 1985). Further, larval food quality is important to the adult insect because its effects can carry over to affect larval performance in the succeeding generation (Slansky & Scriber, 1985).

Thus, the nutritional state of parents can influence the performance of their progeny (Rossiter, 1991a,b; Fox et al., 1995; Carisey & Bauce, 2002). For example, the progeny of gypsy moth (*Lymantria dispar* L.) females that had fed on leaves from defoliated trees dispersed less successfully than those of females that had not suffered such nutritional stress (Diss et al., 1996). At a more fundamental level, as Rossiter (1991b) found, the nutritional experience of gypsy moth parents can influence the length of the pre-feeding larval period, together with the developmental time and pupal mass of the offspring.

Hennigar et al. (2008) found that balsam fir is more prone to being defoliated than is white spruce, red spruce, or black spruce. Although balsam fir is known to be the preferred host of the budworm, field observations (Blais, 1957; Craighead, 1924, cited by Lavallé & Hardy, 1988) and laboratory studies (Koller & Leonard, 1981; Mattson et al., 1991) have found that larvae reared on white spruce develop more rapidly and are larger than those reared on balsam fir. Lower levels of defoliation on white spruce versus balsam fir may be due to faster growth, greater development, and more foliage per unit area in the shoots of spruce compared to those of balsam fir (Greenbank, 1963). In contrast, naturally occurring budbreak and shoot elongation occurs later in black spruce than in balsam fir, making the latter more susceptible to defoliation than the former (Blais, 1957). Thus, susceptibility to spruce budworm attack varies among host species, depending upon differences in phenology and shoot performance.

It has been proposed that balsam fir, white spruce and black spruce are equally susceptible targets for spruce budworm oviposition and that all are suitable for completion of its life cycle (Nealis & Régnière, 2004). However, differences in synchrony between spruce budworm and host tree phenology are responsible for differences in host susceptibility and insect performance (Blais, 1957; Mattson et al., 1991; Nealis & Régnière, 2004). Nevertheless, differences in host nutritional quality may also play an important role. For example, Thomas (1989) found that black spruce was less suitable than white spruce and red spruce as a source of food because of the presence of allelochemicals which reduce budworm performance. Differences in food quality provided by host species can thus affect population dynamics and adaptions of the budworm (Carisey & Bauce, 2002). Understanding the effects of food quality on the performance of spruce budworm progeny may help us in developing methods that reduce the damage caused by this insect. The objectives of this study were to determine 1) if differences in nutritional quality existed among balsam fir, white spruce and black spruce, and 2) if differences in host nutritional quality affected spruce budworm progeny development and survival. We reared budworms in the field to elucidate the importance of host trees on insect performance. Also, a laboratory insect rearing study that used an artificial diet was used to determine whether or not the effect of host tree is passed on to the progeny.

5.4 Materials and methods

5.4.1 Field insect rearing

Our research was conducted in the Montmorency experimental forest (47°19′N, 79°09′W), which is located 60 km north of Quebec City, Canada. This forest is typical of the Laurentide-Onatcheway region (Rowe, 1972), and most of the stands fit Grandtner's (1966) description of the balsam fir-white birch association. We evaluated the effect of food quality on spruce budworm by using foliage of three different host trees: balsam fir, white spruce, and black spruce. Balsam fir and white spruce trees were selected from sites with good quality drainage (Class 3, mesic with seepage), whereas black spruce trees were selected only on sites with poor drainage (Class 5, hydric) because this species only grows on the hydric drainage class in the Laurentide-Onatcheway region (Rowe, 1972). Belanger et al. (2004) should be consulted for further details regarding drainage class. Site selection avoided using stressed trees, which could have altered results of the study. Also, the study site was free of spruce budworm. Six dominant or codominant individuals were randomly selected for each tree species. Trees were at least one km apart, which allowed us to treat them as independent experimental units. This gave three "treatments" (species), each with six replicates, which yielded 18 individuals that included subsamples (pseudoreplication). Two 75 cm-long branches, from the north-northwest aspect of the tree canopy, were selected from the mid-crown of each tree. Each branch was enclosed with a fine-mesh cloth sleeve cage, which served as an enclosure for 20 post-diapausing second-instar larvae (parental generation) (n = 360 larvae). Larvae came from a colony in the Laboratory of Forest Entomology, Laval University. The colony has been maintained with regular introductions (every three years) of wild populations for the last seven years. To simulate normal field emergence following winter diapause, insects were placed in the field cages when 150 degree-days had been accumulated, which is two to three weeks prior to vegetative budbreak in the study area. Branches were cut and brought to the laboratory when 90% of the larvae had turned into pupae. During travel from the forest to the laboratory, pupae were kept under ambient conditions. The dry mass of frass produced in each rearing sleeve cage was recorded, larval mortality was determined, and pupae were sexed and weighed using an electronic balance with 10 µg accuracy (MC 1 Analytic AC 210 S, Sartorius Canada, Mississauga, ON). Results from an earlier study on spruce budworm food utilisation that combined laboratory and field rearing experiments indicated that the rearing technique used in the present study gives an accurate estimate of frass production (Bauce et al., 1994).

5.4.2 Laboratory insect rearing

Spruce budworm second-instar larvae were obtained from the parental generation which had been reared in the Montmorency forest. At emergence, moths were sexed and placed in a rearing room (23°C, 60% RH, L:D 16:8). To increase mating success, two males were placed with one female in a clear plastic vial (9.5 cm high x 4.5 cm in diameter), covered on top with a piece of cheesecloth and on the bottom with a plastic cap. Throughout the oviposition period, the eggs laid by each female were collected every two days using a fine brush and weighed to evaluate total and individual egg mass. Eggs were incubated (23°C, 65% RH and L:D 16:8) for one week and were enclosed in clear plastic boxes (4 x 2.5 x 1.5 cm), the lids of which were lined with cheesecloth that could be used by first-instar larvae for building hibernacula.

Twenty-five post-diapausing second-instar larvae from each selected tree (n = 450 larvae) were reared to pupation in a growth chamber (23°C, 60% RH, L:D 16:8). Male and female post-diapause second-instar larvae emerged in rearing containers which contained an artificial diet (McMorran, 1965). Larvae were monitored twice each day to record mortality and instar. These data were then used to establish the time (hours) from second-instar to the adult stage. Pupae were weighed 8 h after pupation and sexed. After emergence, moths were mated and the eggs that were laid were collected each day. The number of eggs laid by each female during its lifetime, the number of fertile eggs, and the subsequent number of second-instar larvae that entered diapause were recorded. Larvae were placed in an outdoor insectarium near Laval University (46°47′N, 71°18′W) for the duration of their winter diapause and were exposed to low ambient temperatures. Winter survival was evaluated the following spring.

For each host tree, 50 sixth-instar larvae were randomly chosen to determine relative growth rates and relative consumption rates, which were estimated on a dry-mass basis (gravimetric experiment). Newly-moulted sixth-instar larvae were weighed and placed in individual rearing containers (4x2.5x1.5 cm) which contained an artificial diet (McMorran, 1965). Larval developmental time was monitored twice daily. Ingested food and excreted dry faeces that had been produced during larval development were quantified, as described by Bauce et al. (1994).

