UNIVERSITÉ DU QUÉBEC À MONTRÉAL

# THE FEEDING PREFERENCES, BEHAVIOURS AND PERFORMANCES OF THE FOREST TENT CATERPILLAR *Malacosoma disstria* HÜBNER (LEPIDOPTERA: LASIOCAMPIDAE), WHEN INTRODUCED TO SIXTEEN HYBRID POPLARS, *Populus* SPP.

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# LES PRÉFÉRENCES ALIMENTAIRES, LE COMPORTEMENT ET LA PERFORMANCE DE LA LIVRÉE DES FORÊTS, *Malacosoma disstria* HÜBNER (LEPIDOPTERA: LASIOCAMPIDAE), SUR SEIZE PEUPLIERS HYBRIDES, *Populus* SPP.

MÉMOIRE

PRÉSENTÉ

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PAR

MELISSA RALPH

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## RÉSUMÉ

De manière récurrente, les infestations d'insectes causent des dommages importants et à l'occasion la mortalité de leurs hôtes. Ce sujet est d'intérêt particulier pour l'industrie forestière, car la productivité diminue et les quantités de bois peuvent devenir insuffisantes pour satisfaire la demande. Au Québec, les plantations de peupliers sont d'importantes sources d'approvisionnement pour la bois d'œuvre et de pâte à papier, c'est pour ces raisons que des espèces du genre *Populus* ont été croisées pour créer des peupliers hybrides qui seraient plus tolérants aux stress abiotiques et biotiques. Les conditions météorologiques, les agents pathogènes et les différences dans la qualité des fibres ont été examinés sur des clones hybrides, mais seulement quelques études concernant les vulnérabilités aux insectes ont été complétées. Actuellement, le ministère des ressources naturelles et de la faune du Québec étudie les susceptibilités de ces peupliers hybrides envers les insectes nuisibles. Dans la présente étude, les préférences alimentaires de la livrée des forêts, *Malacosoma disstria,* un défoliateur important du peuplier en Amérique du Nord, seront étudiées sur différents clones de peupliers hybrides. Les caractéristiques physiques foliaires de ces clones hybrides, telles que la teneur en eau, la longueur du pétiole, et la longueur et la largeur des feuilles, seront mesurées, et des tests de performance seront effectués avec des larves de la livrée des forêts. Aussi, des tests sans-choix et de comportements seront réalisés et étudiés avec l'hôte principal de la livrée des forêts, le peuplier faux-tremble, *Populus tremuloides*. Les résultats démontrent que le feuillage de certains peupliers hybrides a été préféré de façon différenciée par les larves de *M. disstria*. Le groupe d'hybrides le moins préféré et choisi provoquant constamment des réponses dissuasives, et où aussi le taux de survie était le plus bas, était composé principalement de clones ayant un lien parental avec des peupliers baumiers ou japonais. Les groupes d'hybrides modérément et hautement préférés qui ont été principalement acceptés (consommés) par les chenilles comprenaient des parents hybrides liés avec les peupliers deltoides ou euraméricains. Ces résultats peuvent potentiellement améliorer la sélection des clones de peupliers hybrides qui présentent des susceptibilités faibles pour les larves de la livrée des forêts et peuvent maintenir une productivité élevée au cours des années d'épidémies.



Mots-clés: les clones de peupliers hybrides, *Populus* spp., la livrée des forêt, *Malacosoma disstria*, les préférences alimentaires, des tests de performance, des tests sans-choix

## ABSTRACT

Insect infestations are able to repeatedly cause serious damage and even death to their hosts. This subject is of particular interest for the forestry industry, as productivity diminishes and the quantity of wood may become insufficient to satisfy demand. In Quebec, poplar plantations serve as an important source for lumber and pulp and paper products; it is for these reasons that the species of the genus *Populus* have been crossed to create hybrid poplars that are more tolerant to abiotic and biotic stresses. Meteorological influences, the effects of pathogenic agents and differences in fibre quality have been examined on the hybrid clones; however, only a few studies have been completed regarding their vulnerabilities to insects. Currently, the ministère des ressources naturelles et de la faune du Québec is investigating the susceptibilities of these hybrid poplars towards damaging insects. In the present study, the feeding preferences of the forest tent caterpillar, *Malacosoma disstria*, an important poplar defoliator in North America, will be studied when introduced to different hybrid poplars. The physical foliar characteristics of the hybrid clones, such as moisture, petiole length, leaf diameter and length, will be measured, and performance tests will be conducted on the forest tent larvae. Also, no-choice tests and behaviours will be realized and studied against the forest tent caterpillar's primary host, *Populus tremuloides*. Our results demonstrate that *M. disstria* larvae differentially preferred certain hybrid poplar foliar. The hybrid groups composed of clones crossed with balsam or Japanese poplars were least preferred and chosen, constantly provoking dissuasive responses and resulting in low survival. The moderately and highly preferred hybrid groups that were mostly accepted (consumed) by the caterpillars were composed of clones with a parental tie to deltoïdes or Euramerican poplars. These results could potentially improve hybrid poplar clonal selection, determining which hybrids present weak susceptibilities to forest tent larvae and could maintain higher productivity during epidemic years.



Keywords: hybrid poplar clones, *Populus* spp., forest tent caterpillar, *Malacosoma disstria*, feeding preferences, performance tests, no-choice tests

# CHAPITRE 1

# INTRODUCTION GÉNÉRALE

## 1.1 La problématique

En Amérique du nord, les arbres sont exposés à plusieurs facteurs affectant leur survie et leur taux de croissance. Ils sont soumis à des conditions météorologiques extrêmes, des bactéries ou des champignons infectieux, ainsi qu'à des infestations d'insectes (Dickmann and Stuart 1983, Robison 1993, Dickmann 2002). Les épidémies d'insectes sont l'un des facteurs qui peut avoir une durée plus longue et des effets désastreux. Par exemple, la dendroctone du pin, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), a détruit 8.9 millions d'hectares de la forêt boréale dans le nord de la Colombie Britannique et de l'Alberta en 2009 (Walton 2011). De même, la tordeuse des bourgeons d'épinette, *Choristoneura fumiferana* Clemens (Lepidoptera : Totricidae), défolie son hôte causant une diminution du taux de croissance (Morris et al. 1963). Pendant des années d'épidémies sévères de *C. fumiferana* les arbres défoliés peuvent mourir (Morris et al. 1963). Récemment, une infestation de la livrée des forêts, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), a ravagé des peupliers et des érables à sucre dans quelques secteurs des basses Laurentides au nord de Montréal, Québec (MRNF 2010). Dans ce cas, le nombre de chenilles était tellement élevé qu'elles ont envahi les routes et les poteaux de télécommunication, et, dès le début de juillet, il n'y avait aucune feuille sur plusieurs arbres (MRNF 2010). Durant les années d'épidémies, la livrée des forêts est un problème majeur pour l'industrie utilisant le peuplier, car ce sont ces arbres que les chenilles attaqueront préférentiellement (Cerezke 1991, Roland 2000). Conséquemment, l'industrie forestière doit se préparer pour les événements futurs qui peuvent causer la diminution de la productivité de cette essence forestière.

Les peupliers préférés pour la fabrication de pâtes et papiers sont généralement les espèces qui ont une forte croissance mais qui sont aussi souvent sensibles à plusieurs maladies et aux insectes ravageurs (Dickmann 2002). En réponse, la silviculture du peuplier au Québec a comme objectif produit des hybrides qui ont été sélectionnés pour leur résistance envers les pathogènes et les ravageurs, un taux de croissance élevé, une bonne adaptation aux variations climatiques et un bois solide. Les peupliers indigènes qui ont été croisés sont le *Populus balsamifera* L (Figure 1.1), le *Populus trichocarpa* Torr & Gray (Figure 1.2) et le *Populus deltoides* Batr (Figure 1.3). Les espèces de peupliers introduits et qui ont été croisés sont le *Populus maximowiczii* Henry et le *Populus nigra* L..

## 1.2 Les peupliers hybrides du Québec

Comme les peupliers hybrides au Québec peuvent être issus de différentes espèces parentales indigènes et exotiques (voir Annexe 2), leur vulnérabilité envers les insectes ravageurs peuvent aussi différer. Il est présumé que les hybrides croisés avec *P. balsamifera* auront une plus forte tolérance aux insectes parce que les peupliers baumiers ont une forte fragrance et qu'ils sécrètent une résine collante au niveau de leurs bourgeons et de leurs jeunes feuilles (Dickmann and Stuart 1983). Fait intéressant, il a été documenté que les Amérindiens brûlaient les bourgeons et l'écorce des peupliers baumiers pour éloigner les insectes volants (Dickmann 2002). La remarque à l'effet que les insectes restaient à distance de la fumée parfumée soutient l'hypothèse de Bryant et Kuropat (1980) qui est que les bourgeons résineux et les feuilles de *P. balsamifera* diminuent les interactions avec les animaux.

Il est aussi suggéré que les peupliers hybrides issus de *P. trichocarpa* ou *P. deltoides* seront considérés comme une source de nourriture adéquate pour les insectes ravageurs. Même si le feuillage de *P. trichocarpa* contient une résine similaire à celle du *P. balsamifera,* il y a plusieurs insectes défoliateurs et perce-bois qui s'y alimentent (Maini and Cayford 1968, Furniss and Carolin 1977). Il y a également plusieurs espèces d'insectes ravageurs qui se retrouvent et s'alimentent sur le feuillage de *P. deltoides* (Morris et al. 1975).

Lorsque l'on considère les espèces de peupliers exotiques parentaux utilisées pour l'hybridation, soit *P. maximowiczii* (provenant du Japon) et *P. nigra* (provenant de l'Eurasie), il est très difficile de prédire leurs interactions avec les insectes nord-américains car peu d'études ont été réalisées.

### 1.3 L'espèce à l'étude: *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae)

Les épidémies de la livrée des forêts causent des dommages importants à leurs hôtes feuillus et ce à des intervalles entre 6 et 16 ans (Meeker 1997). Le cycle de vie de *M. disstria* comprend un développement embryonnaire pendant l'hiver suivi par cinq à six stades larvaires (d'une durée d'environ quatre jours chacun) débutant à la fin d'avril et se terminant par une transformation en pupe et l'éclosion d'un papillon adulte vers le début de juillet (Fitzgerald 1995). Ce sont les stades larvaires qui sont les plus intéressants à étudier, car ils ont la capacité de défolier leurs hôtes (les papillons adultes ne mangent pas) (Fitzgerald 1995, Meeker 1997). La livrée des forêts est distribuée dans les mêmes zones que son hôte préféré, le peuplier faux-tremble, *Populus tremuloides* Michaux, aux États-Unis et le Canada (Figure 1.4) (Meeker 1997). Les chenilles de *M. disstria* sont nomades et construisent leurs propres tentes pour se reposer, se réguler la température et pour se protéger contre le ennemis naturels (Fitzgerald 1995). Pour les trois premiers stades, les larves *M. disstria* démontrent des caractéristiques grégaires; elles mangent en groupe et laissent des traces de soie derrières elles pour communiquer avec les autres membres de la colonie (Fitzgerald 1995, Colasurdo and Despland 2005). Les chemins de soie aident à garder la cohésion coloniale et ils sont utilisés comme source de liaison entre les sites de repas et de repos; l'installation d'une tente proche d'une source de nourriture démontre la satisfaction d'un repas (Fitzgerald and Edgerly 1979, Fitzgerald 1995, Colasurdo and Despland 2005). Pour éviter les interactions avec les parasites ou les prédateurs, les chenilles *M. disstria* mangent en particulier tôt le matin (vers 6hrs) et tard dans la soirée (vers 22hrs) (Fitzgerald et al. 1988, Peters and Despland 2006, Trottier 2010). Les activités de la livrée des forêts suivant la consommation d'un repas satisfaisant incluent la fabrication d'une tente et du repos, dont un cycle complet se reproduit à chaque trois heures (Fitzgerald 1980).

**1.4 Le comportement alimentaire**

La livrée des forêts utilise ses sens olfactifs et gustatifs pour repérer ses hôtes. Les larves de lépidoptères peuvent sentir et goûter, par contre une larve ne peut pas sentir l'odeur d'un arbre voisin dans son environnement (Dethier 1937). Des sensilles olfactives (récepteurs de phéromones) ont été retrouvées sur les segments terminaux des antennes, des maxillaires et des tarses des chenilles (Dethier 1937, Chapman 1995a). Il est supposé que les larves des lépidoptères peuvent seulement sentir leurs hôtes par le toucher ou le goûter, par contre des mouvements de la tête, l'élévation des derniers segments et l'immobilité ont été observés lorsque les chenilles ont été présentés avec l'odeur d'un aliment non-désiré (McIndoo 1919, Dethier 1937, Bernays and Chapman 1994, Chapman 1995a). Les études précédentes sur plusieurs chenilles, comme Isia isabella L (Lepidoptera: Arctiidae) et *Anosia plexippus* L. (Lepidoptera: Nymphalidae), ont démontré que le processus d'olfaction et de réaction envers une odeur se produit en moins d'une minute (Dethier 1937, Chapman 1995a). Si une chenille sent l'odeur agréable d'un hôte potentiel, elle le mangera, par contre, si l'hôte a une odeur inacceptable, une chenille décidera de se déplacer vers une autre source (Dethier 1937, Waldbauer and Friedman 1991, Chapman 1995a).

La gustation des chenilles implique l'analyse des phagostimulants et des composés secondaires (toxines ou phéromones) (Bernays and Chapman 1994, Strauss and Agrawal 1999, Chapman 2003). Les larves de lépidoptères sont capables de gouter et d'établir la qualité et la chimie d'un repas en palpant un hôte potentiel avec leur bouche qui est composée de plusieurs sensilles (Figure 1.5) (Dethier 1937, Bernays and Chapman 1994, Chapman 1995a, 2003). Si un hôte est trouvé acceptable après les palpations, une chenille goutera le repas pour mieux évaluer les caractéristiques chimiques qui sont présentes (Chapman 1995a). Les glucides sont les phagostimulants primaires qui informent les chenilles d'un choix d'hôte approprié (Panzuto and Albert 1997, Panzuto et al. 2002). Toutes les larves de lépidoptère ont des sensilles sensibles aux sucres, celles-ci suscitent une réponse stimulant la continuité de l'alimentation lorsqu'elles sont stimulées (Panzuto and Albert 1997, Panzuto et al. 2002). Aussi, les protéines (acides aminés) peuvent être considérées comme phagostimulants même si elles ne sont pas détecté au goût, car elles semblent

déterminer la durée d'un repas et les intervalles de consommation (Bernays and Chapman 1994, Despland and Noseworthy 2006, Trottier 2010).

Contrairement aux phagostimulants, les composés secondaires, comme les alcaloïdes, les tannins, les acides phénoliques et les flavonoïdes, réagissent comme des toxines quand ils sont ingérés par les chenilles (Bernays and Chapman 1994, Strauss and Agrawal 1999, Panzuto et al. 2002, Chapman 2003, Trottier 2010). Par exemple, Arimura et al. (2004) ont découvert que l'alimentation de la livrée de la forêt, sur du feuillage de peuplier hybride *Populus trichocarpa* croisé avec *P. deltoides,* produisait des émissions locales systémiques de produits volatiles secondaires des gènes synthéases terpéniques comme mécanisme de défense. Les phéromones et les signaux de défenses sont aussi considérés comme des composés secondaires, ils peuvent cependant stimuler la réponse de l'hôte (Chapman 2003). De plus, il semble que chaque espèce possède des réponses spécifiques qui induisent des effets phagostimulants (Chapman 2003). Chapman (2003) a trouvé que des chenilles qui se nourrissent exclusivement sur les espèces de *Rosecea* Juss, avaient des neurones gustatifs particulièrement sensibles au sorbitol, un composé spécifique à ces arbres. Les glucides et les tannins sont soumis à plusieurs études concernant les signaux de réponse qu'ils provoquent dans les insectes, car ces deux substances sont des composés primaires dans la diète d'une larve de lépidoptère (Karowe 1989a, Panzuto 2002, Despland and Noseworthy 2006). Panzuto et al. (2002) ont démontré que les glucides en grande quantité ralentissent la croissance des larves *Choristoneura rosceana* (Lepidoptera: Tortricidae). Ceci est dû au fait qu'une diète plus riche en glucides qu'en protéines (et inversement) diminue le taux de croissance et de survie des larves lépidoptères, en particulier chez les larves de *M. disstria* (Despland and Noseworthy 2006). Les tannins en concentration de 0.5% et plus, démontrent un taux de mortalité élevé et une diminution de croissance significative aussi chez les larves de *M. disstria* (Karowe 1989a).

Les chenilles choisissent un hôte par rapport à leur texture et le pourcentage d'eau présent. Hunter et Lechowicz (1992) ont trouvé que les larves de *Lymantria dispar* L. (Lepidoptera: Lymantriidae) évitaient le feuillage robuste et ayant un faible quantité d'eau.

Peeters et al. (2007) ont aussi démontré que les insectes sont réticents à consommer des feuilles qui sont fortement texturées (avec un contenu haut en fibre, lignine et cellulose). La structure d'une feuille semble affecter le choix alimentaire de la chenille; Peeters (2002b) a découvert que les insectes broyeurs évitaient les feuilles avec des surfaces hautement lignifiés (les veines), des cuticules épaisses et de tissus vasculaires profonds. De plus, la surface des feuilles possédant des trichomes (petits poils) peut affecter la préférence d'un hôte potentiel (Levin 1973, Peeters 2002b).