Relative growth rate (RGR) and relative consumption rate (RCR) were determined from the following formulae:

RGR = G/(MW*hours (developmental time)),

RCR = I/(MW*hours (developmental time)),

Where:

G = Gained mass = (final mass-initial mass)

MW = Mean larval mass = G/log (final mass/initial mass)

I = Ingested food

Linear or non-linear regression was used to predict the numerator as a function of the denominator for each ratio so that an adjusted ratio could be calculated on the basis of a common denominator, thereby enabling indices to be compared (Bauce et al., 1994).

5.4.3 Chemical analysis of the foliage

For chemical analysis of the foliage, we collected mid-crown branches from each tree that had been selected for field rearing. Foliar chemical content was determined on each sample tree using north-northwest facing mid-crown branches which had not been infested by budworm. Foliar chemistry was determined twice during each growing season: 15 days after insect installation, and when budworm infested-branches were collected (at pupal stage). For chemical determinations, 3 g of fresh current-year foliage were collected from each sample tree (*n* = 18 samples per collection date). The samples were returned to the laboratory on dry ice, flash-frozen in liquid nitrogen, freeze-dried, ground in a Wiley mill (maintained below -30^{o}C to avoid deterioration of polyphenolics), and maintained at -20^{o}C until they were analysed for protein, mineral nutrients (P, K, Ca, Mg), total soluble sugars, total tannins, hydrolysable tannins, condensed tannins, and total phenolic content using the methodologies described in Bauce (1996) and Bauce et al. (2006). Two subsamples of 15 current-year twigs were collected from each sample tree to determine moisture content. Two additional subsamples of fresh current-year twigs were collected on each tree, placed in crimped sealed vials, and kept at -20^{o}C until the needles could be analysed for monoterpenes using gas chromatographic techniques described in Bauce et al. (1994). Extracts were analysed with a Varian GC3900 gas chromatograph equipped with a flame ionisation detector and a 30 m x 0.25 mm fused silica capillary column (supelco SPB-5), controlled by a Varian Workstation running Galaxie software. Three µl aliquots were injected into the column and carried by hydrogen (split 1:20). Column temperature was programmed to increase at 2°C/min from 60°C to a final temperature of 110°C, which was maintained for 3 min. Monoterpenes were identified by comparing retention times with authentic standards (Aldrich Chemical Co. Inc., Milwaukee, WI, USA) under identical conditions Our identifications were confirmed at the LASEVE laboratory (Université du Québec à Chicoutimi) using data obtained from a gas chromatography/mass spectrometry system. Quantification of monoterpenes was based on injecting known amounts of authentic compounds under identical conditions and determining response factors for each monoterpene relative to known amounts of the internal standard, tetradecane. The results are expressed as percent dry weight.

5.4.4 Statistical analyses

Multiple responses for each property were averaged for each tree to avoid pseudoreplication (i.e., the tree was the experimental unit). Normality and homogeneity of variance tests were performed before data were subjected to multivariate analysis of variance (MANOVA), with individual trees as experimental units. In the case of chemical analysis, the data were analysed using a split-plot complete randomised factorial design with 6 replicates, with block(tree species) as the error term. The main plots corresponded to tree species (3), and the sub-plots to collection date (2). MANOVA was performed on each of the following groups of variables: parental generation performance, progeny performance, gravimetric experiment (males and females were analysed separately), host tree monoterpenes, host tree tannins and phenols, and nutrient elements. Furthermore, monoterpenes were divided into two groups because there were not sufficient degrees of freedom to perform MANOVA on a single group. The first group corresponded to monoterpenes reported as oviposition stimulants to the budworm in the scientific literature (group 1: α-pinene, β-pinene, limonene, myrcene, thujone) (Städler, 1974; Grant et al., 2007), whereas the second group corresponded to monoterpenes reported as feeding deterrents to the insect (group 2: camphene, terpinolene, δ-3-carene, bornyl acetate, borneol) (Bauce et al., 1994; Mattson et al., 1991). If MANOVA found a significant effect in a group of variables, data from that group were analysed using Analysis of Variance (ANOVA) to determine which variables were affected by the factors that were studied. Duncan's test was used for comparison of means. When data did not meet assumptions of normality and homogeneity of variance, the tests were performed on ranked data (PROC GLM). Mortality was analysed in a generalised linear model for binary response data, assuming that the random component in the model has a binomial distribution, followed by two-by-two contrasts for comparing differences between treatments (PROC GENMOD, SAS Institute, 2003).

Canonical correlation analysis (CCA) examined the degree to which components of each group of insect performance variables were correlated with each foliar chemistry group of variables (PROC CANCORR, SAS Institute, 2003). For each group, we used only the variables that were statistically different among host tree species because the large number of variables in these groups compared to the relatively small number of repetitions did not permit the use of CCA on the entire data set. Finally, the variables developmental time (DT), development time of the sixth-instar (DT6) and total development time (TDT) were transformed into developmental rate (DR), development rate of the sixth-instar (DR6), and total development rate (TDR) by using the following formulae: DR= 1/DT; DR6= 1/DT6; and TDR= 1/TDT.

5.5 Results

5.5.1 Field insect rearing

Results of MANOVA on field insect rearing measurements indicated that host species had a significant effect on spruce budworm performance (Wilks' Lambda: $F_{(14,\ 18)}$= 5.34, P=<0.01). For both sexes, the larval developmental period was approximately four days shorter on white spruce than on black spruce and balsam fir (Table 5.1). Male larvae that fed on white spruce were about 12% heavier than larvae that fed on balsam fir and 19% heavier than those that fed on black spruce. Males also had a shorter developmental time. Further, male spruce budworm fed on black spruce had a lower pupal mass than males fed on the other hosts. Larvae that fed on white spruce exhibited higher realised fecundity, but lower fertility than larvae fed on the other hosts. Female pupal mass (Table 5.1), egg mass ($F_{(2,15)}$= 1.25, P=0.31) and total mortality ($\chi^2_{(2)}$=3.08, P=0.21) did not differ among the three host trees species.

Table 5.1 Spruce budworm performance tabulated by host species (mean ± SEM)

Parameter	Host tree					
	Balsam fir (47)*	White spruce (57)	Black spruce (54)	*F*	*df*	*P*
Female development time (h)	1104.17 ± 7.83a	1011.50 ± 13.90b	1104.29 ± 10.79a	23.16	2, 15	<0.01
Male development time (h)	1078.05 ± 3.61a	989.16 ± 9.07b	1087.83 ± 18.93a	19.54	2, 15	<0.01
Female pupal mass (mg)	94.00 ± 3.00a	110.0 ± 7.00a	94.00 ± 4.00a	2.85	2, 15	NS
Male pupal mass (mg)	73.00 ± 1.00ab	83.00 ± 2.00a	67.00 ± 6.00b	4.19	2, 15	<0.04
Fertility (%)[2]	58.32 ± 1.70a	52.00 ± 1.67b	57.00 ± 0.63a	5.47	2, 15	<0.02
Fecundity[1]	135.55 ± 12.86b	182.80 ± 10.85a	159.78 ± 10.07ab	4.35	2, 15	<0.04

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan's multiple range test.

[1]Total number of eggs laid by a female moth

[2]Total number of viable larvae produced by a female moth

* Number of larvae in parentheses

5.5.2 Laboratory insect rearing

Host tree species affected spruce budworm performance in laboratory reared larvae (Wilks' Lambda: $F_{(12,\ 18)}$= 3.22, P=<0.02). Budworm progeny from parents reared on balsam fir exhibited the greatest female pupal mass, while budworms from parents reared on white spruce showed shorter developmental time for both sexes (Table 5.2). Also, larvae with parents reared on black spruce had a longer developmental time, greater mortality and lower pupal mass than those reared on the other hosts. Finally, fertility ($F_{(2,15)}$= 2.56, P=0.110), fecundity ($F_{(2,15)}$= 1.12, P=0.352) and winter larvae survival ($F_{(2,15)}$= 0.24, P=0.792) were not significantly affected by the parental host tree.

Table 5.2 Spruce budworm performance in laboratory tabulated by host species (mean ± SEM)

Parameter	Host tree					
	Balsam fir (103)•	White spruce (108)	Black spruce (91)	*F*	*df*	*P*
Female development time (h)	626.83 ± 10.67b	606.00 ± 4.22b	690.00 ± 37.14a	3.8	2, 15	<0.05
Male development time (h)	610.80 ± 10.46b	596.00 ± 17.70b	674.50 ± 23.15a	5.21	2, 15	<0.03
Female pupal mass (mg)	123.00 ± 8.00a	120.00 ± 4.00ab	95.00 ± 8.00b	3.92	2, 15	<0.05
Male pupal mass (mg)	76.00 ± 3.00a	78.00 ± 4.00a	62.00 ± 3.00b	5.45	2, 15	<0.02
Mortality (%)[1,2]	31.29 ± 3.81a	27.92 ± 3.60a	39.60 ± 4.02a	4.89*	2	<0.10

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan's multiple range test.

[1] Mortality was analysed in a generalised linear model for binary response data, followed by two-by-two contrasts (PROC GENMOD).

[2] Test was considered statistically significant at P<0.1

*Chi-square value

• Number of larvae in parentheses

Host tree species also had a significant effect on performance of female (Wilks' Lambda: $F_{(14, 8)}$= 3.83, P=<0.04) and male (Wilks' Lambda: $F_{(14, 14)}$= 3.86, P=<0.01) larvae used in the gravimetric experiment. Females that were obtained from parents reared on balsam fir had shorter total developmental time and reached sixth-instar 10h and 86h earlier than those with parents fed on white and black spruce, respectively (Table 5.3). Females obtained from parents reared on black spruce had 53 and 65% higher RGR than those whose parents had fed on balsam fir and white spruce, respectively. No differences were detected among parental host species in terms of female sixth-instar initial ($F_{(2,15)}$= 0.74, P=0.503) and final masses ($F_{(2,15)}$= 0.38, P=0.694), RCR ($F_{(2,15)}$= 3.52, P=0.069) and pupal developmental time ($F_{(2,15)}$= 1.20, P=0.341).

Males obtained from parents reared on balsam fir had 10% higher sixth-instar initial mass than those with parents reared on white spruce and 46% higher than those with parents reared on black spruce (Table 5.4). They also reached sixth-instar stage 14h and 84h earlier, and had a shorter total developmental time than those with parents fed on white and black spruce, respectively. In contrast, males obtained from parents reared on black spruce had 87% and 59% higher RGR than those with parents fed on balsam fir and white spruce, respectively. No differences in male sixth-instar final mass ($F_{(2,15)}$= 1.15, P=0.346), RCR ($F_{(2,15)}$= 0.17, P=0.846) and pupal developmental time ($F_{(2,15)}$= 1.47, P=0.267) were detected among parental host species. Finally, larvae of parents reared on black spruce exhibited greater mortality than those whose parents were reared on balsam fir and white spruce.

Table 5.3 Female spruce budworm performance and indices in laboratory tabulated by host species (mean ± SEM)

Parameter	Host tree					
	Balsam fir (16)*	White spruce (15)	Black Spruce (11)	*F*	*df*	*P*
Initial mass (mg)[1]	56.92 ± 4.01a	54.12 ± 5.25a	47.87 ± 7.12a	0.74	2,15	NS
Development time sixth-instar (h)[2]	258.48 ± 8.32b	268.50 ± 10.78b	344.40 ± 5.67a	29.36	2,15	<0.01
Final mass (mg)[3]	90.52 ± 6.63a	90.95 ± 2.72a	98.82 ± 10.95a	0.38	2,15	NS
RGR (mg/mg*h)	0.0012 ± 0.0003b	0.0009 ± 0.0002b	0.0026 ± 0.0004a	5.58	2,15	<0.03
RCR (mg/mg*h)	0.015 ± 0.003a	0.004 ± 0.001a	0.019 ± 0.005a	3.52	2,15	NS
Total development time (h)[4]	420.24 ± 11.69b	456.50 ± 22.72b	520.20 ± 15.90a	9.36	2,15	<0.01

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan's multiple range test.

[1] Larval mass at the beginning of the sixth-instar

[2] Developmental time from second to sixth-instar

[3] Pupal mass

[4] Developmental time from second-instar to pupal stage

* Number of larvae in parentheses

Table 5.4 Male spruce budworm performance and indices in laboratory tabulated by host species (mean ± SEM)

Parameter	Host tree					
	Balsam fir (28)•	White spruce (33)	Black Spruce (22)	*F*	*Df*	*P*
Initial mass (mg)[1]	57.05 ± 3.03a	51.05 ± 4.11a	30.67 ± 1.99b	13.67	2,15	<0.01
Development time sixth-instar (h)[2]	241.80 ± 4.70b	255.71 ± 8.69b	325.49 ± 20.63a	14.74	2,15	<0.01
Final mass (mg)[3]	64.50 ± 2.91a	63.45 ± 2.16a	57.20 ± 5.76a	1.15	2,15	NS
RGR (mg/mg*h)	0.0002 ± 0.00005b	0.0007 ± 0.0002b	0.0018 ± 0.0004a	8.33	2,15	<0.01
RCR (mg/mg*h)	0.015 ± 0.003a	0.014 ± 0.002a	0.018 ± 0.007a	0.17	2,15	NS
Total development time (h)[4]	425.16 ± 14.49b	404.69 ± 5.49b	489.92 ± 5.19a	15.65	2,15	<0.01
Mortality (%)[6]	12.00 ± 5.23b	2.04 ± 2.04c	33.33 ± 6.66a	19.69*	2	<0.01

Values in each row followed by the same letter do not differ significantly at P<0.05 according Duncan's multiple range test.