Les larves de *M. disstria* consommeront et auront des comportements différents selon l'acceptation d'un hôte. Si un repas est très désirable, les chenilles de *M. disstria* produiront un chemin riche en phéromones pour encourager les autres membres de la colonie à suivre, là ils mangeront la presque la totalité du feuillage, sauf les nervures et le pétiole (Heinrich 1979, Fitzgerald 1995, Colasurdo and Despland 2005, Trottier 2010). La livrée des forêts mange de trois façons: un repas préféré sera très troué ou beaucoup consommé, une source modérée sera grignotée en périphérie et un repas non-désiré se limitera à quelques grignotages (Robison 1993).

### 1.5 Les objectifs et les hypothèses

Le but de cette étude était d'examiner les susceptibilités de seize clones de peupliers hybrides en utilisant des chenilles de *M. disstria* pour plusieurs expériences. Ces susceptibilités ont été investigué en deux volets principaux (les chapitres 2 et 3).

Le chapitre 2 examinera la tolérance du feuillage de peupliers hybrides envers les chenilles de stades 4 (2010) et 5 (2009), dans le temps, en réalisant des essais de non-choix et de deux-choix, et ce en observant leurs comportements et en identifiant leurs caractéristiques foliaires (la taille des feuilles, la taille des pétioles, la quantité d'eau présente dans les feuilles). Une échelle de préférence sera créée par la suite et utilisée pour des comparaisons entre les deux années d'études (2009 et 2010) et dans le temps (3ième à 7ième semaine en 2010).

Le chapitre 3 portera sur la performance (survie et durées des stades larvaires) de livrées des forêts qui ont été élevées sur six clones hybrides différents; les études se dérouleront en deux étapes: débutant au stade néonatal et au quatrième stade larvaire.

Nos principales hypothèses sont les suivantes:

1) Si les larves de *M. disstria* démonteront des préférences variées entre les différents feuilles de peupliers hybrides, cette discrimination devrait être due aux croisements des arbres parentales qui causent des variations physiques et chimiques foliaires.

2) S'il y a une présence de discrimination, les larves de *M. disstria* devraient généralement défavorisées et auront des performances moindres lorsque élevées sur des peupliers hybrides issus de croisements avec *P. balsamifera.* Aussi, il est suggéré que les chenilles de *M. disstria* préfèreront et auront une meilleure performance lorsque nourries d'hybrides issus de *P. deltoides* ou *P. trichocarpa,* car il y a plusieurs espèces d'insectes qui s'alimentent sur leur feuillages (Maini and Cayford 1968, Morris et al. 1975, Furniss and Carolin 1977).

**Figure 1.1** — Le peuplier baumier, *P. balsamifera* L., est l'espèce le plus nordique quand on considère les espèces Tacamahaca indigènes de l'amérique du Nord. Les peupliers baumiers sont retrouvés à travers le haut des États-Unis, dans le Canada et l'Alaska (Dickmann and Stuart 1983, USEPA 1999).

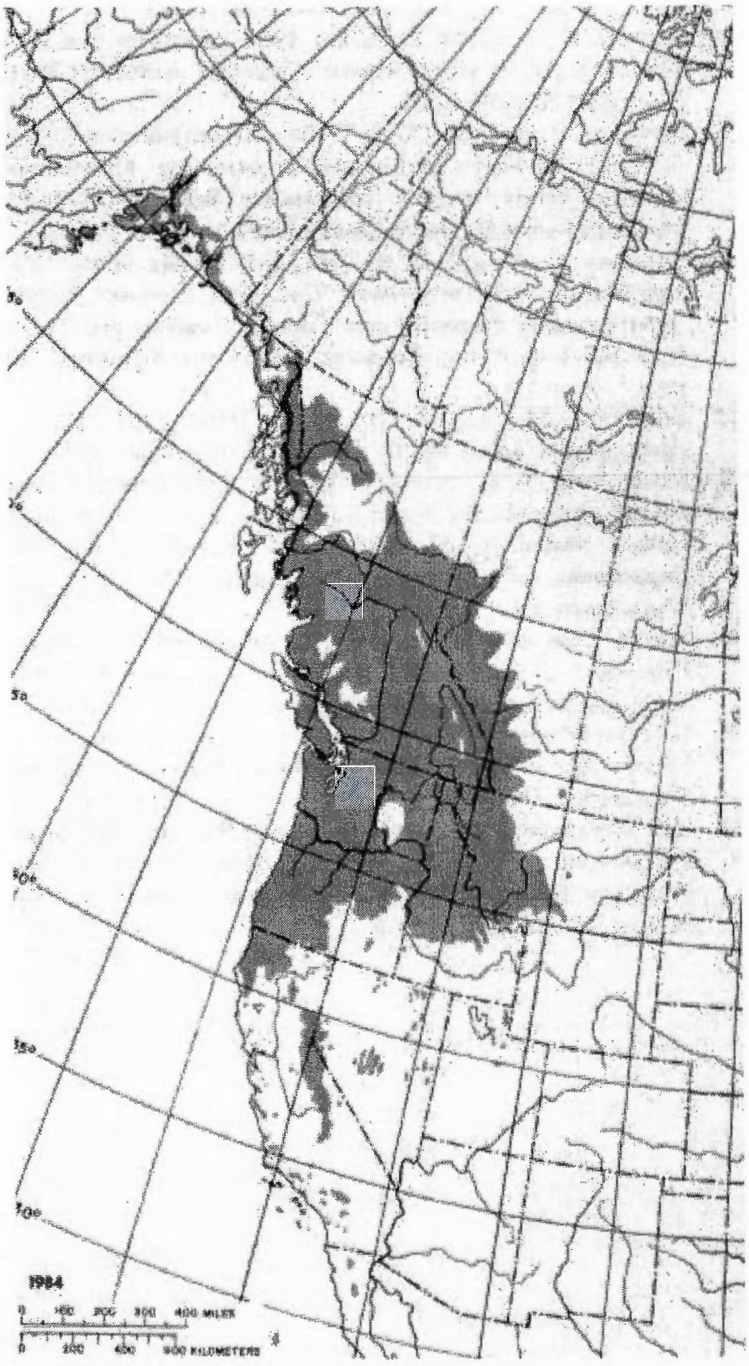



**Figure 1.2** — Le peuplier noir, *P. trichocarpa* Torr. & Gray (Tacamahaca), est l'espèce de peuplier Américain le plus à l'ouest dans les États-Unis et le Canada (USEPA 1999).

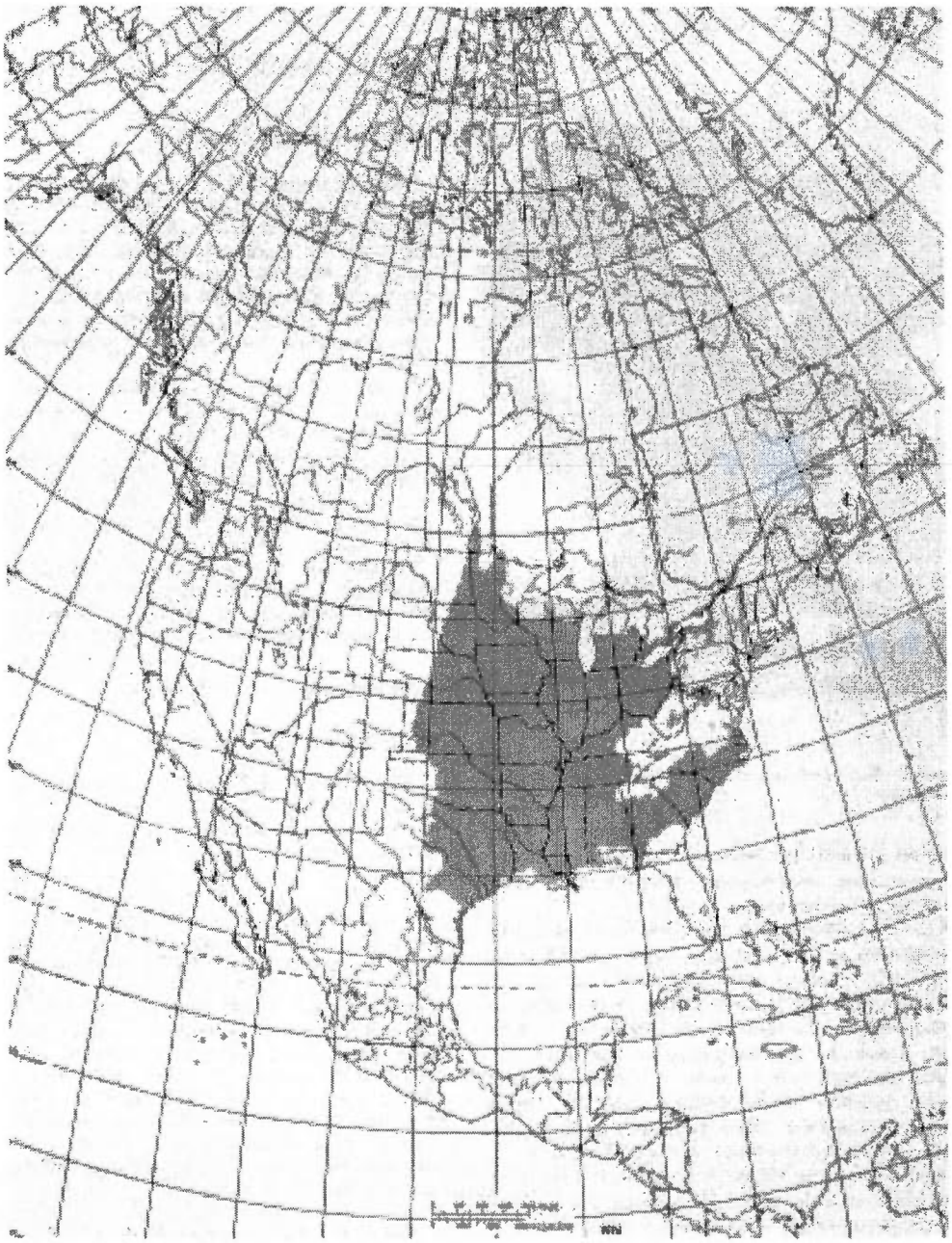


**Figure 1.3** — Dans l'est les peupliers deltoides, *P. deltoides* Batr. (Aigeros), ont une vie très courte. Par contre, ils sont commercialement favorisés pour leur taux de croissance très rapide. Cette espèce de peuplier est indigène de l'Amérique du Nord, trouvée dans les forêts de feuillus et dans plusieurs plantations forestières dans l'est des États-Unis et au sud du Canada (Dickmann and Stuart 1983, USEPA 1999).

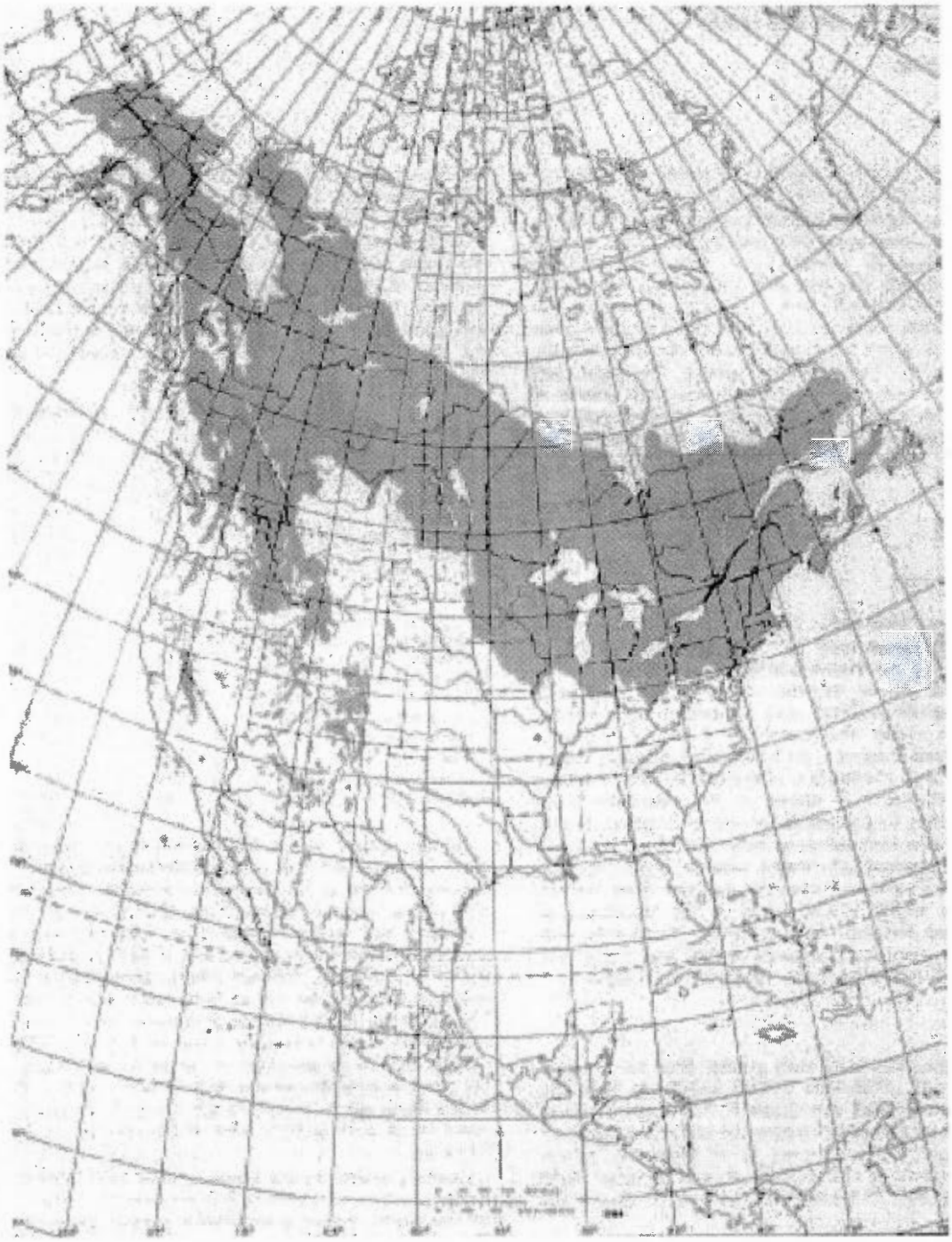


**Figure 1.4** — Le peuplier faux-tremble *P. tremuloides* Michx., de la section de peuplier Leuce et de la sous-section Trepidae, est l'espèce d'arbre indigène la plus répandu en Amérique du Nord (USEPA 1999).

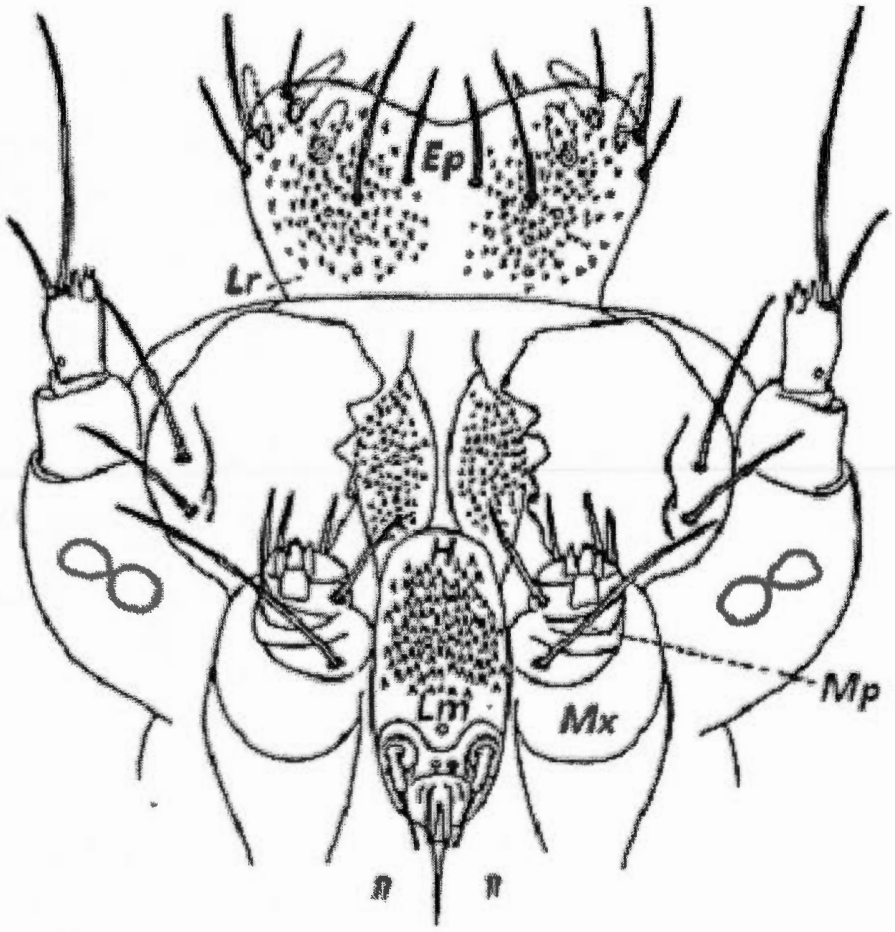



**Figure 1.5** — La cavité buccale d'une larve de lépidoptère contient: des sensilles gustatoires trouvées dans l'épipharynx (Ep), un labre (Lr), une hypopharynx (H), des maxillaires (Mx), des palpes maxillaires (Mp), et un labium (Lm) (Dethier 1937).