[1] Larval mass at the beginning of the sixth-instar

[2] Developmental time from second to sixth-instar

[3] Pupal mass

[4] Developmental time from second-instar to pupal stage

[5]Mortality (males and females included) was analysed in a generalised linear model for binary response data, followed by two-by-two contrasts (PROC GENMOD).

*Chi-square value

• Number of larvae in parentheses

5.5.3 Foliar chemical analysis

Host tree species were significantly different in terms of their foliar chemistry (Table 5.5 and 5.6). Balsam fir foliage contained higher concentrations of N, Ca, total tannins, and total hydrolysable tannins than the other hosts, whereas black spruce foliage had higher concentrations of P, Mg, and total phenolics (Table 5). Potassium ($F_{(2,21)}$= 0.33, P=>0.05), and sugars ($F_{(2,21)}$= 3.54, P=>0.05) did not differ among host trees. As for monoterpenes, black spruce had high concentrations of camphene, bornyl acetate and myrcene (Table 6). Balsam fir also had high concentrations of certain monoterpenes, including α- and β-pinene.

Table 5.5 Nutrient, tannins and phenolic contents according to host species (Balsam fir, white spruce and black spruce) (mean ± SEM). Foliar chemistry was determined twice during each growing season: 15 days after insect installation, and when budworm infested-branches were collected (at pupal stage). A total of 6 trees were chosen at random from each host species (*n*=18 samples per collection date). Data were analyzed using multivariate analysis of variance (MANOVA). If MANOVA found a significant effect in these groups of variables, data from that group were analysed using analysis of variance (ANOVA) to determine which variables were affected by the factors that were studied (host species and collection date).

	Content of foliage			*P*[1]					
Parameter	Balsam fir	White spruce	Black spruce	Host tree effect		Collection effect		Interaction	
N (% dry mass)	2.19 ± 0.14a	1.9 ± 0.16b	2.04 ± 0.33ab	<0.03		<0.01		<0.01	
P (μg/g)	2874.19 ± 230.81a	2577.04 ± 243.13b	3055.63 ± 527.52a	<0.03		<0.01		<0.01	
Ca (μg/g)	1796.53 ± 268.22a	1142.63 ± 153.44b	1221.13 ± 126.54b	<0.01		<0.01		<0.01	
Mg (μg/g)	973.46 ± 18.70c	1138.79 ± 46.22b	1247.5 ± 93.14a	<0.01		<0.01		<0.01	
				Wilks' λ[2]	0.008	Wilks' λ	0.012	Wilks' λ	0.027
				$F_{(12,8)}$	6.61	$F_{(6,4)}$	51.07	$F_{(12,8)}$	3.3
				P	<0.01	*P*	<0.01	*P*	<0.05
Allelochemical compounds									
Total tannins (cm2)	8.58 ± 2.09a	7.89 ± 2.25a	2.77 ± 2.31b	<0.01		<0.01		<0.01	
Total hydrolysable tannins (cm^2)	7.26 ± 1.76a	6.6 ± 1.87a	2.15 ± 1.61b	<0.04		<0.01		<0.01	
Total phenolics (% dry mass)	5.9 ± 1.39b	6.65 ± 1.86b	12.95 ± 2.07a	<0.02		<0.01		<0.01	
				Wilks' λ[3]	0.098	Wilks' λ	0.058	Wilks' λ	0.082
				$F_{(6,14)}$	5.51	$F_{(3,7)}$	37.71	$F_{(12,8)}$	5.8
				P	<0.01	*P*	<0.01	*P*	<0.01

Values in each row followed by the same letter do not differ significantly at $P<0.05$ according Duncan's multiple range test.

[1] *P*-value is for univariate analysis of variance.

[2] Results of MANOVA for group of nutrients.

[3] Results of MANOVA for group of tannins and phenolics.

There were marked shifts in host foliar chemistry over the growing season, but temporal variation differed among host tree species (Table 5.5). Variation in foliar chemistry over the sampling dates was detected for N, P, Mg, Ca, total tannins, total hydrolysable tannins, and total phenolics (Table 5). The interactions between date and host species were also significant for those compounds, further indicating that seasonal trends differed among the hosts. Seasonal declines were observed in all three hosts for N (47%), P (51%), and Mg (17%), with the foliage of black spruce being the most affected. Seasonal elevation in concentrations were observed for Ca (121%), total tannins (2477%), total hydrolysable tannins (2415%), and total phenolics (1395%), with the foliage of balsam fir showing the greatest increases.

With respect to monoterpenes, date of collection affected deterrent monoterpenes, whereas the date by host species interaction affected oviposition-stimulating monoterpenes (Table 6). Variations in monoterpenes over sampling dates were detected for myrcene, camphene and bornyl acetate, whereas a date by host species interaction was detected for α-pinene, β-pinene, limonene, and myrcene (Table 5.6). Black spruce foliage retained the highest concentrations of deterrent monoterpenes, such as camphene, and bornyl acetate, throughout the growing season (Table 5.6).

Table 5.6 Monoterpene contents according to host species (Balsam fir, white spruce and black spruce) (mean ± SEM). Foliar chemistry was determined twice during each growing season: 15 days after insect installation, and when budworm infested-branches were collected (at pupal stage). A total of 6 trees were chosen at random from each host species (*n*=18 samples per collection date). Data were analyzed using multivariate analysis of variance (MANOVA). If MANOVA found a significant effect in these groups of variables, data from that group were analysed using analysis of variance (ANOVA) to determine which variables were affected by the factors that were studied (host species and collection date).

	Content of foliage			*P*[1]					
Parameter	Balsam fir	White spruce	Black spruce	Host tree effect		Collection effect		Interaction	
Monoterpenes (Stimulants)									
α-pinene (ng/mg)	4183.62 ± 341.08a	1261.44 ± 139.27c	3315.51 ± 477.61b	<0.01		NS		<0.01	
β-pinene (ng/mg)	8515.92 ± 837.18a	285.08 ± 31.27b	1353.35 ± 275.56b	<0.01		NS		<0.01	
Myrcene (ng/mg)	428.5 ± 77.71b	318.19 ± 56.30b	3284.12 ± 710.77a	<0.01		<0.04		<0.05	
Limonene-β-phellandren (ng/mg)	3613.75 ± 248.82a	2817.60 ± 298.57b	2227.1 ± 145.09b	<0.01		NS		<0.01	
				Wilks' λ[2]	0.001	Wilks' λ	0.225	Wilks' λ	0.044
				$F_{(10,10)}$	29.03	$F_{(6,4)}$	3.45	$F_{(12,8)}$	3.73
Monoterpenes (Deterrents)				*P*	<0.01	*P*	NS	*P*	<0.03
Camphene (ng/mg)	1273.65 ± 112.39b	891.97 ± 195.74b	3322.13 ± 930.13a	<0.01		<0.01		<0.01	
Bomyl acetate (ng/mg)	2559.7 ± 135.54b	2649.49 ± 455.83b	6975.13 ± 1756.18a	<0.01		<0.01		<0.03	
				Wilks' λ[3]	0.045	Wilks' λ	0.043	Wilks' λ	0.116
				$F_{(10,10)}$	3.71	$F_{(5,5)}$	22.11	$F_{(10,10)}$	1.92
				P	<0.03	*P*	<0.01	*P*	NS

Values in each row followed by the same letter do not differ significantly at *P*<0.05 according Duncan's multiple range test.

[1] *P*-value is for univariate analysis of variance.

[2] Results of MANOVA for group of monoterpenes stimulants.

[3] Results of MANOVA for group of monoterpenes deterrents.

5.5.4 Canonical correlation analysis

The canonical correlation analysis (CCA) showed a significant correlation between parental generation performance and nutrient only ($R_c^2 = 0.96$, Wilks' Lambda: $F_{(40, 24)}= 1.89$, $P=<0.05$). The first canonical variate for parental performance was positively associated with female (r=0.78) and male (r=0.68) developmental rate, and fecundity (r=0.93), whereas the first canonical variate for nutrients was negatively associated with Ca on the first (r=-0.51) and second (r=-0.56) collection dates. Scores on the first canonical variate of parental performance for Ca for the first (r=-0.49) and second (r=-0.55) collection dates suggest that Ca has a negative effect on female and male developmental rate, and fecundity. Canonical redundancy analyses (CRA) indicated that the nutrient data set extracted 44.12% of the variance in the parental performance data set.

As for progeny, their performance was significantly correlated with deterrent monoterpenes only ($R_c^2 = 0.91$, Wilks' Lambda: $F_{(16, 22)}= 2.91$, $P=<0.02$). The first canonical variate for progeny performance was negatively associated with female developmental rate (r=-0.16), and male pupal mass (r=-0.11), and positively associated with female pupal mass (r=0.95), whereas the first canonical variate for deterrent monoterpenes was positively associated with camphene (r=0.99) and bornyl acetate (r=0.54) at the second collection. The analysis of correlations between the first canonical variate of progeny performance and camphene (r =0.94) and bornyl acetate (r =0.52) suggests that these monoterpenes have a negative effect on female developmental rate and male pupal mass, while they have a positive effect, surprisingly, on female pupal mass. CRA indicated that the proportion of variance in progeny performance explained by the nutrient data set was 21.79%.

Finally, CCA indicated that only female performance in the gravimetric experiment data set had a significant correlation with deterrent monoterpenes ($R_c^2 = 0.86$, Wilks' Lambda: $F_{(12, 16)}= 4.44$, $P=<0.01$) and tannin and phenol ($R_c^2 = 0.96$, Wilks' Lambda: $F_{(18, 11)}= 2.72$, $P=<0.05$). The first canonical variate for female performance was positively associated with developmental rate of sixth-instar larvae (r=0.71), total developmental rate (r=0.46), and relative growth rate (r=0.47), whereas the first canonical variate for deterrent monoterpenes was negatively associated with bornyl acetate (r =-0.53) on the first collection date. Scores for bornyl acetate (r =-0.49) on the first collection date for the first canonical variate of female performance suggest that this monoterpene has a negative effect on the three variables of female performance. CRA indicated that the nutrient data set extracted 27.49% of the variance in the progeny performance date set.

With respect to correlations between female performance and tannin and phenols, the first canonical variate for female performance was positively associated with relative growth rate (r=0.86), whereas the first canonical variate for tannin and phenol was positively associated with total tannins (r=0.81) and total hydrolysable tannins (r=0.56) on the first collection date and negatively associated with total phenolics on the second collection date (r=-0.27). Scores for these elements suggest that total tannins (r=0.80) and total hydrolysable tannins (r=0.55) at the first collection have a positive effect and that total phenolics at the second collection (r=-0.26) have a negative effect on relative growth rate. CRA indicated that the proportion of variance in female performance explained by nutrient data set was 21.79%.

5.6 Discussion

Results of this experiment show that budworm larvae that fed on white spruce foliage performed best in terms of fitness indicators, as expressed in the shorter larval developmental time for both sexes, and high male pupal mass, compared with larvae that fed upon black spruce and balsam fir. Shorter developmental time may be important to larval survival because the duration of larval exposure is reduced with respect to predators, pathogens, and other potentially harmful agents (Slansky, 1990). Moreover, developmental time may alter the adult’s ability to mate, and the timing and rate of reproduction, together with its fecundity and dispersal abilities (Slansky & Scriber, 1985). Furthermore, male insect mass may affect fecundity because it has been discovered that male body size affects female fecundity (Fox et al., 1995; Delisle & Hardy, 1997).

Foliar analyses revealed significant differences among host species. For example, balsam fir had higher concentrations of N and Ca, whereas black spruce contained greater concentrations of camphene, bornyl acetate, and total phenolics than did the other hosts. Canonical correlation analysis suggests that Ca might play an important role in budworm performance by reducing developmental rate and fecundity. Mattson et al. (1991) hypothesised that high concentrations of calcium might interfere with the uptake of micronutrients, such as iron and zinc, which are known to be important catalysts of several enzyme reactions (Mattson & Scriber 1987). Moreover, nitrogen is by far the most important nutrient for insect growth and survival (Mattson & Scriber 1987). In fact, larvae of spruce budworm fed on a diet containing sufficient nitrogen have higher growth rates and shorter developmental times (Bidon, 1993; Mattson et al., 1991; Bauce et al., 1994, Carisey & Bauce, 1997a,b). Nevertheless, the lack of strong correlation between insect performance and the other nutrients suggests that a proper balance of nutrients would be more important to spruce budworm than a high concentration of a given nutrient. For example, Clancy (1992) reported that western spruce budworm response to increased N in artificial diets was neither positively linear nor convex; rather, response was dependent on levels of minerals in the diets. Thus, the stronger seasonal decline of nutrients such as N, P and Mg in black spruce may affect budworm performance by making its foliage nutritionally unbalanced and, therefore, less suitable for the insect than the foliage of the other hosts.

The effects of secondary compounds on insect progeny appeared to be stronger than nutrients, as reflected in the negative correlations between monoterpenes, such as camphene and bornyl acetate, and female developmental rate and pupal mass. Surprisingly, these monoterpenes also had a positive effect on female pupal mass. This effect was not consistent with results from previous studies, which have found that bornyl acetate and camphene exert deleterious or toxic effects on budworm larvae, including higher mortality and lower growth rates (Mattson et al., 1991; Bauce et al., 1994; Carisey & Bauce, 1997a). Furthermore, some phenolics such as pungenin are feeding deterrents for spruce budworm and can cause a reduction in consumption, thereby affecting the size of females (Strunz et al., 1986).

Mortality did not differ among the host trees, but we could observe that larvae fed on balsam fir exhibited slightly higher mortality (60.83%) than those fed on black (55%) and white (52.5%) spruce. This result is not in accordance with previous works, which have reported higher larval mortality in black spruce (Blais, 1957; Nealis & Régnière, 2004; Henningar et al., 2008) compared to other spruce budworm host trees. Late budbreak of black spruce has frequently been suggested as the most important factor responsible for high larval mortality and reduced defoliation on this species compared with balsam fir and white spruce because this phenological delay forces budworms to mine old foliage, which is less suitable food source (Blais, 1957; Greenbank, 1963).