CHAPITRE 2

# THE FEEDING PREFERENCES AND BEHAVIOURS OVER TIME OF THE FOREST TENT CATERPILLAR, *MALACOSOMA DISSTRIA* HÜBNER (LEPIDOPTERA: LASIOCAMPIDAE) , WHEN INTRODUCED TO SIXTEEN HYBRID POPLARS, *POPULUS* SPP., FROM QUEBEC

## 2.1 Abstract

Insect outbreaks have the ability to devastate entire forests and the potential to damage hybrid poplar plantations used for the forestry industry in Quebec. This paper investigates the susceptibilities of sixteen hybrid poplars towards a predominant *Populus* pest in North America, the forest tent caterpillar, *Malacosoma disstria*. In order to assess a preference gradient, consumption experiments during the Spring of 2009 and 2010 were conducted and compared. In 2010, two-choice assays, foliar characteristics (cross-section, leaf and petiole lengths, leaf water content), and larval behavioural observations were also performed over the course of 3, 5, and 7 weeks following respective hybrid clone budbreak dates. Preference rankings remained consistent from 2009 to 2010 and over time in 2010 ($X^2$ = 5.53, df = 3, p = 0.137). Low leaf consumption and water content, increased initial searching and lengthly leaf tasting behaviours were related to less preferred hybrid foliage of *Populus balsamifera* parentage. Increased initial consumption, water content, and completed foraging cycles were related to higher preferred foliage of *P. euramericana* parentage. In two-choice assays, previously ranked highly preferred foliage was consistently chosen against lower preferred foliage (Z = -4.46, N = 30, p < 0.001). In 2010, as leaves aged, all foliar measurements (cross-section and petiole length) increased except for leaf length, and leaf water content decreased. The work presented here suggests that hybrid poplars crossed with *P. balsamifera*, *P. maximowiczii* or *P. deltoides* parentage be cultivated for Quebec's forestry industry in order to minimize potential entomological destructions.

## 2.2 Introduction

The increasing demands for lumber and paper products have encouraged the growth of hybrid poplar silviculture in Quebec (Vallée 1995a, Vallée 1995b, Zhang et al 2003). Both endogenic (North American) and exogenic (European, Asian) *Populus* spp. have been

crossed to produce such hybrid poplars. Current hybrids used in these plantations have been selected for rapid growth rates, tolerance to abiotic stresses and pathological diseases, and strong fiber in order to satisfy the growing needs of the forest industry (Vallée 1995a, Vallée 1995b, Johnson 2000, Zhang et al. 2003, DRF-MRNF 2005, Broderick et al. 2010). As parental specimens originate from different geographical regions around the world, it is possible that a broad range of entomological host suitabilities exists amongst the hybrid poplar clones.

Previous investigations have demonstrated that non-native *Populus* parents may render hybrid poplars resistant against insect predators. For example, both the poplar-and-willow borer, *Cryptorhynchus lapathy* L. (Coleoptera: Curulionidae), and poplar aphids, *Chaitrophorus leucolmelas* Koch (Homoptera: Aphididae), are less likely to establish in high densities on hybrid poplars crossed with *P. maximowiczii* Henry parentage from Japan (Ramirez et al. 2004, Broberg et al. 2005, Hannon et al. 2008). Robison and Raffa (1994) have reported varying entomological susceptibilities of hybrid poplars from Wisconsin: forest tent caterpillars, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), consumed little and survived poorly on hosts crossed with *P. simonii* Carr. (Asian) and *P. berolinensis* Dipp. (European) or *P. nigra* L. (European) and *P. maximowiczii* (Asian), and the opposite was observed when *P. nigra* var. *Charkowiensis* and *P. berolinesis* or both parents from *P. deltoides* Batr. (North American) were crossed (Robison 1993). It is therefore important to assess the vulnerabilities of Quebec's hybrid poplar silviculture against *M. disstria* in order to understand and prepare for such interactions.

The forest tent caterpillar is an important aspen defoliator across Canada and the mid-to-northern United States (Batzer and Morris 1978, Cerezke 1991, Meeker 1997, Roland 2000). During outbreak years, mature *M. disstria* larvae can severely defoliate their hosts from late May to early July, decreasing tree growth rates and occasionally causing tree mortalities (Hidahl and Reeks 1960, Hogg and Brandt 2002, Moulinier et al. 2011). Moulinier et al. (2011) found that forest tent caterpillar infestations contributed significantly to canopy degeneration in deciduous stands of northwestern Quebec from 1998 – 2003; trees

defoliated for several years exhibited stand gaps comparable to those of aspen stands aged 120-124 years (Kneeshaw and Bergeron 1998, Hill et al. 2005). It is hypothesized that Quebec hybrid poplars are likely subject to *M. disstria* as well, parental hybrid clone differences may play a role in differential susceptibilities towards insects, particularly those that are exogenous to North America's ecology. As such hybrid poplar clones are crosses between different exogenous or endogenous *Populus* specimens to North America, differing budbreak periods are expected. As Lepidopteran larvae have synchronized emersion times with deciduous leaf flushing in the early Spring (Lechowicz 1984), this may cause difficulty for such larvae to consume hybrid foliage that may emerge much earlier or later in the season. For example, Lechowicz and Hunter (1992) found that the window of opportunity of gypsy moth larvae to consume alternative hosts was greatly decreased on a daily basis due to continuously changing foliar properties.

This study investigates clonal leaf traits and forest tent larval preferences and behaviours with reference to various hybrid poplar forage and seasonal variation in hybrid leaf quality. In order to examine any differences amongst Quebec hybrid poplars, *M. disstria* larvae were subjected to consumption, two-choice and behavioural assays towards sixteen clones in 2009 and three-, five-, and seven-weeks after their respective budbreak dates in 2010.

## 2.3 Materials and Methods

Experiments were conducted under laboratory settings at UQAM Biological Science Department from April to July 2009 and 2010. For all experiments, forest tent larvae were used once then discarded into a central rearing bin. Statistical analyses were performed via SPSS 18 Statistical Software.

### 2.3.1 Vernal Season of 2009

#### 2.3.1.1 Egg mass collection

In 2008, egg masses were collected from Mont Saint-Hilaire (45°57N, 73°19W) and overwintered outdoors in a brown paper bag until March 2009, when egg masses were brought indoors to be refrigerated. Before use, egg masses were sterilized in a sodium hypochlorite solution as per Grisdale (Grisdale 1985) in order to decrease mortality due to pathogen infection. Prior to hatching, four to five egg bands were placed into 9cm x 9cm x 3cm containers with a young branch of *Populus tremuloides* Michaux. leafing buds held in a water-filled 1.5mL microcentrifuge tube (Figure 2). Once hatched, neonatal larvae from different egg masses were randomized via aggregation, diminishing any maternal effects present, such as differing maternal diets or egg vitellogin concentrations which have been found to influence the fitness of Lepidopteran larvae (Wellington 1965, Rossiter et al. 1993). Neonatal larvae were reared on an ad libitum diet of young *P. tremuloides* foliage at 22°C, 70% R.H., 16L:8D regime, until their second instar, where larvae were transferred in groups of fifteen individuals to larger 25cm x 14cm x 10cm chambers and kept under similar conditions.

Following *M. disstria*'s second molt (to third instar), containers were randomly placed and maintained in 18°C, 60% R.H., 16L:8D or 20°C, 70% R.H., 16L:8D rearing conditions in order to uphold larval numbers. It has been demonstrated that forest tent larval development is lengthened at cooler temperatures; however, their activities and performance remains at the same standards, at 18°C and 20°C, as caterpillars subjected to higher temperatures (Levesque et al. 2002). Caterpillars were reared on *P. tremuloides* foliage synchronized with natural leaf phenology, for example, neonatal larvae were fed recently eclosed buds, whereas third instar larvae were fed foliage twelve days after budbreak, representing the approximate four day duration of each caterpillar instar (Fitzgerald 1995).

**2.3.1.2 Foliage collection**

*M. disstria* larvae were consistently reared on *P. tremuloides* foliage, their preferred host in the field (Meeker 1997). Young budding branches and foliage were collected from aspen stands north of Montreal (45°72N, 73°66W).

**2.3.1.2 Hybrid poplar clones**

In early May 2009, three to five clones of sixteen hybrid poplar saplings aged of one to two years old were collected from Ripon, Quebec, supplied from the government of Quebec (DRF-MRNF 2005) and grown in the UQAM greenhouse (Table I). Young trees were transplanted from small to larger pots, diameter 40cm by depth 35cm, filled with sand and peat-moss in a 1:2 ratio, respectively. Hybrid clones were not subject to insecticides or fungicides until after experiments were completed; however they did receive a constant supply of general nitrogen, phosphorus and potassium fertilizer in ratios of 20:20:20.

**2.3.1.3 Consumption experiments**

Fifth instar *M. disstria* larvae (n = 204) were individually introduced to a 20mm leaf disc, punched from lightly veinated surfaces (Figure 2.2a) and placed on a pin under a large petri base (Figure 2.2b). Leaf discs originated from sixteen different hybrid poplars or *P. tremuloides* (control) leaves. Twelve replicates per foliage type were conducted, where experimental setups were laid out on a laboratory countertop and contained randomly chosen leaf disks (so that disks under petris next to a setup may or may not have been similar). Once all control disks were 50% consumed, the experiment ended and visual percentages of remaining leaf disk portions from hybrid poplars were estimated, and all leaf disc portions were oven dried (for 72 hours at 60°C) and weighed. The weight of a dried hybrid leaf disc was compared to that of the mean of all dried control leaf discs multiplied by the percentage of hybrid leaf disc remaining when 50% of all control discs were consumed, via the below calculation:

$$\text{Percent consumption} = \frac{\text{Weight of dried hybrid leaf disc} \times \text{Percent of hybrid leaf disc remaining}}{\text{Mean dried weight of control leaf discs}}$$

Average percent consumptions were calculated in order to rank forest tent caterpillar hybrid poplar preferences.

Leaves chosen for experiments were randomly selected from different positions on their respective saplings, removing the different preference effects that may be present between sun- and shade-leaves which has previously been found to affect *M. disstria* preference when fed sugar maple (Fortin and Mauffette 2002). A randomized selection of hybrid poplar leaves were chosen from various saplings of a given clone; Hwang and Lindroth (1997) found that among-clone variation of thirteen aspen clones differentially affected both *M. disstria* and *Lymntria dispar* L. (Lepidoptera: Lymantriidae) larval performance.

#### 2.3.1.4 Statistical Analysis

Hybrid poplar clones were ranked in order of preference by comparing their average consumed percentages via a nonparametric Kruskal-Wallis test.

### 2.3.2 Vernal season of 2010

#### 2.3.2.1 *M. disstria* larvae collection

Unusually warm temperatures caused trees to bud early and *M. disstria* eggs to hatch at the beginning of April much early when compared with average forest tent hatching times around the beginning of May (Fitzgerald 1995). Following extremely warm conditions, much cooler temperatures and wet weather conditions set in, allowing for young instars to be captured until mid-May due to slowed larval development (Levesque et al. 2002). All caterpillars were reared similar to prior experiments from 2009. Unfed and newly hatched neonatal larvae were collected from sugar maple stands in Saint-Esprit (45°91N, 73°65W) on

April 8th 2010. Second and third instar larvae were collected from sugar maple and aspen stands in Saint-Esprit as needed.

#### 2.3.2.2 Foliage collection

*M. disstria* larvae were consistently reared on *P. tremuloides* foliage collected from Saint-Esprit aspen stands. When foliage demands were high during later caterpillar instars, mature forage was collected from a small stand of *P. tremuloides* trees found in Montreal-West (45.43°N, 73.61°W).

#### 2.3.2.3 Hybrid poplar clones

Sixteen hybrid poplar clones from 2009 (Table I), under similar field temperatures, were kept inside the UQAM greenhouse until the beginning of December 2009, where plants were brought to the UQAM rooftop to overwinter outside until early April 2010 when they were brought back inside to the greenhouse. During 2010, clones ranged from two to three years of age and were treated (insecticide, fungicide and fertilizer) only after experiments were completed, as in 2009.

#### 2.3.2.4 Consumption experiments

Fourth instar forest tent larvae (n = 529) were individually introduced to a whole hybrid poplar or *P. tremuloides* leaf under a 20cm diameter petri base and were allowed to consume for 24 hours (Figure 2.3). Each leaf was kept hydrated via an attached water-filled flourist vial where stems were inserted from under the petri base (Figure 2.3). Twelve replicates were conducted for each of the sixteen hybrid poplars and trembling aspen, where experimental setups were laid out on a laboratory countertop and contained randomly chosen leaves (so that leaves under petris next to a setup may or may not have been similar). Caterpillars were subjected to consumption experiments as hybrid leaves matured, at 3-, 5- and 7-weeks following their respective budbreak dates (Table II). As only three hybrid

saplings were available for some clones, E3333 and E3570 were not tested during the third week, MB915302 was not tested during the fifth week and MB915313 was only tested during the fifth week.

Leaves were chosen for experiments as in 2009. Every leaf was scanned before and after experiments in order to calculate leaf areas consumed, to measure leaf cross-section, length and petiole length via Adobe Photoshop CS4 selection and measurement tools, and to rank the caterpillars' preferences. Leaves were also weighed before consumption (wet weight) in order to measure percent water content of leaves at the end of experiments. After 24 hours, leaves, or remaining leaf fragments and stem if a given leaf was entirely consumed, were oven dried (for 72 hours at 60°C) and weighed; percent leaf water content was subsequently calculated by the performing formulae (converting consumed dry leaf weights into unconsumed dry leaf weights, and subsequently calculating leaf water content):

$$\text{Unconsumed leaf dry weight} = \frac{\text{Dry weight of consumed leaf} \times \text{Unconsumed leaf area}}{\text{Consumed leaf area}}$$

$$\text{Percent water content} = \frac{\text{Unconsumed leaf wet weight} - \text{Unconsumed leaf dry weight}}{\text{Unconsumed leaf wet weight}} \times 100\%$$

**2.3.2.5 Statistical analysis**

Hybrid poplar clones were ranked in order of preference by comparing their mean consumed leaf areas from calculated non-parametric Kruskal-Wallis tests for each week following budbreak that was studied. Phenological influences on *M. disstria* leaf area consumptions and foliar traits were compared via stepwise multiple regression analyses (alpha significance level of 0.05), nonparametric Kruskal-Wallis tests and post-hoc Mann-Whitney U-tests (Bonferonni correction was applied, alpha significance level of 0.025).

**2.3.2.6 Two-choice experiments**

Two variations of a two-choice experiment were conducted where four fourth instar caterpillars were placed at the base of a Y-branch and allowed two hours to consume 5-week old leaves placed at both ends (Figure 2.4). The Y-branch, of approximately 30cm high and expanding approximately 40cm wide, was broken from *P. tremuloides* foliage collected from St-Esprit or Montreal-West and sterilized by wetting the branch with rubbing alcohol and allowing it to air dry in order to remove any previous trails that could have been made by tent caterpillars in the field (Fitzgerald 1995). The initial experiment involved a choice of *P. tremuloides* on one random side of the branch and a previously highly (EM915508), intermediately (E3656, EM916401, MB915319, BM915005) or less (BM3374) preferred hybrid poplar choice on the other end; six treatments and a control group were replicated sixteen times (n = 448). The control group consisted of comparing two leaves of *P. tremuloides* foliage at the ends of the Y-branch. All experimental setups were conducted on a laboratory countertop where the different treatments and control groups were randomly stationed.

The second variation contrasted the choice of a higher preferred (EM915508, E3656, or *P. tremuloides*) versus a less preferred (BM3374, MB915319, or *Acer rubrum* L., respectively) hybrid poplar leaf where two treatments (EM915508 versus BM3374 and E3656 versus MB915319) and a control group (*P. tremuloides* versus *A. rubrum*) were replicated ten times (n = 120). *A. rubrum* leaves served as a non-preferred host in the control treatment because they contain ethyl m-digallate which acts as a resistance factor against insects, particularly the forest tent caterpillar (Nicol 1996, Nicol et al. 1997, Mamdouh et al. 2001). All experimental setups were randomly stationed on a laboratory countertop, similar to the initial two-choice experiments.

Leaves were chosen for assays as in consumption experiments of 2009 and 2010.

#### 2.3.2.7 Statistical analysis

For every treatment, nonparametric Wilcoxon signed rank paired t-tests were performed against higher and less preferred foliage choices (alpha significance level of 0.05), where leaves were ranked as being unconsumed, between 1-50% consumed and 51-100% consumed on a scale of 0 to 2, respectively.

#### 2.3.2.8 Behavioural experiments

Behavioural analyses were conducted concurrently during consumption experiments. The behaviours of *M. disstria* larvae were documented within 15 minutes of leaf presentation (initial response) and at times 30, 45, 60, 90, 120, 150, 180, 210, 240, 270, 300, 330, and 360 minutes, where an overall average was calculated from combining behaviours and comparing them between individuals (6-hour average response). At any given time, a caterpillar was found to be consuming, searching or resting (Table III).

#### 2.3.2.9 Statistical analysis

A nonparametric Kruskal-Wallis test was used to determine whether there were significant differences in initial and average 6-hour caterpillar behaviour as hybrid poplar foliage aged (alpha significance level of 0.05). In order to assess how initial and average 6-hour responses changed with leaf phenology, nonparametric Kruskal-Wallis tests and post-hoc Mann-Whitney U-tests were calculated and compared amongst preference groups (Bonferonni correction was applied, alpha significance level of 0.025).

### 2.3.3 Comparisons of vernal seasons 2009 and 2010

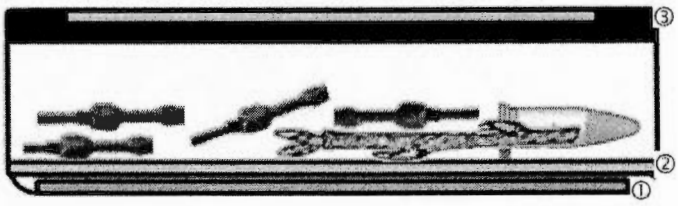
It was pertinent to compare hybrid preference rankings from 2009 to 2010, as saplings aged from one year to the other. Regarding aspen chemistry, Donaldson et al. (2006)

found that tannin concentrations doubled within a sapling's first five years and that phenolic glycoside levels were highest in young trees.