Nevertheless, Lawrence et al. (1997) found that late budbreak (i.e., budbreak follows larval emergence by several weeks) does not significantly affect post-diapause spruce budworm survival. By contrast, early budbreak (i.e., budbreak occurs prior to or during larval emergence) dramatically reduced budworm survival and body mass because larvae start feeding too late to take advantage of the high levels of foliar nitrogen, which diminishes rapidly during and immediately following budbreak. This same pattern has been observed by Bauce (unpublished data) in white spruce. The results reported by Lawrence et al. (1997) may thus be explained by the ability of young budworms to mine 1- and 2-year-old foliage, where they obtained the required amount of nitrogen from nitrogen-rich tissues under the nitrogen-poor outer needle layer (Trier & Mattson, 1997). Acquisition of nitrogen is more important than sugars for young larvae (Albert & Bauce, 1994), thereby allowing larvae to survive up to four weeks prior to budbreak (Trier & Mattson, 1997). This ability of young budworms may explain larval mortality on black spruce. Likewise, the use of sleeve cages may have reduced the loss of early-stage larvae by preventing the redistribution of budworms among more suitable host trees.

An earlier study on spruce budworm (Carisey & Bauce, 2002) suggests that the nutritional experience of the parents may affect the performance of the progeny. The laboratory rearing results indicate that progeny with parents fed on black spruce exhibited longer developmental times and greater mortality, and had lower pupal masses. Despite reaching the sixth-instar later, the progeny of parents that fed on black spruce also exhibited higher RGR than progeny of parents fed on balsam fir and white spruce, suggesting the existence of a nutritional-based parental effect. Canonical correlation analysis suggests that concentrations of bornyl acetate and phenolics in the foliage fed upon by the parental generation might have affected offspring performance.

The poorer performance exhibited by the offspring of parents fed on black spruce points to this species as poor quality food for spruce budworm. The nutritional quality of this host may have caused a reduction in the quantity or quality of reserves which the parents provided to their eggs. Egg provisioning is very important because it represents the sole energy source available to the progeny for embryogenesis and maintenance prior to hatching. Besides, these reserves can affect larval survival, development and behaviour (Rossiter, 1991a).

The lack of significant differences between the parental generations fed on balsam fir and black spruce does not concur with previous research, which has shown that larvae fed on black spruce foliage performed more poorly than those fed on other budworm host species (Blais 1957; Thomas 1989). However, a similar phenomenon has been reported by Carisey & Bauce (2002). They found that the parental generation did not show significant differences between the two poorest artificial diets that were used, but its progeny was affected by them. Unfortunately, the parameters measured in the current study do not allow us to explain the cause of this pattern. Examination of the nutritional composition of eggs and feeding behaviour of the progeny may help us to explain the parental effects reported in this study. These results also show the importance of studying effects of food quality on at least two generations to fully understand the effect that this variable exerts on insect performance; otherwise, we could have concluded that black spruce is an optimal source of food for spruce budworm.

In conclusion, our results demonstrate that black spruce foliage is an inferior food for budworm. This is because of the negative effects that black spruce imposed on the progeny of those insects that had been reared on it. These effects are not readily apparent if only one generation is studied. It is necessary to incorporate this phenomenon into budworm control, particularly by adjusting predictive models accordingly. We have shown that, for budworm and doubtless for other lepidopteran forest pests, carry-over effects cannot be ignored.

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6. Conclusion

L'éclaircie a souvent été recommandée pour réduire la vulnérabilité des peuplements contre les ravageurs forestiers tels que le dendroctone du pin ponderosa (*Dendroctonus ponderosae*) (Larsson et al. 1983, Mitchell et al. 1983, Waring et Pitman 1985), la guêpe *Sirex noctilio* (Dodds et al. 2007, Villacide et Corley 2006), la spongieuse (*Lymantria dispar*) (Liebhold et al. 1998), la tordeuse de l'ouest (Carlson et al. 1985, Mason et al. 1992) et la TBE (Crook et al. 1979, Bauce 1996, Bauce et al. 2001). On croit que l'effet positif de cette technique sylvicole sur la vigueur des arbres résiduels devrait les rendre plus résistants à l'attaque des ravageurs. Cependant, les résultats de plusieurs études visant à déterminer l'effet de cette technique sur la résistance des arbres hôtes à la TBE sont contradictoires (voir section 1.3.1).

Cette étude nous a permis de mieux cerner l'impact de l'éclaircie sur la vigueur des essences hôtes de la TBE et sur la performance de ce ravageur forestier. De plus, elle nous a éclairés sur la raison selon laquelle des études précédentes ont rapporté des résultats contradictoires. Un an après l'éclaircie, cette technique sylvicole produit une réduction de l'antibiose chez le sapin baumier. Nous avons constaté une diminution de la concentration de certains monoterpènes tels que le bornyl acétate. Cette réponse de l'arbre permet à l'insecte de consommer davantage de feuillage. Ainsi, cette diminution de la quantité de feuillage résiduel restant aux arbres pour faire la photosynthèse se traduit par une réduction de la résistance du sapin baumier à la TBE. Cependant, cet effet varie en fonction de la qualité de drainage du site. Les sapins qui poussent dans les sites hydriques ont montré une réponse positive au traitement (stimulation de la production foliaire) un an après son application, probablement parce que cette espèce est mal adaptée pour croître sur les sites humides (Hix et al. 1987). Autrement dit, l'éclaircie a produit un effet positif sur les arbres résiduels en diminuant la concurrence pour les ressources disponibles qui sont limitées dans ce type de sites. Ces résultats nous permettent de mieux comprendre les conclusions de certaines études selon lesquelles l'éclaircie réduit la résistance des arbres hôtes à la TBE (Piene 1989, MacLean et Piene 1995). Ils nous confirment également qu'il ne serait pas recommandé de pratiquer une éclaircie un an avant ou durant une épidémie de ce ravageur forestier, à moins de s'assurer qu'une protection au Bt soit appliquée pendant cette période de faible résistance à l'insecte. Par ailleurs, l'épinette blanche et l'épinette noire n'ont pas été significativement affectées par ce traitement sylvicole un an après son application, mais on a observé une légère augmentation de la production foliaire chez l'épinette blanche et l'effet contraire chez l'épinette noire. Bien que l'épinette blanche et l'épinette noire n'aient pas été significativement affectées par le traitement, il serait opportun de mener l'éclaircie après que les femelles aient pondu leurs œufs afin d'éviter une pression excessive des insectes sur les arbres restants.

Trois ans après l'éclaircie, le sapin baumier et l'épinette blanche réagissent au traitement en augmentant considérablement leur production foliaire. Cette augmentation permet aux arbres résiduels de ces deux essences de conserver une bonne quantité de feuillage pour la photosynthèse, ce qui accroit leur capacité à supporter les dégâts engendrés par la TBE. Cette tolérance accrue s'est traduite par une augmentation globale de la résistance de ces essences à ce ravageur forestier. Cette réponse a été observée malgré l'effet positif de l'éclaircie sur la performance de l'insecte. En effet, les chrysalides provenant de sites ayant été éclaircis ont présenté un poids supérieur par rapport à celles provenant de sites témoins. Cependant, l'effet de l'intensité de l'éclaircie sur la tolérance des arbres hôtes et sur la performance des insectes varie en fonction de la qualité du drainage. En effet, l'effet est davantage positif dans les sites bien drainés, car les arbres qui y poussent produisent plus de feuillage, leur permettant de faire face plus efficacement aux attaques de ce défoliateur. L'effet positif de cette technique sylvicole sur la tolérance des arbres hôtes, accompagné du retour de l'antibiose à son niveau prétraitement tel que rapporté dans d'autres études (Bauce 1996, Bauce et al. 2001), suggère que l'éclaircie pourrait être utilisée en tant que mesure préventive visant à minimiser les dommages provoqués par la TBE.

Quatre ans après le traitement, l'épinette noire a commencé à montrer une réponse positive significative au traitement en augmentant sa production foliaire par rapport aux arbres provenant de sites témoins. L'augmentation foliaire chez l'épinette noire compense la quantité de feuillage détruit par la TBE, ce qui, à son tour, a augmenté sa tolérance à cet insecte pendant au moins 2 ans. Une réponse similaire a été observée chez le sapin baumier poussant dans les sites soumis à une intensité légère et forte d'éclaircie dans toutes les classes de drainage. Cette augmentation de la tolérance a persisté jusqu'à la fin de la période d'étude. En revanche, seules les épinettes blanches poussant dans la classe de drainage subhydrique ont montré une réponse positive à l'éclaircie de 2007 à la fin de l'étude. La tolérance accrue est perdue chez l'épinette blanche dans les sites mésiques six ans après le traitement.

Les résultats présentés ici suggèrent que la tolérance est plus importante que la défense pour la résistance à la TBE des arbres hôtes utilisés dans cette étude. L'antibiose commence à se stabiliser trois ans après le traitement, mais la performance de l'insecte n'a pas été affectée (Chapitre 2). Cela peut se produire en raison d'une compensation des effets négatifs de l'augmentation de la concentration de composés secondaires sur la qualité du feuillage par les effets positifs d'une concentration plus élevée de nutriments foliaires tels que l'azote et le phosphore. D'autre part, il a été suggéré que la tolérance joue un rôle plus important que la défense dans la résistance des plantes ligneuses que celui qui a été assigné à ce mécanisme par le passé, car les herbivores les repèrent facilement en raison de leur grande taille et de leur longévité (Feeny 1976). De plus, leurs mécanismes de défense ne peuvent pas éliminer complètement les dommages causés par les herbivores (Bauce et al. 2001, Haukioja et Koricheva 2001) Ainsi, leur capacité à tolérer et à se remettre de la défoliation devient très importante pour les arbres. Compte tenu de l'importance de la tolérance en tant que mécanisme de résistance, des traitements conçus pour l'augmenter (comme l'éclaircie) devraient parvenir à réduire la vulnérabilité des arbres à la TBE. C'est pourquoi, l'utilisation de ce type de traitements devrait être encouragée pour réduire les pertes produites par cet insecte.

Quant à l'impact de la qualité nutritionnelle du feuillage sur la performance de l'insecte, les résultats du chapitre 4 montrent que le feuillage de l'épinette noire contient des concentrations plus élevées de monoterpènes déterrents et de phénols toxiques par rapport à celui du sapin baumier et de l'épinette blanche. Cette observation suggère que l'épinette noire est une source de nourriture pauvre pour la TBE étant donné les effets négatifs observés chez la progéniture des insectes nourris sur le feuillage de cette essence. Cette réponse suggère que la phénologie tardive de l'épinette noire n'est pas le seul mécanisme de défense utilisé par cette essence pour se protéger de l'attaque de ce ravageur, mais qu'encore l'antibiose pourrait jouer un rôle important dans la défense de l'épinette noire. Cette étude a aussi montré que, pour la tordeuse des bourgeons de l'épinette et sans doute pour d'autres lépidoptères ravageurs forestiers, les effets d'entraînement (carry-over effects) ne peuvent pas être ignorés. Des études supplémentaires sont nécessaires pour bien comprendre les rôles de ces mécanismes de défense dans la résistance accrue de cette espèce arborescente et comment ils seraient affectés dans un contexte de changement climatique. Les informations ainsi recueillies nous permettront de déterminer si l'épinette noire sera plus ou moins susceptible à la TBE. Cette information est importante car elle nous permettra d'évaluer l'impact de la TBE sur les forêts d'épinette noire situées au nord du Canada. En effet, ces forêts nordiques pourraient devenir susceptibles à la TBE dans le cas où l'augmentation prédite de la température permet à l'insecte de se déplacer vers le nord et d'atteindre ces forêts. Aujourd'hui, celles-ci sont naturellement protégées contre ce défoliateur en raison des conditions climatiques plus froides qui y prévalent et qui ne sont pas adéquates pour le développement de la TBE.

6.1 Répercussions sur la gestion des forêts

Les gestionnaires forestiers doivent choisir les meilleures options de gestion pour optimiser les fonctions des forêts et maximiser leur valeur, tout en réduisant les dégâts causés par les insectes. Ces décisions peuvent influencer la susceptibilité des forêts aux dégâts des insectes nuisibles. Toutefois, les informations concernant l'impact des pratiques sylvicoles, telles que l'éclaircie, sur la vulnérabilité des arbres et des peuplements à la TBE sont contradictoires. Nos résultats suggèrent que l'éclaircie peut être utilisée comme mesure préventive visant à augmenter la résistance globale des arbres hôtes et, par conséquent, à réduire la vulnérabilité des arbres et des peuplements. La figure x (chapitre 3) résume la quantité moyenne de feuillage résiduel dans les peuplements témoins et la réponse au traitement des trois espèces d'arbres hôtes utilisées dans cette étude en fonction de la qualité de drainage du site et de l'intensité des éclaircies par an. La variation de la résistance du peuplement est obtenue en comparant la quantité de feuillage résiduel dans les peuplements éclaircis à celui des peuplements témoins. Les résultats (exprimés en pourcentage) sont ensuite classés selon une échelle de résistance. Ce système de classification permet aux gestionnaires forestiers de déterminer si l’éclaircie produit un impact positif ou négatif sur les arbres résiduels et comment cet effet évolue au fil du temps selon les différentes qualités de drainage du site. Cela peut faciliter la prise de décision sur quand et où effectuer ce traitement sylvicole et quelle est la meilleure intensité pour obtenir l'augmentation désirée de la résistance. Par exemple, supposons qu'un gestionnaire forestier dispose d'un peuplement composé d’individus de sapin baumier et d'épinette noire qui poussent dans un site hydrique et qu’il veut déterminer l'effet de l'éclaircie sur la résistance du peuplement à la TBE. En vérifiant le système de classification de résistance (figure 6 chapitre 3), on peut observer que l'éclaircie augmente la résistance du sapin baumier un an après le traitement, mais que l’éclaircie de forte intensité produit les hausses de résistance les plus élevées tout au long de la période d’étude (6 ans). Quant à l'épinette noire, l'éclaircie produit une réduction légère de la résistance un an après le traitement, mais cette dernière augmente trois ans après l'éclaircie. Cependant, cette résistance accrue commence à disparaître à la sixième année. Par conséquent, le gestionnaire forestier pourrait pratiquer une éclaircie afin d’augmenter la résistance du peuplement sans nécessiter l’utilisation de traitements complémentaires pour protéger les arbres contre la TBE. Même si la résistance de l’épinette noire est affectée négativement la première année, cette espèce est moins encline à être défoliée par la tordeuse. En effet, son débourrement tardif (Blais 1957, Greenbank 1963) et son feuillage riche en composés toxiques peuvent nuire à la performance de l’insecte (Thomas, 1989, Chapitre 4) et la rende moins susceptible, ce qui se traduit par une défoliation et une réduction de la croissance plus faibles par rapport au sapin baumier (Henningar et al. 2008, Pothier et al. 2012). Toutefois, si l’éclaircie est appliquée dans un peuplement pur de sapin baumier poussant dans un site mésique ou subhygrique, il serait recommandé de mener ce traitement sylvicole accompagné d’arrosages aériens de l’insecticide microbien Bt pour protéger les arbres résiduels pendant la période de faible résistance à l’insecte (Figure 4.6 chapitre 3).