#### 2.3.3.1 Statistical analysis

Differences in preference rankings amongst hybrid poplar clones from 2009 and 2010 were compared via a Friedman test (alpha significance level of 0.05).

(a)




(b)

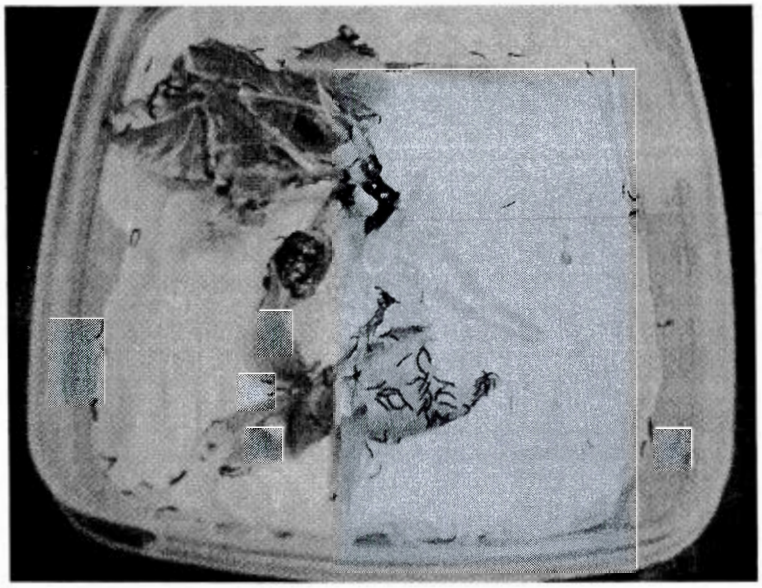


**Figure 2.1** — (a) Containers were underlain with a moist towelette① and wax paper② to ensure adequate humidity; a 6cm x 6cm square was cut out of the covers and nylon was hot glued onto the top③ for air exchange to occur.

(b) Aerial view of a neonatal to second instar rearing chamber.

**Table 2.1** — Hybrid poplar clones with their respective identifications and poplar sections used for laboratory experiments. Endogenic hybrid parents include *P. balsamifera* L., *P. trichocarpa* Torr. & Gray and *P. deltoides* Bartr.. Exogenic hybrid parents include *P. maximowiczii* Henry and *P. nigra* L.. *P. euramericana* is the hybrid specimen result from a cross between *P. deltoides* and *P. nigra*.

| *Clonal ID* | *Hybrid Poplar Parentage* | *Respective Populus Sections* |
|---|---|---|
| BM3374 | *P. balsamifera* x *P. maximowiczii* | Tacamahaca x Tacamahaca |
| BM915005 | *P. balsamifera* x *P. maximowiczii* | Tacamahaca x Tacamahaca |
| MB915302 | *P. maximowiczii* x *P. balsamifera* | Tacamahaca x Tacamahaca |
| MB915313 | *P. maximowiczii* x *P. balsamifera* | Tacamahaca x Tacamahaca |
| MB915319 | *P. maximowiczii* x *P. balsamifera* | Tacamahaca x Tacamahaca |
| NM3729 | *P. nigra* x *P. maximowiczii* | Aigeiros x Tacamahaca |
| E131 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| E3308 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| E3333 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| E3570 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| E3585 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| E3656 | *P. deltoides* x *P. nigra* | Aigeiros x Aigeiros |
| EM916401 | *P. euramericana* x *P. maximowiczii* | Aigeiros x Tacamahaca |
| EM915508 | *P. euramericana* x *P. maximowiczii* | Aigeiros x Tacamahaca |
| I3225 | *P. trichocarpa* x *P. deltoides* | Tacamahaca x Aigeiros |
| I3230 | *P. trichocarpa* x *P. deltoides* | Tacamahaca x Aigeiros |

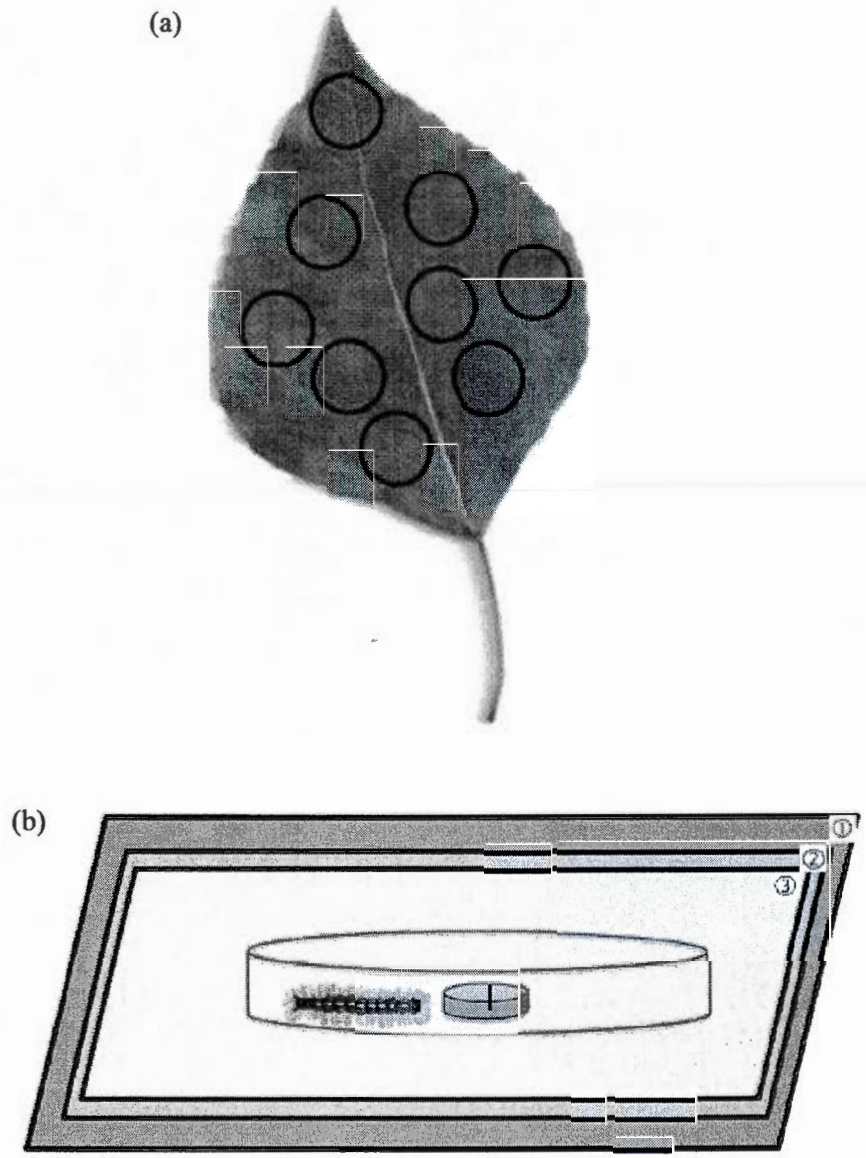
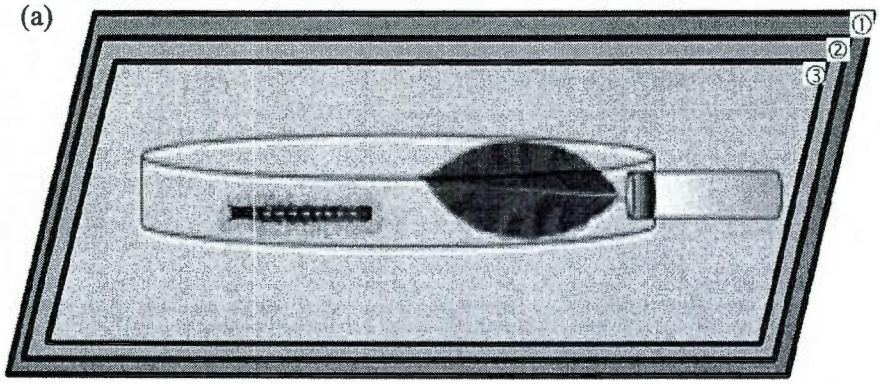



**Figure 2.2** — (a) Using a leather punch, leaf discs were taken from areas surrounding the tough middle vein.

(b) Leaf discs were pinned to a Styrofoam board① covered by a moistened towelette② and wax paper③ to maximize disc moisture.

(a)




(b)

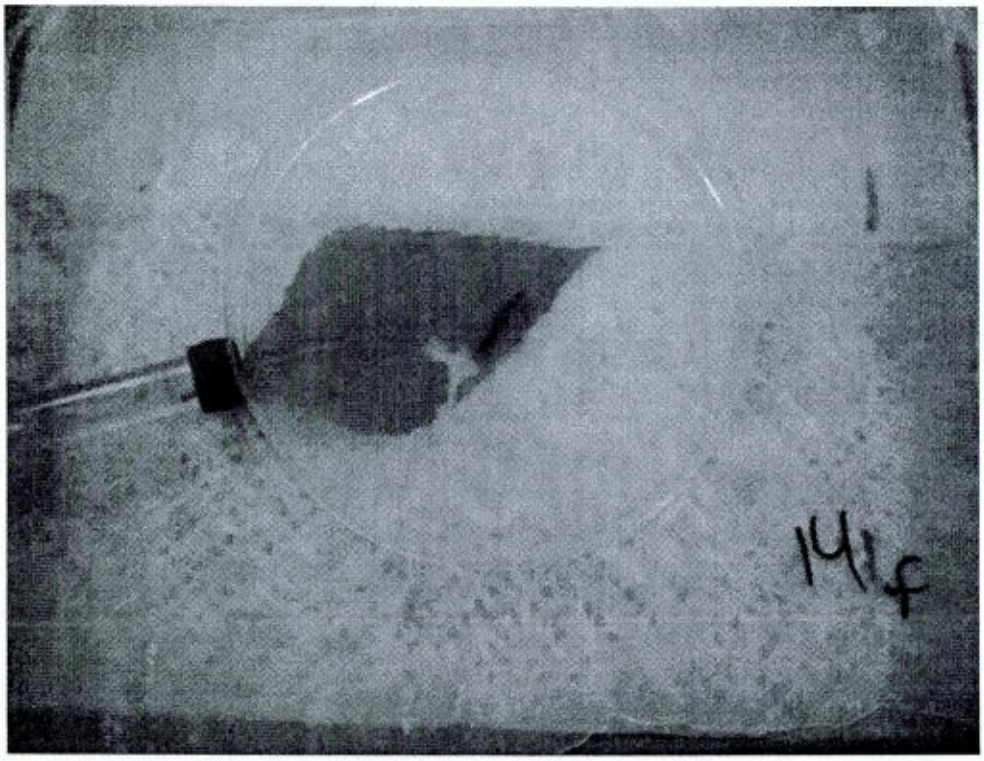


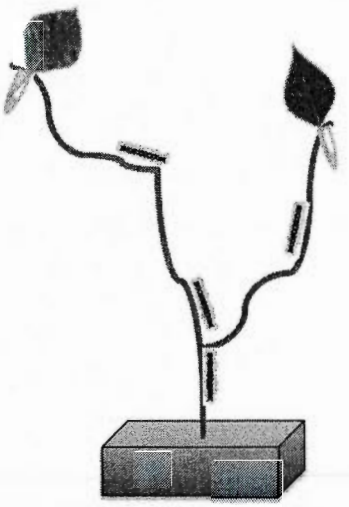

**Figure 2.3** — (a) Leaf stems were inserted into florist vials filled with water, glued over a 1cm diameter hole on the side of a 20cm diameter petri base. The experimental chamber was placed onto Styrofoam board① covered by a moistened towelette② and wax paper③ to maintain adequate humidity.

(b) Aerial view of fourth instar leaf consumption experiments.

**Table 2.2** — All hybrid poplars and *P. tremuloides* (control) underwent budbreak over the month of April 2010; leaf out dates varied over a span of 13 days.

| *Clonal ID* | *Budbreak (April)* |
|---|---|
| *Control* | 8 |
| BM3374 | 7 |
| BM915005 | 10 |
| MB915302 | 11 |
| MB915313 | 10 |
| MB915319 | 7 |
| NM3729 | 11 |
| E131 | 16 |
| E3308 | 21 |
| E3333 | 16 |
| E3570 | 19 |
| E3585 | 16 |
| E3656 | 14 |
| EM916401 | 5 |
| EM915508 | 9 |
| I3225 | 14 |
| I3230 | 14 |

(a)



(b)

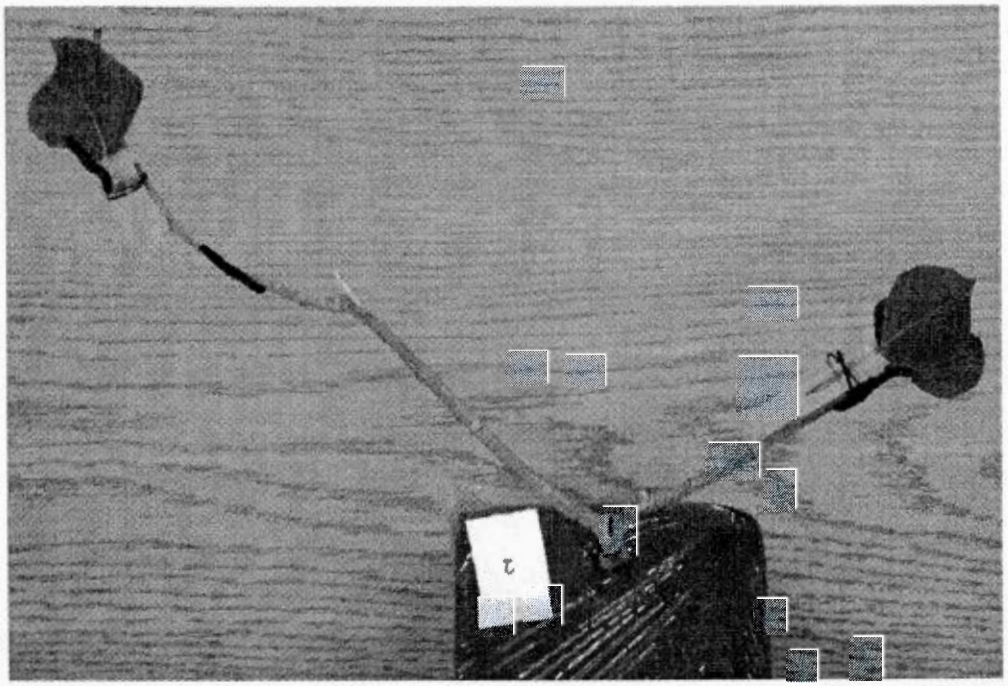


**Figure 2.4** — (a) The Y-branch was placed into a foam base for support and petroleum jelly was rubbed at the base of the branch to ensure the presence of caterpillars (larvae avoided the jelly as it was sticky and reduced mobility).

(b) Aerial view of the two-choice experimental set-up.

**Table 2.3** — Description of forest tent caterpillar behaviours observed during behavioural experiments.

| *Behaviour* | *Description* |
|---|---|
| Consuming | · individual is nibbling or eating<br>· mandibles are cutting through leaf surface |
| Searching | · individual is in constant locomotion, walking<br>· prolegs are moving |
| Resting | · individual is quiescent, either sleeping or temporarily reposing<br>· prolegs and mandibles are not in motion |

## 2.4 Results

### 2.4.1 Vernal season of 2009

#### 2.4.1.1 Consumption experiments

Calculated nonparametric Kruskal-Wallis tests found that comparative percent consumptions were significantly different amongst hybrid poplars ($X^2 = 43.31$, df = 16, p = 0.001) (Table IV, Figure 2.5). Three preference groups (high: E3308, E3570, EM915508, E3656, intermediate: E3333, I3225, I3230, E3585, E131, EM916401, MB915319, BM915005 and low: NM3729, BM3374, MB915302, MB915313) were created based on Kruskal-Wallis mean ranks of the calculated percent consumptions (groups will henceforth remain the same) (Table IV).

### 2.4.2 Vernal season of 2010

#### 2.4.2.1 Consumption experiments

Reported nonparametric Kruskal-Wallis tests showed that *M. disstria* consumptions were different across different hybrid foliage and over 3- ($X^2 = 97.35$, df = 13, $p < 0.001$), 5- ($X^2 = 103.70$, df = 15, $p < 0.001$) and 7-weeks ($X^2 = 71.77$, df = 15, $p < 0.001$) following budbreak (Table V, Figure 2.6). Hybrid poplars were subsequently ranked into preference groups based on Kruskal-Wallis mean ranks of leaf areas consumed over 24 hours (Table V).

Foliar characteristics were journalized (Table VI) and stepwise multiple regression analyses showed that leaf length, petiole length and water content predicted 29.4% and 47.7% of *M. disstria*'s leaf area consumptions 3- and 5-weeks after budbreak, respectively (Table VIIa, VIIb). A stepwise multiple regression also demonstrated that petiole length, at a leaf age of 7-weeks, was the only influential factor contributing to 19.4% of leaf consumption (Table VIIc).

A comparison amongst changes in leaf areas consumed and foliar characteristics from different preference groups, via nonparametric Kruskal-Wallis tests, showed that leaf area consumption, petiole length and water content changed significantly in all groups, while cross-section differed only amongst highly preferred foliage (Table VIII). Leaf length did not change significantly amongst all preference groups as leaves aged. Mann-Whitney U-tests found that consistent similar trends occurred within preference groups (Table IX); leaf consumption significantly decreased from 5- vs. 7-week and 3- vs. 7-week old foliage, percent water content decreased significantly from 5- vs. 7-week old foliage and petiole length never changed from 5- vs. 7-week old foliage. Within the high preference group, cross section significantly increased from 3- vs. 5-weeks, petiole length also increased from 3- vs. 5- and 3- vs. 7-weeks and percent water content significantly decreased from 3- vs. 7-weeks (Table IXa). In the intermediate preference group it was found that leaf area consumption significantly decreased from 3- vs. 5-week old foliage, that petiole length significantly increased from 3- vs. 5-weeks and that percent water content significantly decreased from 3- vs. 5- and 3- vs. 7-week old foliage (Table IXb). Less preferred foliage also showed a significant drop in leaf area consumed from 3- vs. 5-week old foliage, and increased leaf cross section from 5- vs. 7- and 3- vs. 7-weeks and an increased petiole length over 3- vs. 7-weeks (Table IXc).

#### 2.4.2.2 Two-choice experiments

Nonparametric Wilcoxon signed rank t-tests showed that *P. tremuloides* was consistently chosen over any of the hybrid poplars from all preference groups in the initial two-choice set-up ($Z = -8.37$, $N = 112$, $p < 0.001$) (Table Xa). Similar tests also found that the second variation of the two-choice experiments consistently showed that the higher preferred foliage was chosen significantly more than the lower preferred foliage ($Z = -4.46$, $N = 30$, $p < 0.001$) (Table Xb).

### 2.4.2.3 Behavioural experiments

A series of nonparametric Kruskal-Wallis tests showed that *M. disstria*'s initial behaviour significantly differed significantly across preference groups (Table XI, Figure 2.7). Significant initial behaviour differences were found via a nonparametric Kruskal-Wallis test across preference groups (Table XI, Figure 2.7). Commonly, a significant decrease in the initial behaviour of consuming was observed when *M. disstria* was fed 5- vs. 7- and 3- vs. 7-week old foliage, and initial behaviour remained constant when fed 3- vs. 5-week old foliage (Table XI, Figure 2.7).

Nonparametric Kruskal-Wallis tests also found that *M. disstria*'s average 6-hour behaviour differed significantly across preference groups (Table XII, Figure 2.8). Commonly, a significant increase in the overall behaviour of consuming was observed across preference groups from 3- vs. 5-weeks and no change in behaviour was found from 5- vs. 7-weeks (Table XII, Figure 2.8). A significant increase in consuming behaviour was shown for highly and intermediately preferred foliage from 3- vs. 7-weeks (Table XII, Figure 2.8).

### 2.4.3 Comparisons of vernal seasons 2009 and 2010

A Friedman chi-square test amongst preferred ranks in 2009 and at 3-, 5- and 7-weeks after budbreak in 2010, confirmed that preference order was consistent ($X^2 = 5.53$, df = 3, $p = 0.137$) even though different techniques were used in the 2009 versus 2010 experiments and leaves were studied over a 4-week duration in 2010.

**Table 2.4** — Mean percent consumption (± SE) of hybrid poplars and control were ranked in order of preference and divided into three groups (the control group served as a reference) in 2009.

| *Preference Group* | *Tree Identification* | *Mean Percent Consumption (%)* | *Preference Ranking* |
|---|---|---|---|
| (Control) | *P. tremuloides* | 50.000 ± 0.000 | 4 |
| High | E3308 | 62.116 ± 2.219 | 3 |
| | E3570 | 48.458 ± 2.478 | 5 |
| | EM915508 | 73.504 ± 14.741 | 1 |
| | E3656 | 62.395 ± 6.859 | 2 |
| Intermediate | E3333 | 38.674 ± 12.948 | 8 |
| | I3225 | 21.950 ± 5.042 | 10 |
| | I3230 | 36.027 ± 8.617 | 9 |
| | E3585 | 47.333 ± 7.197 | 6 |
| | E131 | 17.496 ± 2.465 | 11 |
| | EM916401 | 44.822 ± 17.555 | 7 |
| | MB915319 | 15.430 ± 5.929 | 13 |
| | BM915005 | 8.972 ± 2.320 | 14 |
| Low | NM3729 | 16.557 ± 6.501 | 12 |
| | BM3374 | 5.595 ± 1.087 | 16 |
| | MB915302 | 8.328 ± 2.738 | 15 |
| | MB915313 | 2.711 ± 1.256 | 17 |

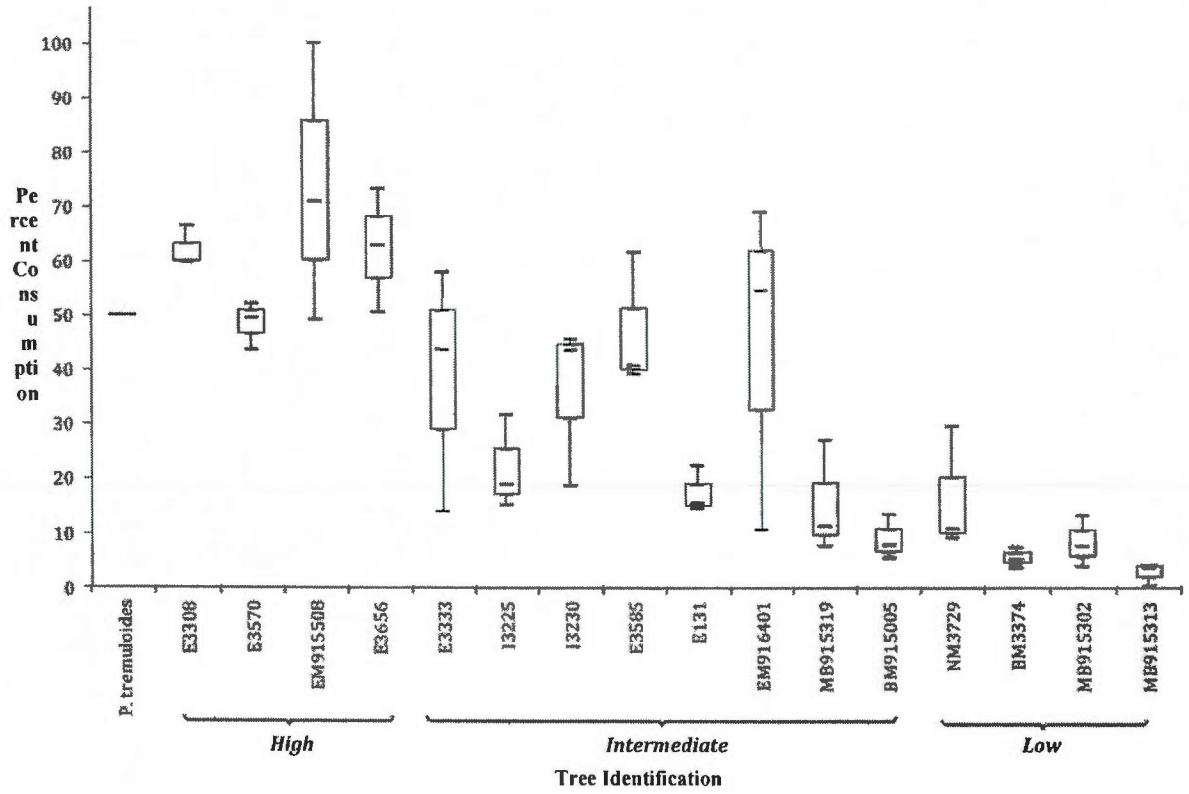



**Figure 2.5** — Box-and-whisker plots for hybrid poplar clones, ordered by preference groups in 2009.

**Table 2.5** — Consumed leaf areas, in $mm^2$, (± SE) of hybrid poplar clones over 24-hour consumption trials for (a) 3-week, (b) 5-week and (c) 7-week old foliage. Hybrids were ranked in order of preference and divided into three groups (the control group served as a reference) in 2010.

| | *Preference Group* | *Tree Identification* | *Initial Leaf Area* | *Leaf Area Consumed* | *Preference Rank* |
|---|---|---|---|---|---|
| (a) | (Control) | *P. tremuloides* | 1993.64 ± 77.37 | 920.30 ± 64.10 | 2 |
| | High | E3308 | 1921.71 ± 131.95 | 1021.69 ± 88.69 | 1 |
| | | E3570 | | | |
| | | EM915508 | 2597.23 ± 234.16 | 686.48 ± 45.03 | 6 |
| | | E3656 | 3247.38 ± 253.67 | 594.75 ± 159.95 | 7 |
| | Intermediate | E3333 | | | |
| | | I3225 | 4257.72 ± 727.01 | 808.42 ± 98.47 | 4 |
| | | I3230 | 5181.30 ± 759.87 | 587.81 ± 130.65 | 8 |
| | | E3585 | 2574.98 ± 242.99 | 868.86 ± 381.37 | 3 |
| | | E131 | 1617.14 ± 221.59 | 787.28 ± 119.87 | 5 |
| | | EM916401 | 4089.88 ± 344.85 | 219.16 ± 43.92 | 14 |
| | | MB915319 | 4752.72 ± 376.16 | 248.08 ± 88.10 | 11 |
| | | BM915005 | 2832.23 ± 114.00 | 477.03 ± 86.51 | 9 |
| | Low | NM3729 | 3752.15 ± 228.91 | 231.44 ± 69.39 | 13 |
| | | BM3374 | 2593.39 ± 176.78 | 282.83 ± 72.50 | 10 |
| | | MB915302 | 2300.66 ± 105.43 | 236.03 ± 86.17 | 12 |
| | | MB915313 | | | |
| (b) | (Control) | *P. tremuloides* | 1928.29 ± 166.13 | 728.93 ± 79.63 | 3 |
| | High | E3308 | 2836.56 ± 106.96 | 687.47 ± 146.45 | 4 |
| | | E3570 | 4393.90 ± 491.19 | 1057.44 ± 161.16 | 1 |
| | | EM915508 | 2322.74 ± 110.29 | 202.12 ± 81.78 | 11 |
| | | E3656 | 2720.09 ± 332.22 | 361.00 ± 101.83 | 9 |
| | Intermediate | E3333 | 2073.32 ± 99.29 | 998.86 ± 160.54 | 2 |
| | | I3225 | 4654.79 ± 713.27 | 489.94 ± 127.81 | 6 |
| | | I3230 | 4182.41 ± 326.56 | 400.55 ± 130.14 | 8 |
| | | E3585 | 2633.75 ± 63.60 | 429.63 ± 158.73 | 7 |
| | | E131 | 1992.22 ± 94.45 | 568.88 ± 194.14 | 5 |
| | | EM916401 | 2703.98 ± 57.44 | 112.03 ± 47.22 | 12 |
| | | MB915319 | 3399.06 ± 430.81 | 65.45 ± 20.25 | 13 |
| | | BM915005 | 2112.80 ± 377.15 | 210.28 ± 127.15 | 10 |
| | Low | NM3729 | 3829.75 ± 190.17 | 48.13 ± 22.91 | 14 |
| | | BM3374 | 2472.81 ± 222.89 | 41.70 ± 25.61 | 15 |
| | | MB915302 | | | |
| | | MB915313 | 3592.54 ± 297.07 | 27.50 ± 16.88 | 16 |

| | | | | | |
|---|---|---|---|---|---|
| (c) | (Control) | *P. tremuloides* | 2663.27 ± 86.08 | 327.32 ± 52.53 | 1 |
| | High | E3308 | 2858.86 ± 269.50 | 186.71 ± 101.59 | 3 |
| | | E3570 | 2893.78 218.06 | 169.59 36.70 | 5 |
| | | EM915508 | 2388.15 ± 62.42 | 170.57 ± 53.60 | 4 |
| | | E3656 | 2788.68 ± 224.54 | 68.15 ± 35.05 | 11 |
| | Intermediate | E3333 | 2159.79 ± 208.43 | 244.67 ± 80.71 | 2 |
| | | I3225 | 4740.09 ± 626.11 | 73.44 ± 19.01 | 10 |
| | | I3230 | 4067.78 ± 332.79 | 90.50 ± 31.96 | 7 |
| | | E3585 | 2665.89 ± 88.81 | 90.72 ± 59.97 | 6 |
| | | E131 | 1785.64 ± 97.55 | 81.42 ± 47.22 | 8 |
| | | EM916401 | 2384.07 ± 149.14 | 41.03 ± 20.93 | 14 |
| | | MB915319 | 2331.80 ± 157.23 | 74.32 ± 42.78 | 9 |
| | | BM915005 | 2658.85 ± 130.10 | 48.81 ± 33.74 | 13 |
| | Low | NM3729 | 3445.96 ± 165.08 | 19.27 ± 17.89 | 15 |
| | | BM3374 | 2196.85 ± 130.12 | 61.27 ± 41.27 | 12 |
| | | MB915302 | 3698.06 ± 368.92 | 0.00 ± 0.00 | 16 |
| | | MB915313 | | | |

(a)

(b)

(c)

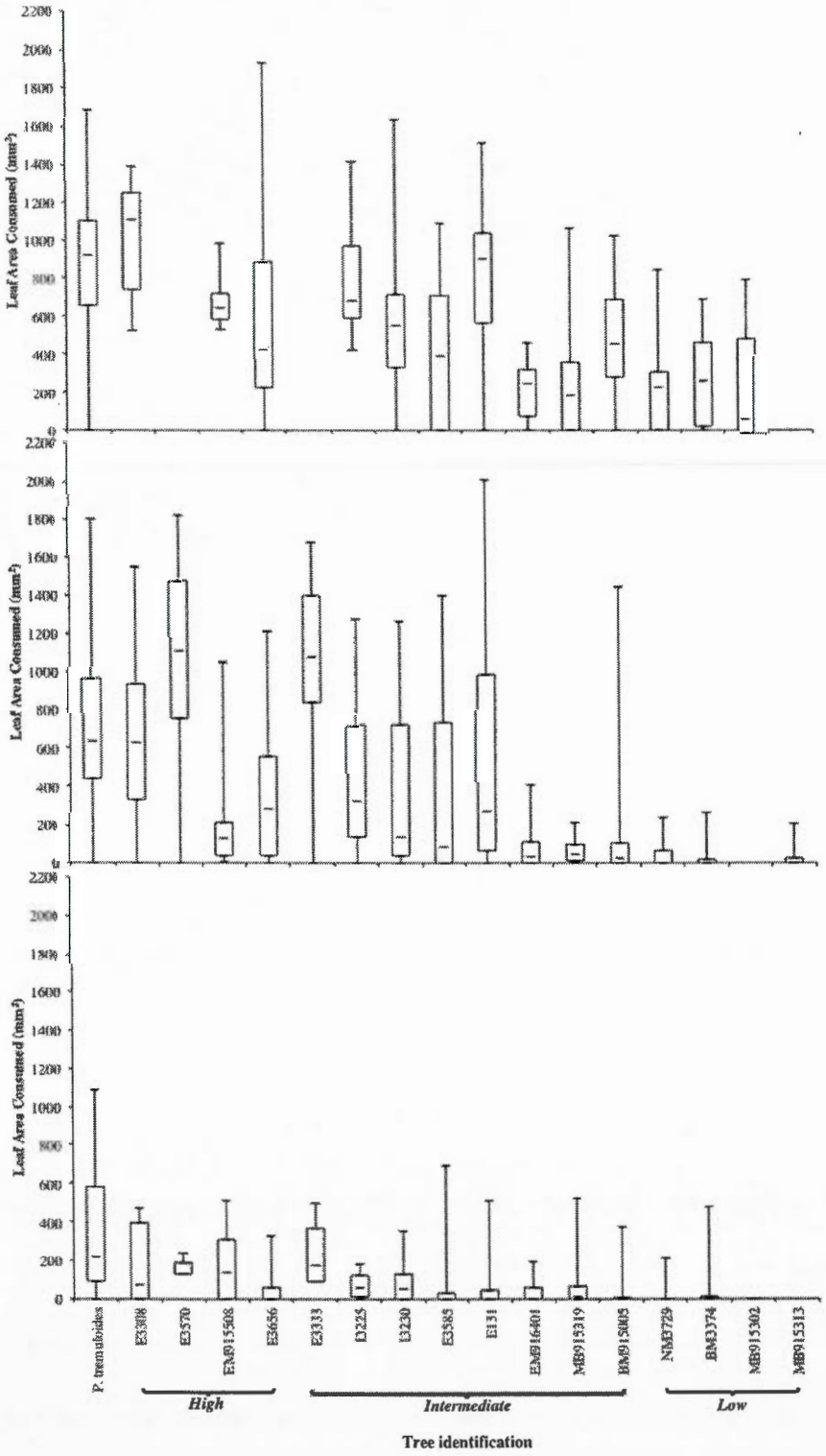

Leaf Area Consumed (mm²)
P. tremuloides
E3308
E3570
EM915508
E3636
E3333
E3225
E3230
E3585
E131
EM916401
MB918319
BM915005
NM3729
BM3374
MB915302
MB915313
High
Intermediate
Low
Tree identification

**Figure 2.6** — Box-and-whisker plots for hybrid poplar clone leaf consumptions over 24-hours, ordered by preference groups for foliage aged (a) 3-weeks, (b) 5-weeks and (c) 7-weeks in 2010.