L'efficacité de l'éclaircie sera toutefois très différente selon le moment et le lieu du traitement, c'est-à-dire avant ou pendant une épidémie. L'éclaircie sera plus efficace pour réduire les dommages provoqués par la TBE si elle est menée pendant la phase de faible densité des populations de la TBE, sinon elle peut accroître la vulnérabilité à l'insecte (Piene, 1989; MacLean et Piene, 1995, Bauce 1996, Chapitre 1). Bien qu'il ait été prouvé que cette pratique sylvicole est efficace pour augmenter la résistance au niveau de l'arbre et du peuplement, nous ne connaissons pas les impacts de cette technique au niveau du paysage ou si elle peut altérer les infestations de la tordeuse. Il est peu probable que les épidémies de la TBE puissent être éliminées en utilisant des pratiques sylvicoles. Cependant, ces pratiques peuvent influencer l'ampleur, la périodicité ou la durée des épidémies (Robert et al. 2012). Les traitements sylvicoles à l'échelle du peuplement ne peuvent pas par eux-mêmes influencer les infestations des défoliateurs (Muzika et Liebhold 2000), mais l'effet cumulatif de ces pratiques à l'échelle du paysage peut affecter les infestations de TBE (Robert et al. 2012) et, par conséquent, en réduire les impacts. Par exemple, Campbell et al. (2008) ont constaté que le contenu en feuillus aux environs des peuplements de sapins baumier-épinettes diminue de manière significative la réduction de la croissance provoquée par la TBE sur ceux-ci. Cela suggère que l'augmentation du contenu en feuillus dans les paysages forestiers pourrait être utile pour réduire l'impact des épidémies de la TBE sur l'approvisionnement en bois. En outre, la fragmentation du paysage créée par l'aménagement forestier peut retarder la réponse des ennemis naturels à l'augmentation des populations de tordeuse (Capuccino et al. 1998), ce qui pourrait affecter l'intensité et la durée des épidémies de ce ravageur forestier (Robert et al. 2012). La bonne sélection de ces pratiques, ainsi que le moment et les échelles où elles sont appliquées sont, par conséquent, essentiels pour parvenir à une réduction des pertes de bois et de la mortalité des arbres. C'est pourquoi, les plans d'aménagement forestier visant à réduire les dommages provoqués par ce défoliateur devraient envisager l'utilisation de différentes techniques sylvicoles en même temps, comme l'éclaircie, l'augmentation des espèces non hôtes et l'application des arrosages aériens de Bt, pour réussir à réduire la vulnérabilité du paysage à l'insecte.

En conclusion, les résultats de cette étude appuient l'idée selon laquelle l'éclaircie pourrait être utilisée pour augmenter la résistance des arbres et des peuplements pendant la phase de faible densité des populations de TBE. Cette technique a non seulement augmenté la résistance du sapin baumier et de l'épinette noire à la TBE, mais elle fait en sorte que cette résistance accrue dure plusieurs années chez ces deux espèces. La même réponse a été observée chez les individus d'épinettes blanches qui poussent dans des sites subhygriques. L'augmentation de la résistance des arbres hôtes est importante, car elle permet de diminuer leur susceptibilité et celle des peuplements à la TBE en permettant aux arbres de résister et de se remettre plus rapidement de la défoliation. De plus, cela permet d’atténuer les pertes de bois attribuées à la mortalité des arbres et aux réductions de croissance en volume dans les peuplements. Le système de classification de résistance proposé dans cette étude peut être utile pour les aménagistes forestiers afin de planifier les temps d’application de l'éclaircie et les arrosages aériens de Bt permettant de réduire l'impact de la TBE au niveau du peuplement. Cependant, l'éclaircie doit être accompagnée par d'autres pratiques sylvicoles visant à réduire l'impact de ce défoliateur au niveau du paysage, sinon la mise en œuvre de cette technique sylvicole seule pourrait produire l'effet inverse. Finalement, il faut garder à l'esprit que nos résultats s'appliquent à une population de la TBE de taille moyenne, c’est-à-dire 20 larves par branche. Un certain degré d'incertitude persiste quant à savoir si cette résistance supplémentaire sera suffisante dans le cas où les arbres hôtes sont confrontés à des densités plus élevées de cet insecte ou si tous les arbres dans le peuplement vont réagir de la même manière au traitement. L'épidémie en cours dans l'est du Québec fournit une bonne occasion de tester nos conclusions.

Les résultats du chapitre 4 démontrent que le feuillage de l'épinette noire est un aliment de qualité inférieure pour la tordeuse par rapport au feuillage du sapin baumier et de l’épinette blanche. Ce phénomène se produit en raison des effets négatifs que le feuillage de l'épinette noire entraîne sur la descendance des insectes élevés sur cette diète. Ces effets ne sont pas apparents si une seule génération est étudiée. Il est nécessaire d’intégrer ce phénomène dans les méthodes de contrôle de ce ravageur forestier, en particulier en ajustant en conséquence les modèles prédictifs. Ces résultats nous permettent de mieux comprendre les mécanismes de défense des principaux hôtes de la TBE et leurs effets sur l'insecte. Une meilleure compréhension de ces mécanismes et de leurs effets sur ce ravageur est très importante afin de déterminer l'impact du changement climatique sur la résistance des essences hôtes de la TBE, de développer des méthodes visant à réduire les dommages causés par cet insecte, d'estimer les dommages à venir sous différents scénarios de réchauffement climatique et de développer et mettre en œuvre des mesures d'adaptation afin de protéger et conserver nos forêts des perturbations naturelles provoquées par les ravageurs.

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