**Table 2.6** — Mean foliar traits (± SE) of (a) 3-week, (b) 5-week and (c) 7-week old foliage in 2010.

| | *Clonal ID* | *Cross-section* | *Length* | *Petiole length* | *Water content* |
|---|---|---|---|---|---|
| (a) | *Control* | 4.08 ± 0.11 | 4.45 ± 0.11 | 3.54 ± 0.13 | 0.845 ± 0.016 |
| | BM3374 | 4.90 ± 0.50 | 9.79 ± 1.12 | 1.86 ± 0.21 | 0.814 ± 0.009 |
| | BM915005 | 4.31 ± 0.07 | 9.25 ± 0.15 | 1.07 ± 0.09 | 0.810 ± 0.006 |
| | MB915302 | 4.11 ± 0.08 | 8.01 ± 0.13 | 1.19 ± 0.09 | 0.802 ± 0.012 |
| | MB915313 | | | | |
| | MB915319 | 6.26 ± 0.26 | 10.66 ± 0.26 | 2.35 ± 0.18 | 0.805 ± 0.005 |
| | NM3729 | 6.20 ± 0.18 | 7.68 ± 0.23 | 1.90 ± 0.13 | 0.798 ± 0.005 |
| | E131 | 4.48 ± 0.08 | 5.45 ± 0.07 | 1.47 ± 0.05 | 0.899 ± 0.006 |
| | E3308 | 4.00 ± 0.22 | 5.09 ± 0.26 | 1.63 ± 0.32 | 0.926 ± 0.011 |
| | E3333 | | | | |
| | E3570 | | | | |
| | E3585 | 5.77 ± 0.19 | 6.84 ± 0.24 | 1.99 ± 0.11 | 0.875 ± 0.009 |
| | E3656 | 6.63 ± 0.21 | 7.17 ± 0.20 | 2.68 ± 0.07 | 0.868 ± 0.012 |
| | EM916401 | 5.06 ± 0.12 | 11.22 ± 0.42 | 1.42 ± 0.08 | 0.786 ± 0.015 |
| | EM915508 | 5.14 ± 0.15 | 8.19 ± 0.21 | 1.46 ± 0.07 | 0.829 ± 0.010 |
| | I3225 | 5.74 ± 0.38 | 9.53 ± 0.57 | 2.50 ± 0.19 | 0.828 ± 0.037 |
| | I3230 | 6.92 ± 0.38 | 10.91 ± 0.45 | 2.60 ± 0.16 | 0.840 ± 0.016 |
| (b) | *Control* | 5.43 ± 0.17 | 5.77 ± 0.11 | 3.90 ± 0.13 | 0.844 ± 0.010 |
| | BM3374 | 4.48 ± 0.18 | 8.90 ± 0.23 | 1.20 ± 0.21 | 0.778 ± 0.017 |
| | BM915005 | 4.37 ± 0.13 | 9.97 ± 0.24 | 1.40 ± 0.14 | 0.751 ± 0.011 |
| | MB915302 | | | | |
| | MB915313 | 4.89 ± 0.23 | 9.32 ± 0.27 | 1.18 ± 0.13 | 0.752 ± 0.022 |
| | MB915319 | 5.11 ± 0.24 | 9.44 ± 0.35 | 1.99 ± 0.18 | 0.739 ± 0.014 |
| | NM3729 | 6.38 ± 0.24 | 7.50 ± 0.18 | 2.16 ± 0.13 | 0.751 ± 0.002 |
| | E131 | 5.01 ± 0.04 | 6.49 ± 0.06 | 2.32 ± 0.06 | 0.878 ± 0.003 |
| | E3308 | 6.10 ± 0.17 | 7.63 ± 0.18 | 2.85 ± 0.14 | 0.869 ± 0.006 |
| | E3333 | 5.26 ± 0.16 | 6.46 ± 0.20 | 2.67 ± 0.19 | 0.905 ± 0.010 |
| | E3570 | 7.81 ± 0.49 | 8.30 ± 0.45 | 3.46 ± 0.23 | 0.873 ± 0.010 |
| | E3585 | 6.18 ± 0.23 | 7.82 ± 0.18 | 2.56 ± 0.06 | 0.671 ± 0.074 |
| | E3656 | 6.68 ± 0.32 | 6.98 ± 0.35 | 2.88 ± 0.14 | 0.860 ± 0.012 |
| | EM916401 | 4.59 ± 0.14 | 10.32 ± 0.42 | 1.51 ± 0.16 | 0.737 ± 0.019 |
| | EM915508 | 4.88 ± 0.12 | 7.90 ± 0.26 | 1.34 ± 0.12 | 0.779 ± 0.009 |
| | I3225 | 6.80 ± 0.32 | 11.32 ± 0.47 | 3.32 ± 0.19 | 0.813 ± 0.016 |
| | I3230 | 6.97 ± 0.31 | 12.02 ± 0.58 | 3.07 ± 0.15 | 0.842 ± 0.005 |

(c)

| | | | | |
|---|---|---|---|---|
| *Control* | 4.24 ± 0.15 | 4.96 ± 0.13 | 3.50 ± 0.17 | 0.586 ± 0.034 |
| BM3374 | 3.79 ± 0.16 | 8.68 ± 0.22 | 0.83 ± 0.06 | 0.803 ± 0.012 |
| BM915005 | 4.35 ± 0.11 | 9.04 ± 0.18 | 1.40 ± 0.07 | 0.763 ± 0.004 |
| MB915302 | 3.74 ± 0.25 | 8.00 ± 0.58 | 1.00 ± 0.09 | 0.806 ± 0.015 |
| MB915313 | | | | |
| MB915319 | 4.70 ± 0.20 | 8.27 ± 0.15 | 1.66 ± 0.11 | 0.739 ± 0.023 |
| NM3729 | 5.32 ± 0.22 | 6.97 ± 0.26 | 1.80 ± 0.11 | 0.753 ± 0.019 |
| E131 | 5.89 ± 0.07 | 6.87 ± 0.10 | 2.76 ± 0.07 | 0.506 ± 0.029 |
| E3308 | 6.05 ± 0.20 | 6.92 ± 0.46 | 3.19 ± 0.18 | 0.890 ± 0.030 |
| E3333 | 5.07 ± 0.26 | 6.49 ± 0.31 | 2.62 ± 0.37 | 0.839 ± 0.006 |
| E3570 | 6.14 ± 0.28 | 7.39 ± 0.32 | 2.90 ± 0.59 | 0.803 ± 0.017 |
| E3585 | 6.70 ± 0.30 | 8.09 ± 0.16 | 2.39 ± 0.07 | 0.831 ± 0.012 |
| E3656 | 6.92 ± 0.41 | 7.86 ± 0.43 | 2.98 ± 0.17 | 0.824 ± 0.015 |
| EM916401 | 3.88 ± 0.16 | 8.62 ± 0.25 | 1.40 ± 0.19 | 0.756 ± 0.025 |
| EM915508 | 4.90 ± 0.04 | 7.46 ± 0.16 | 1.61 ± 0.10 | 0.751 ± 0.013 |
| I3225 | 6.33 ± 0.24 | 8.73 ± 0.56 | 2.91 ± 0.16 | 0.399 ± 0.041 |
| I3230 | 5.56 ± 0.31 | 9.97 ± 0.58 | 2.37 ± 0.13 | 0.813 ± 0.005 |

**Table 2.7** — (a) 3-week old foliage consumptions ($y$) are significantly (*) explained by leaf length ($x_1$), petiole length ($x_2$) and water content ($x_3$), where the linear regression equation is $y = -314.0 - 38.5x_1 + 95.4x_2 + 1212.5x_3 + \varepsilon$.

(b) 5-week old foliage consumptions ($y$) are significantly explained by leaf length ($x_1$), petiole length ($x_2$) and water content ($x_3$), where the linear regression equation is $y = -231.2 - 18.1x_1 + 79.4x_2 + 588.7x_3 + \varepsilon$.

(c) 7-week old foliage consumptions ($y$) are significantly explained by leaf length ($x$), where the linear regression equation is $y = 33.4 + 15.5x + \varepsilon$.

(a)

| *Regression model* | *Sum of squares* | *F* | *df* | *p* |
|---|---|---|---|---|
| Adjusted $R^2 = 0.2937$ | 6595234.2 | 26.6433 | 3 | < 0.001* |
| Error | 15017337.3 | | 182 | |

| *Parameters* | *Sum of squares* | *F* | *df* | *p* | *Estimate* |
|---|---|---|---|---|---|
| Leaf length | 1746883.1 | 21.1710 | 1 | < 0.001* | -38.5282 |
| Petiole length | 1519257.0 | 18.4214 | 1 | < 0.001* | 95.4084 |
| Water content | 1291264.2 | 15.6493 | 1 | < 0.001* | 1212.5383 |

(b)

| *Regression model* | *Sum of squares* | *F* | *df* | *p* |
|---|---|---|---|---|
| Adjusted $R^2 = 0.4768$ | 3518791.7 | 64.1811 | 3 | < 0.001* |
| Error | 3746439.7 | | 205 | |

| *Parameters* | *Sum of squares* | *F* | *df* | *p* | *Estimate* |
|---|---|---|---|---|---|
| Leaf length | 282796.9 | 21.1710 | 1 | < 0.001* | -18.1498 |
| Petiole length | 1351189.2 | 18.4214 | 1 | < 0.001* | 79.3917 |
| Water content | 573792.0 | 15.6493 | 1 | < 0.001* | 588.6705 |

(c)

| *Regression model* | *Sum of squares* | *F* | *df* | *p* |
|---|---|---|---|---|
| Adjusted $R^2 = 0.1896$ | 46437.2 | 44.2783 | 1 | < 0.001* |
| Error | 192971.6 | | 184 | |

| *Parameters* | *Sum of squares* | *F* | *df* | *p* | *Estimate* |
|---|---|---|---|---|---|
| Petiole length | 46437.2 | 44.2783 | 1 | < 0.001* | 15.4695 |

**Table 2.8** — Nonparametric Kruskal-Wallis tests showed that foliar cross-section, water content, petiole length and consumed leaf areas over 24-hours of highly preferred foliage differed significantly (*) with leaf age. Leaf areas consumed, petiole length and water content changed significantly for intermediately ranked foliage over time. Only leaf length did not differ significantly amongst less preferred foliage.

| *Experiment /* | *High preference* | | | *Intermediate preference* | | | *Low preference* | | |
|---|---|---|---|---|---|---|---|---|---|
| *Characteristic* | $X^2$ | *df* | *p* | $X^2$ | *df* | *p* | $X^2$ | *df* | *p* |
| Leaf area consumed | 28.895 | 2 | < 0.001* | 70.242 | 2 | < 0.001* | 30.130 | 2 | < 0.001* |
| Cross-section | 15.278 | 2 | < 0.001* | 0.883 | 2 | 0.643 | 12.954 | 2 | 0.002* |
| Length | 3.412 | 2 | 0.182 | 5.206 | 2 | 0.074 | 6.391 | 2 | 0.051 |
| Petiole length | 13.298 | 2 | 0.001* | 12.565 | 2 | 0.002* | 8.872 | 2 | 0.012* |
| Water content | 15.100 | 2 | 0.001* | 43.225 | 2 | < 0.001* | 20.206 | 2 | < 0.001* |

**Table 2.9** — Mann-Whitney U-tests found that common significant (*) trends occurred amongst (a) high, (b) intermediate and (c) low quality foliage over different leaf ages; differences amongst preference classes were also observed.

(a)

| *Experiment/ Characteristic* | *Leaf age comparisons* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *3- vs 5-weeks* | | | *5- vs 7-weeks* | | | *3- vs 7-weeks* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| Leaf area consumed | -2.173 | 0.030 | – | -3.581 | < 0.001* | ↓ | -5.432 | < 0.001* | ↓ |
| Cross-section | -3.670 | < 0.001* | ↑ | -2.009 | 0.045 | – | -2.163 | 0.031 | – |
| Length | -1.028 | 0.304 | – | -1.847 | 0.065 | – | -0.365 | 0.715 | – |
| Petiole length | -3.395 | 0.001* | ↑ | -1.231 | 0.218 | – | -2.179 | 0.007* | ↑ |
| Water content | -1.977 | 0.048 | – | -2.462 | 0.014* | ↓ | -3.771 | < 0.001* | ↓ |

(b)

| *Experiment/ Characteristic* | *Leaf age comparisons* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *3- vs 5-weeks* | | | *5- vs 7-weeks* | | | *3- vs 7-weeks* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| Leaf area consumed | -3.645 | < 0.001* | ↓ | -2.125 | < 0.001* | ↓ | -8.231 | < 0.001* | ↓ |
| Cross-section | -0.052 | 0.958 | – | -0.826 | 0.409 | – | -0.799 | 0.424 | – |
| Length | -0.108 | 0.914 | – | -1.974 | 0.048 | – | -1.978 | 0.048 | – |
| Petiole length | -3.460 | 0.001* | ↑ | -1.522 | 0.128 | – | -2.141 | 0.032 | – |
| Water content | -2.241 | 0.025* | ↓ | -4.143 | < 0.001* | ↓ | -6.592 | < 0.001* | ↓ |

(c)

| *Experiment/ Characteristic* | *Leaf age comparisons* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *3- vs 5-weeks* | | | *5- vs 7-weeks* | | | *3- vs 7-weeks* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| Leaf area consumed | -3.093 | 0.002* | ↓ | -3.412 | 0.001* | ↓ | -5.128 | < 0.001* | ↓ |
| Cross-section | -1.098 | 0.272 | – | -3.480 | 0.001* | ↑ | -2.455 | 0.014* | ↑ |
| Length | -1.920 | 0.055 | – | -2.309 | 0.026* | – | -0.755 | 0.451 | – |
| Petiole length | -0.608 | 0.543 | – | -1.672 | 0.094 | – | -3.231 | 0.001* | ↑ |
| Water content | -0.460 | 0.030 | – | -2.169 | 0.009* | ↓ | -1.385 | 0.166 | – |

**Table 2.10** — Mean two-choice rankings (± SE) when caterpillars were allowed to choose between two leaves, of either (a) hybrid poplar or *P. tremuloides* option or (b) two hybrid poplar options, for a 2-hour duration.

(a)

| *Hybrid leaf choice* | *Mean hybrid ranking* | *Mean P. tremuloides ranking* |
|---|---|---|
| BM3374 | 0.063 ± 0.063 | 2.000 ± 0.000 |
| MB915319 | 0.188 ± 0.101 | 1.875 ± 0.125 |
| BM915005 | 0.125 ± 0.085 | 2.000 ± 0.000 |
| EM916401 | 0.063 ± 0.063 | 2.000 ± 0.000 |
| EM915508 | 0.250 ± 0.144 | 1.938 ± 0.063 |
| E3656 | 1.000 ± 0.258 | 1.875 ± 0.125 |
| *P. tremuloides* | 1.875 ± 0.125 | 1.625 ± 0.202 |

(b)

| *Choice 1* | *Mean choice 1 ranking* | *Choice 2* | *Mean choice 2 ranking* |
|---|---|---|---|
| BM3374 | 0.000 ± 0.000 | EM915508 | 1.200 ± 0.291 |
| MB915319 | 0.100 ± 0.100 | E3656 | 1.200 ± 0.291 |
| *P. tremuloides* | 1.800 ± 0.133 | *A. rubrum* | 0.000 ± 0.000 |

**Table 2.11** — Nonparametric Kruskal-Wallis tests showed that initial and 6-hour caterpillar behaviours differed significantly (*) amongst preference groups.

| *Characteristic* | *High preference* | | | *Intermediate preference* | | | *Low preference* | | |
|---|---|---|---|---|---|---|---|---|---|
| | $X^2$ | *df* | *p* | $X^2$ | *df* | *p* | $X^2$ | *df* | *p* |
| Initial behaviour | 17.464 | 2 | < 0.001* | 90.013 | 2 | < 0.001* | 13.947 | 2 | 0.001* |
| Behaviour over 6-hours | 22.091 | 2 | < 0.001* | 24.447 | 2 | < 0.001* | 8.458 | 2 | 0.015* |

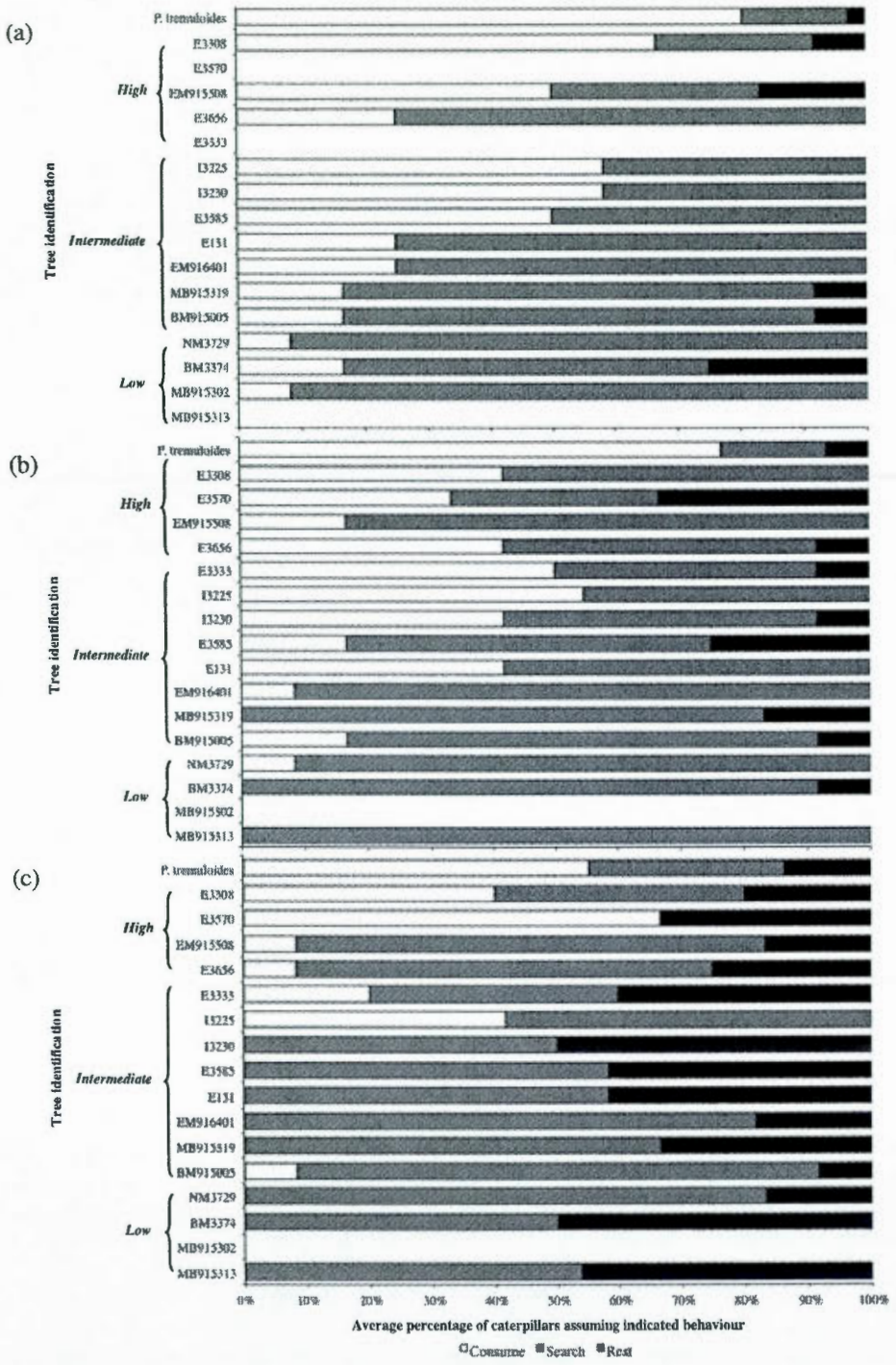



**Figure 2.7** — Stacked histograms of caterpillars' initial behaviour when introduced to different hybrid poplars, ordered by preference groups, at (a) 3-weeks (b) 5-weeks and (c) 7-weeks of leaf age.

**Table 2.12** — Non-parametric Mann-Whitney U-tests found that common significant (*) behavioural trends occurred amongst (a) high, (b) intermediate and (c) low quality foliage over different leaf ages; differences amongst preference classes were also observed.

(a)

| *Leaf age comparisons* | *Experiment / Characteristic* | | | | | |
|---|---|---|---|---|---|---|
| | *Initial behaviour* | | | *Behaviour over 6-hours* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| *3- vs 5 weeks* | -1.703 | 0.089 | – | -4.606 | < 0.001* | ↑ |
| *5- vs 7-weeks* | -3.295 | 0.001* | ↓ | -0.149 | 0.881 | – |
| *3- vs 7-weeks* | -3.786 | < 0.001* | ↓ | -3.300 | 0.001* | ↑ |

(b)

| *Leaf age comparisons* | *Experiment / Characteristic* | | | | | |
|---|---|---|---|---|---|---|
| | *Initial behaviour* | | | *Behaviour over 6-hours* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| *3- vs 5 weeks* | -1.233 | 0.217 | – | -4.076 | < 0.001* | ↑ |
| *5- vs 7-weeks* | -7.608 | < 0.001* | ↓ | -0.576 | 0.565 | – |
| *3- vs 7-weeks* | -8.617 | < 0.001* | ↓ | -4.481 | < 0.001* | ↑ |

(c)

| *Leaf age comparisons* | *Experiment / Characteristic* | | | | | |
|---|---|---|---|---|---|---|
| | *Initial behaviour* | | | *Behaviour over 6-hours* | | |
| | *Z* | *p* | *Var* | *Z* | *p* | *Var* |
| *3- vs 5 weeks* | -0.343 | 0.731 | – | -2.828 | 0.005* | ↑ |
| *5- vs 7-weeks* | -3.249 | 0.001* | ↓ | -1.542 | 0.123 | – |
| *3- vs 7-weeks* | -2.892 | 0.004* | ↓ | -1.517 | 0.129 | – |

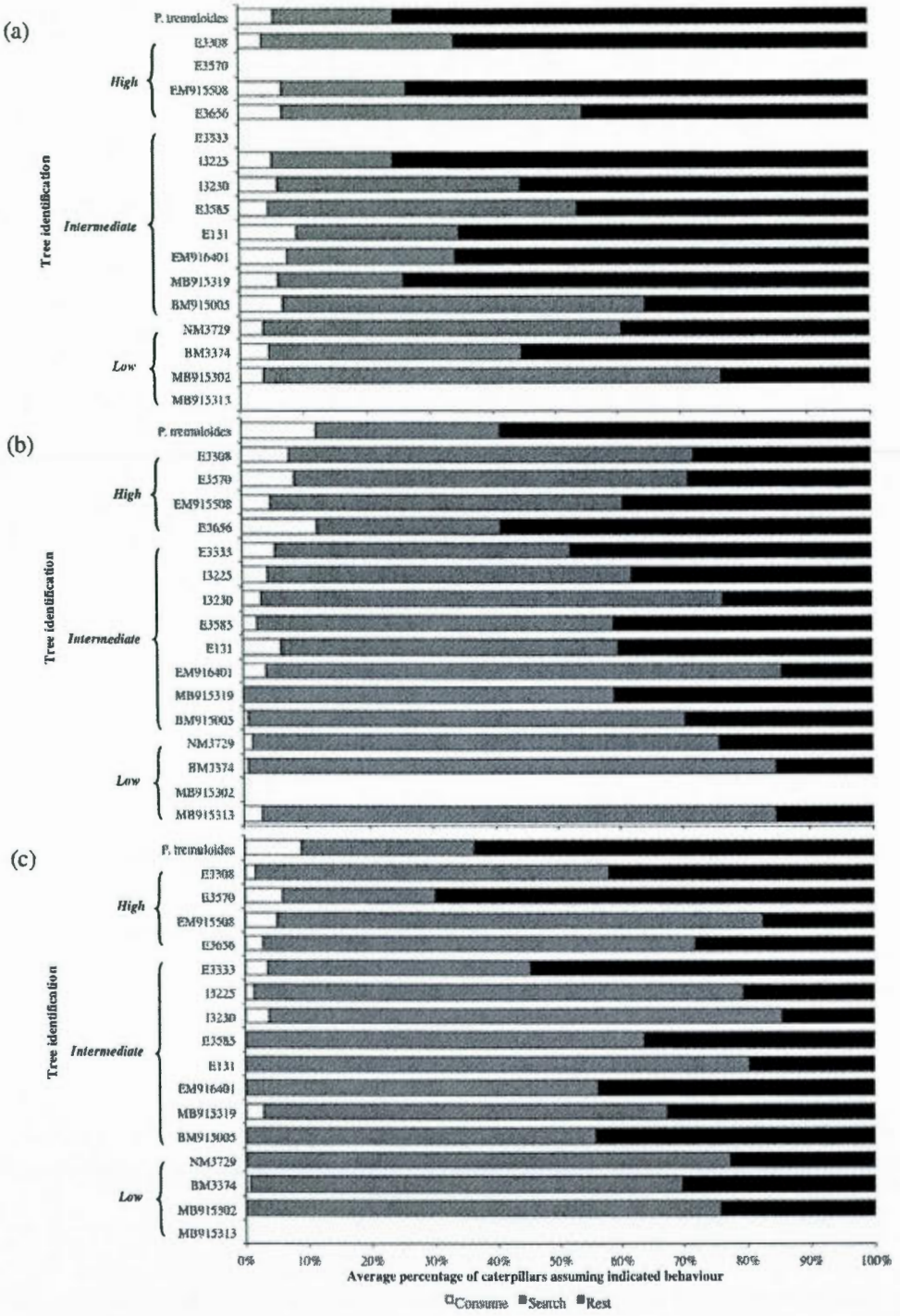



**Figure 2.8** — Stacked histograms of caterpillars' mean six-hour behaviour (resting, searching or consuming) when introduced to different hybrid poplars, ordered by preference groups, at (a) 3-weeks (b) 5-weeks and (c) 7-weeks of leaf age.

## 2.5 Discussion

In the current study, consumed leaf areas were found to significantly decrease once leaves were 5-weeks old and such a decrease was also found in the percent water content of the foliage. This relationship is similar to Haukioja et al's (2002) study where *Epirrita autumnata* Bkh. (Lepidoptera: Geometridae) larvae consumed significantly less foliage when presented mature leaves at low percent water contents. For both intermediate and low preference groups, foliar consumption significantly decreased at 5-weeks following budbreak, which could be associated with a loss in leaf water content or an increase in tannic acid presence (Karowe 1989a, Robison 1993, Haukioja et al. 2002). Tannins are present in later poplar foliage and act as insect deterrents, particularly towards the forest tent caterpillar (Karowe 1989a, Robison 1993). For example, concentrations as low as 0.5% in tannins, which usually presents itself in later foliage, have been shown to reduce the performance and consumption of *M. disstria* larvae (Karowe 1989a). As expected, there were significant size increases in hybrid poplar leaf characteristics (cross-section, length, petiole length) over time, which indicates that the leaves used in the current study were following a similar vernal growth pattern as the poplars in the field. Interestingly, although hybrid leaves increased in size and decreased in water content over time, foliar preference groups from 2009 to 2010, and during a 4-week period in 2010, remained consistent.

It is important to note that hybrid poplar susceptibilities did not significantly differ over a year, or change in time, as *M. disstria*'s preferences remained constant. Hybrid poplar parentage influenced the preferences of *M. disstria* in the current study, regardless of year or leaf age. *M. disstria* demonstrated a constant high preference for hybrids crossed with *P. euramericana*, an intermediate preference for those crossed with *P. maximowiczii* and *P. deltoides*, and a low preference for those crossed with *P. balsamifera*. In the field, *P. balsamifera* is avoided by insects, most likely due to its unique fragrance and sticky leaves (Bryant and Kuropat 1980), whereas the forest tent caterpillar has been found to host upon *P. euramericana* foliage in the field (Batzer and Morris 1978). Robison and Raffa (1994) found that hybrid poplars crossed with *P. maximowiczii* parentage have an intermediate susceptibility towards *M. disstria*, and would be beneficial for the forestry industry. The

forest tent caterpillar's strong preferences towards hybrid poplars were also demonstrated when their consumption of differently preferred leaves were compared against each other in two-choice tests.

In the current investigation, *M. disstria*'s field host, *P. tremuloides*, and highly preferred hybrid poplars, were consistently chosen more over less liked hybrid foliage. Such a constant choice shows that, indeed, hybrid leaves differed across preference groups and were composed of foliar characters (mechanical or chemical) that made them differentially palatable/susceptible to caterpillars. Lepidopteran larvae use various senses (chemoreception, tactile, vision) in order to assess an acceptable meal (McIndoo 1919, Dethier 1937, Feeny 1970, Levin 1973, Waldbauer and Friedman 1991, Bernays and Chapman 1994, Chapman 1995a, Strauss and Agrawal 1999, Peeters 2002b, Chapman 2003, Peeters et al. 2007, Reeves 2011), which was observed in *M. disstria*'s behavioural responses towards different hybrid poplar foliage.

Through behavioural experiments, the forest tent caterpillar's activity of consuming on less preferred foliage was initially less when compared to higher favored hybrid leaves, whereas the former resulted in an increased searching behaviour. The initial response of continuing to search for a more palatable meal versus tasting or accepting a given food source, may be explained by the different senses that Lepidopteran larvae possess. For example, chemoreception uses both olfactory and gustatory senses, where pheromones and chemicals (respectively) are analyzed via receptors (McIndoo 1919, Dethier 1937, Waldbauer and Friedman 1991, Bernays and Chapman 1994, Chapman 1995a, Strauss and Agrawal 1999, Chapman 2003). Situated on the terminal antennae segments, maxillae and tarsi of a Lepidopteran larva, olfactory sensillae have been found to react within less than a minute of exposure to an odor (Dethier 1937, Chapman 1995a, 2003). Chapman (1995a) and Waldbauer and Friedman (1991) have shown that an agreeable host will be immediately tasted by a caterpillar, whereas an initially unacceptable host will entice continued searching for another potential meal. Lepidopteran gustatory responses involve the interpretation of phagostimulants and secondary compounds (usually toxins) (Bernays and Chapman 1994,

Strauss and Agrawal 1999, Chapman 2003). Via palpation with their mouth, Lepidopteran larvae are able to establish the chemical composition and quality of a host: phagostimulants (such as carbohydrates and proteins) attract feeding behaviours, whereas as secondary compounds (such as alkaloids, tannins, phenolic acids and flavonoids) are seen as toxins and are less attractive (Bernays and Chapman 1994, Panzuto and Albert 1997, Panzuto et al. 2002, Chapman 2003, Despland and Noseworthy 2006, Trottier 2010). Also, the surface texture and moisture of a leaf determine the acceptance of a caterpillar's host (Hunter and Lechowicz 1992). If a host lacks water content or has a high perforation value (significant amounts of fiber, lignin and cellulose), the preference of a Lepidopteran larva may be negatively impacted and such foliage will be avoided (Levin 1973, Hunter and Lechowicz 1992, Peeters 2002b, Peeters et al. 2007). Recently, vision has also been suggested to be an important cue in a Lepidopteran larva's host selection (Reeves 2011); Yasui et al. (2006) found that *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae) and *Milionia basalis pryeri* Druce (Lepidoptera: Geometridae) larvae were able to differentiate the preferential wavelengths of green silhouettes from a diet containing chlorophyll *b* (which was found to act as a visual stimulus for feeding).

Although a low initial consumption activity was observed when *M. disstria* was fed less preferred foliage, such larvae were found to consume at a much higher frequency over a six hour period when compared to those fed more preferred hybrid leaves. This may be explained by the behavioural increase in nibbling (and not actual feeding) that the forest tent caterpillar uses in order to asses and re-asses a potential host; continuous nibbling without actual feeding demonstrates that a given food source not completely satisfying (Robison 1993). When *M. disstria* larvae were fed highly preferred foliage, they tended to rest for long durations following a large meal. Each bout (consuming and resting followed by searching then re-consuming) lasted approximately three hours and occurred twice during the six hour behavioural observations; such foraging bouts are comparable to the natural bout behaviour of a forest tent caterpillar, where short consumption periods followed by longer quiescent (digestion and resting) phases occur (Fitzgerald 1980). For all preference groups, as leaves matured, the activity of consuming decreased and the desire to initially search for a more acceptable food source increased. Such may be related to the fact that foliar chemistry was

changing as hybrid leaves aged, presenting new chemicals (such as tannins), or other anti-stimulatory secondary compounds, and a decrease in water content, which have been all previously explained as less palatable attributes for a potential meal.

Future investigations regarding hybrid poplar preferences should involve foliar chemistry analyses. The chemical make-up of a leaf strongly affects the consumption and behaviours of a Lepidopteran larva, either attracting or deterring them from a food source (Karowe 1989a, Panzuto et al. 2002). As well, hybrid leaf toughness should be measured in order to determine whether such a mechanical factor is important enough to affect the preference of an individual (Choong 1996).

From the analysis of *M. disstria*'s preferences towards sixteen hybrid poplars in Quebec, it would be beneficial to plant hybrid poplars from *P. balsamifera*, *P. maximowiczii* or *P. deltoides* parentage. Also, *P. balsamifera* crossed hybrids underwent much earlier budbreak periods than most hybrid poplars in this study, which indicates that such foliage, during a shorter vernal season, would be much older and even less palatable for forest tent larvae at their infestation stage. In conclusion, it is suggested that a mixed forest of intermediately and less preferred hybrid poplars be cultivated in order to maximize production and tolerance towards potential entomological destruction.

CHAPITRE 3

# THE FOREST TENT CATERPILLAR'S PERFORMANCE, *MALACOSOMA DISSTRIA* HÜBNER (LEPIDOPTERA: LASIOCAMPIDAE), WHEN THEY ARE FED DIFFERENTLY PREFERRED HYBRID POPLAR, *POPULUS* SPP., FOLIAGE FROM QUEBEC

## 3.1 Abstract

The Quebec forestry industry is constantly threatened by various abiotic and biotic factors, where entomological susceptibilities are one of the most important biotic constraints. The current study investigates the survival and developmental durations of the forest tent caterpillar, *Malacosoma disstria*, a potential host of hybrid poplars in Quebec, when reared on six differently preferred hybrid poplar foliage. Performance experiments were conducted on two starting groups: neonatal and fourth instar larvae were observed until death. Instar durations were significantly longer ($1^{st}$ instar: $Z = -2.960$, $N = 30$, $p = 0.003$, $2^{nd}$ instar: $Z = -3.363$, $N = 25$, $p < 0.001$) and survival was significantly decreased ($X^2 = 38.753$, $df = 2$, $p < 0.001$) when the neonatal groups were fed less preferred foliage containing *Populus balsamifera* parentage. The fourth instar group did not exhibit a difference in survival amongst differently preferred hybrid poplar foliage ($X^2 = 2.978$, $df = 2$, $p = 0.226$), however, instar duration did increase with lower preferred foliage ($4^{th}$ instar: $Z$ -3.733, $N = 48$, $p < 0.001$). The results of this study propose that hybrid poplar clones crossed with a *P. balsamifera* parent could prevent insects from completing their life cycle, which in turn would increase lumber and pulp and paper productivity. Preferably, a mixed hybrid poplar forest is suggested in order to sustain local entomological diversity.

## 3.2 Introduction

Trees belonging to the genus *Populus* have become very important resources for the rapidly growing forestry industry in North America (Dickmann and Stuart 1983, Dickmann 2002, Broderick et al. 2010). The hybridization of two *Populus* spp. occurs readily amongst most endogenic and exogenic poplar sections, where clones created are selected for optimal features such as strong fibre, rapid growth rates, diverse adaptabilities and pathogenic

resistance (Vallée 1995a, Vallée 1995b, Johnson 2000, Zhang et al. 2003, DRF-MRNF 2005, Broderick et al. 2010). However, entomological susceptibilities have been little investigated for such hybrid poplars. Insect outbreaks in 2009 destroyed over 265 121 hectares in Quebec alone (NRC 2011). As poplar production in Quebec had increased tenfold from 1998 to 2003, reaching 2.5 million hectares (DRF-MRNF 2005), and still remains insufficient for forestry industry demands today, it is pertinent that such hybrid trees be investigated for tolerance against insect pests.

Poplar trees are greatly damaged by Lepidopteran species, where larvae have the capability of defoliating thousands of acres of trees during outbreak years. For example, a gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymnatriidae), larva has the capability of consuming at least one square foot of foliage during their lifetime (Hurley et al. 2004). Also, in 2006, the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) was found to have both defoliated and destroyed over 343 000 hectares of hardwood forest at the end of June to the beginning of July in the mid-Vermont region south of Quebec (Wood et al. 2007). Therefore, research regarding the entomological susceptibilities of hybrid poplars towards such insects has already commenced in North America (Robison 1993, Robison and Raffa 1994, Broderick et al. 2010).

Recently, Broderick et al. (2010) found that *L. dispar* larval survival was significantly reduced when reared on hybrid poplar foliage crossed with *P. deltoides* Batr. (North American) and *P. nigra* L (European) parentage than when fed an artificial diet. Robison (1993), having studied fifteen different American hybrid poplars, observed that *M. disstria* larvae developed dissimilarly when presented with different clones. For example, when *M. disstria* was fed hybrid poplar foliage crossed between *P. alba* L and *P. grandidentata* Michaux, of European and North American descents respectively, reduced larval weights and survival were observed (Robison 1993). On the other hand, when larvae were fed hybrid poplars crossed between two *P. deltoides* Batr. parents, an increase in larval weight and survival occurred (Robison 1993). Due to such findings, it is pertinent that

Quebec hybrid poplars also be assessed for their susceptibilities towards epidemiological insect pests.

The current study investigates the development and mortality rates of neonatal and fourth instar *M. disstria* larvae when fed six different hybrid poplar clones from Quebec. A comparison of molt duration and survivability was made against hybrid poplars in order to better understand if hybrid parentage indeed affected the life cycle of the forest tent caterpillar.

## 3.3 Materials and Methods

Experiments were conducted under laboratory settings at UQAM Biological Science Department from April to July 2010.

### 3.3.1 *M. disstria* larvae collection

Unfed and newly hatched neonatal larvae were collected from sugar maple stands in Saint-Esprit (45°91N, 73°65W) on April 8$^{th}$ 2010 and placed into 9cm x 9cm x 3cm containers with a young branch of *Populus tremuloides* Michaux foliage, their preferred host in the field (Meeker 1997), for a maximum of 24 hours under a 22°C, 70% R.H., 16L:8D regime.

Third instar larvae were picked from the same area three weeks later and were placed into 25cm x 14cm x 10cm chambers and kept under a 22°C, 70% R.H., 16L:8D regime, receiving an ad libitum supply of *P. tremuloides* foliage aged 2-weeks until they molted to fourth instar.

### 3.3.2 Hybrid poplar clones

Seven different hybrid poplar clones, under similar field temperatures, were kept inside the UQAM greenhouse in early April 2010. Clones ranged from two to three years of age and were not subject to insecticides or fungicides until after experiments were completed; however they did receive a constant supply of general nitrogen, phosphorus and potassium fertilizer in ratios of 20:20:20.

### 3.3.3 Control foliage collection

Fresh *P. tremuloides* foliage was picked from Saint-Esprit aspen stands (45°91N, 73°65W) at the same time as caterpillars were collected; remaining required foliage for the control treatments were collected every four days until experiments came to an end.

### 3.3.4 Neonatal performance experiments

Groups of 15 neonatal individuals were raised in 10cm diameter petri dishes underlain with moist paper napkin and wax paper to maintain humidity, under a 22°C, 70% R.H., 16L:8D regime. Hybrid poplar preferences were identified via previous consumption experiments from 2009 and 2010 (see Chapter 2). Foliage from one of six differently preferred hybrid poplars (less: BM3374, intermediately: BM915005, MB915319, EM916401, highly: EM915508, E3656) or the control was fed ad libitum to larvae. Six replicates per treatment group (n = 630) were performed, where daily mortalities and instar durations were documented until 22 days following the experimental start date (when most larvae had died).

### 3.3.5 Fourth instar performance experiments

Newly molted fourth instar larvae were raised in groups of three in 25cm x 14cm x 10cm plastic containers, at a 22°C, 70% R.H., 16L:8D regime, and were fed ad libitum foliage from one of six differently preferred hybrid poplars (less: BM3374, NM3729,

intermediately: BM915005, MB915319, EM916401, highly: EM915508) or the control. Twelve replicates per treatment groups were performed (n = 252) where daily mortalities and instar durations were noted until 20 days following the experimental start date (when several larvae began to pupate).

### 3.3.6 Statistical analysis

Kaplan-Meier curves were produced and log-rank tests (alpha significance level of 0.05) were calculated for both performance trials. Nonparametric Kruskal Wallis tests (alpha significance level of 0.05) were performed to compare larval instar durations when larvae were fed foliage from differing preference groups, and Mann-Whitney U-tests (Bonferonni correction was applied for an alpha significance level of 0.025) compared specific groups amongst each other.

## 3.4 Results

### 3.4.1 Neonatal performance experiments

The corresponding Kaplan-Meier curve and log rank test demonstrated that *M. disstria* survival differed significantly amongst at least two hybrid poplar preference groups ($X^2 = 38.754$, df = 2, $p < 0.001$) (Figure 3.1, Table XIII). When compared with the control group, a log rank test showed that larvae fed hybrid foliage survived significantly less than those fed *P. tremuloides* ($X^2 = 75.695$, df = 1, $p < 0.001$) (Table XIV). Nonparametric Kruskal-Wallis tests showed that first and second instar durations differed significantly amongst at least two hybrid poplar preference groups ($X^2 = 12.094$, df = 2, $p = 0.002$ and $X^2 = 12.855$, df = 2, $p = 0.002$, respectively). More specifically, Mann-Whitney U-tests showed that intermediately and highly preferred hybrid groups differed significantly for both instars (Table XV and XVI). The duration of third and fourth instars were not compared amongst preference groups as larvae did not survive until later stages due to infection of the common nuclear polyhedrosis virus (Kukan and Myers 1997).

### 3.4.2 Fourth instar experiments

The produced Kaplan-Meier curve and log rank test showed that forest tent caterpillar survival did not significantly differ across preference groups ($X^2 = 2.978$, df = 2, p = 0.226) (Figure 3.2, Table XVII). However, a log rank test did demonstrate that *M. disstria* larvae fed trembling aspen had a significantly higher survival result than those fed hybrid foliage ($X^2 = 29.249$, df = 1, $p < 0.001$) (Table XVIII). Fourth instar larvae were shown to have significantly different instar durations across at least two preference groups ($X^2 = 12.475$, df = 2, p = 0.002. Instar durations of larvae fed highly preferred hybrid foliage were found to be significantly shorter when compared to intermediately preferred groups and significantly longer when compared to the control, via Mann-Whitney U-tests (Table XIX and XX). Fifth instar and pupation durations were not compared across preference groups, as many larvae did not survive that long due to random parasitic Dipteran (Tachinidae) and Hymenopteran (Ichneumonidae) infections from the field (personal observation).

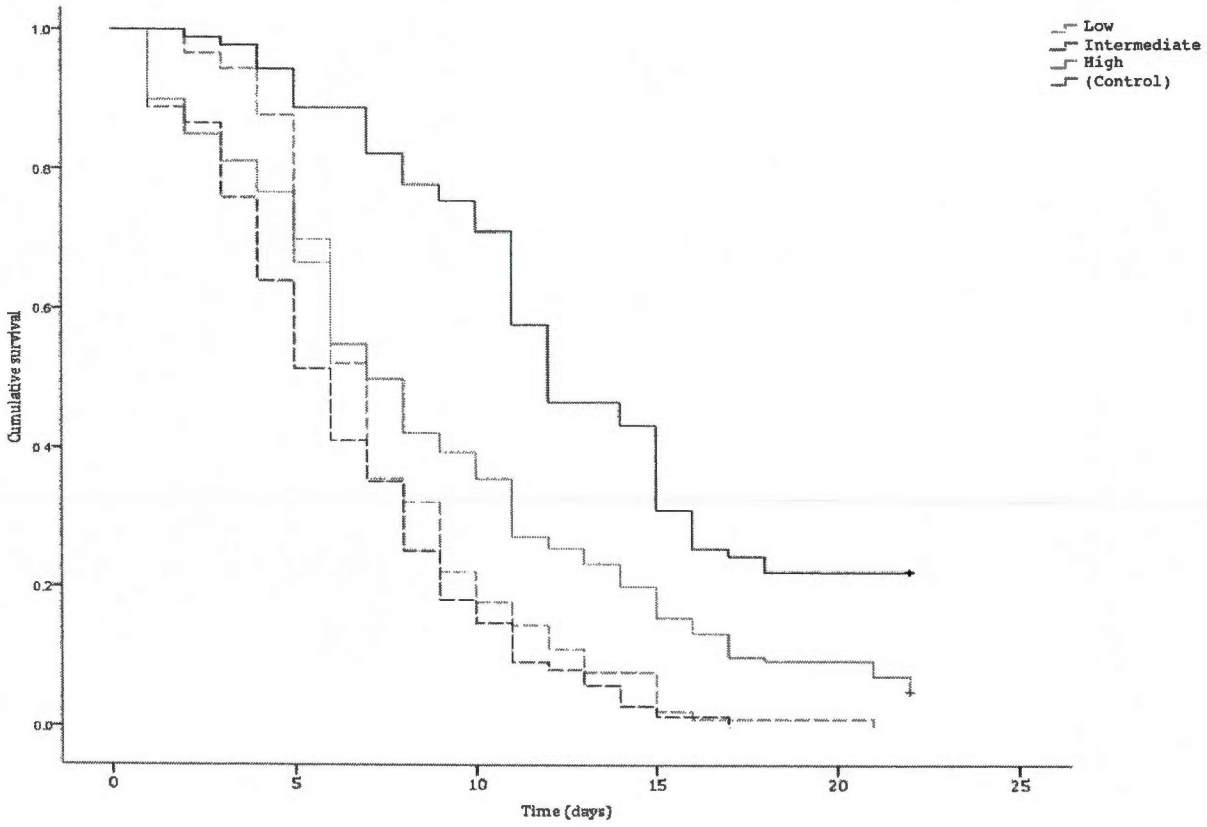



**Figure 3.1** — Kaplan-Meier survival curves of neonatal performance trials across preference groups. *M. disstria* survival differed significantly amongst a least two hybrid poplar preference groups ($X^2 = 38.754$, df = 2, $p < 0.001$).

**Table 3.1** — Average survival (± SE) of forest tent caterpillars beginning at the neonatal stage when reared on a (a) control, highly, (b) intermediately or lowly preferred hybrid poplar diet, over 22 days.

(a)

| *Experimental days alive* | *Mean number of larvae alive per experimental setup* | | |
|---|---|---|---|
| | (Control) | High preference group | |
| | *P. tremuloides* | E3656 | EM915508 |
| 0 | 15.00 ± 0.00 | 15.00 ± 0.00 | 15.00 ± 0.00 |
| 1 | 15.00 ± 0.00 | 13.83 ± 0.48 | 13.17 ± 1.01 |
| 2 | 14.67 ± 0.33 | 12.83 ± 0.70 | 12.67 ± 1.23 |
| 3 | 14.50 ± 0.34 | 12.17 ± 0.87 | 12.17 ± 1.51 |
| 4 | 14.00 ± 0.52 | 11.50 ± 0.67 | 11.50 ± 1.41 |
| 5 | 13.17 ± 0.87 | 8.83 ± 1.14 | 11.17 ± 1.64 |
| 6 | 13.17 ± 0.87 | 5.50 ± 1.45 | 11.00 ± 1.77 |
| 7 | 12.17 ± 0.95 | 4.00 ± 1.34 | 10.67 ± 1.73 |
| 8 | 11.50 ± 0.96 | 3.00 ± 1.10 | 9.17 ± 1.70 |
| 9 | 11.17 ± 1.14 | 2.50 ± 0.89 | 8.33 ± 1.67 |
| 10 | 10.50 ± 1.38 | 2.17 ± 0.75 | 7.83 ± 1.74 |
| 11 | 8.67 ± 1.91 | 1.17 ± 0.75 | 6.83 ± 1.78 |
| 12 | 7.00 ± 2.63 | 1.17 ± 0.75 | 6.50 ± 1.88 |
| 13 | 7.00 ± 2.63 | 0.83 ± 0.65 | 6.00 ± 1.73 |
| 14 | 6.50 ± 2.53 | 0.83 ± 0.65 | 5.00 ± 1.41 |
| 15 | 4.67 ± 2.16 | 0.67 ± 0.67 | 4.00 ± 1.61 |
| 16 | 3.83 ± 2.10 | 0.67 ± 0.67 | 2.67 ± 1.26 |
| 17 | 3.67 ± 2.08 | 0.67 ± 0.67 | 2.33 ± 1.05 |
| 18 | 3.33 ± 2.06 | 0.67 ± 0.67 | 2.17 ± 0.95 |
| 19 | 3.33 ± 2.06 | 0.67 ± 0.67 | 2.17 ± 0.95 |
| 20 | 3.33 ± 2.06 | 0.67 ± 0.67 | 2.17 ± 0.95 |
| 21 | 3.33 ± 2.06 | 0.67 ± 0.67 | 1.50 ± 0.56 |
| 22 | 3.33 ± 2.06 | 0.67 ± 0.67 | 0.83 ± 0.40 |

(b)

| *Experimental days alive* | *Mean number of larvae alive per experimental setup* | | | |
|---|---|---|---|---|
| | Intermediate preference group | | | Low preference group |
| | EM916401 | MB915319 | BM915005 | BM3374 |
| 0 | 15.00 ± 0.00 | 15.00 ± 0.00 | 15.00 ± 0.00 | 15.00 ± 0.00 |
| 1 | 14.17 ± 0.65 | 13.00 ± 1.29 | 13.00 ± 0.77 | 15.00 ± 0.00 |
| 2 | 14.00 ± 0.82 | 12.67 ± 1.20 | 12.50 ± 0.92 | 14.67 ± 0.21 |
| 3 | 12.00 ± 1.63 | 11.17 ± 1.76 | 11.17 ± 0.95 | 14.33 ± 0.33 |
| 4 | 9.33 ± 2.03 | 8.33 ± 2.74 | 9.33 ± 1.26 | 13.33 ± 0.76 |
| 5 | 8.17 ± 1.70 | 5.83 ± 2.63 | 8.33 ± 1.28 | 10.50 ± 1.23 |
| 6 | 6.83 ± 1.62 | 3.83 ± 1.74 | 7.50 ± 1.48 | 7.83 ± 1.01 |
| 7 | 6.33 ± 1.63 | 2.00 ± 1.03 | 7.17 ± 1.62 | 5.33 ± 1.12 |
| 8 | 3.50 ± 1.36 | 1.33 ± 0.99 | 6.00 ± 1.21 | 4.83 ± 0.95 |
| 9 | 3.00 ± 1.24 | 0.00 ± 0.00 | 4.83 ± 1.54 | 3.33 ± 1.20 |
| 10 | 2.00 ± 0.89 | 0.00 ± 0.00 | 4.00 ± 1.57 | 2.67 ± 0.95 |
| 11 | 0.83 ± 0.54 | 0.00 ± 0.00 | 3.00 ± 1.10 | 2.17 ± 0.95 |
| 12 | 0.83 ± 0.54 | 0.00 ± 0.00 | 2.00 ± 1.00 | 1.67 ± 0.76 |
| 13 | 0.33 ± 0.33 | 0.00 ± 0.00 | 2.00 ± 1.00 | 1.17 ± 0.60 |
| 14 | 0.00 ± 0.00 | 0.00 ± 0.00 | 1.17 ± 0.98 | 1.17 ± 0.60 |
| 15 | 0.00 ± 0.00 | 0.00 ± 0.00 | 1.17 ± 0.98 | 0.50 ± 0.34 |
| 16 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.67 ± 0.49 | 0.50 ± 0.34 |
| 17 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.34 |
| 18 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.34 |
| 19 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.34 |
| 20 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.50 ± 0.34 |
| 21 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.33 ± 0.33 |
| 22 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |

**Table 3.2** — Commencing at the neonatal stage, forest tent caterpillar when fed hybrid poplar foliage compared to a preferred host, *P. tremuloides*.

| *Preference group* | *Percent survival* |
|---|---|
| (Control) | 22.2% |
| High | 5.0% |
| Intermediate | 0.0% |
| Low | 0.0% |

**Table 3.3** — Caterpillar instar durations differed significantly (*) when fed highly compared to intermediately preferred foliage.

| *Preference comparison* | *First instar* | | | *Second instar* | | |
|---|---|---|---|---|---|---|
| | *Z* | *N* | *p* | *Z* | *N* | *p* |
| High vs. (Control) | -0.596 | 18 | 0.616 | -1.261 | 18 | 0.250 |
| High vs. Intermediate | -2.960 | 30 | 0.003* | -3.363 | 25 | < 0.001* |
| Intermediate vs. Low | -0.784 | 24 | 0.454 | -2.243 | 19 | 0.022 |

**Table 3.4** — Average molt duration (± SE) of forest tent caterpillars beginning at the neonatal stage when reared on a control or preferentially differing hybrid poplar diet.

| *Preference group* | *Tree identification* | *Mean first instar duration (days)* | *Mean second instar duration (days)* |
|---|---|---|---|
| (Control) | *P. tremuloides* | 4.00 ± 0.00 | 3.83 ± 0.17 |
| High | E3656 | 4.50 ± 0.43 | 4.67 ± 1.52 |
| | EM915508 | 3.17 ± 0.40 | 5.17 ± 2.79 |
| Intermediate | EM916401 | 5.83 ± 0.60 | 16.20 ± 0.73 |
| | MB915319 | 10.33 ± 2.94 | 15.00 ± 0.58 |
| | BM915005 | 5.17 ± 1.01 | 9.80 ± 1.28 |
| Low | BM3374 | 6.33 ± 0.49 | 7.17 ± 2.17 |

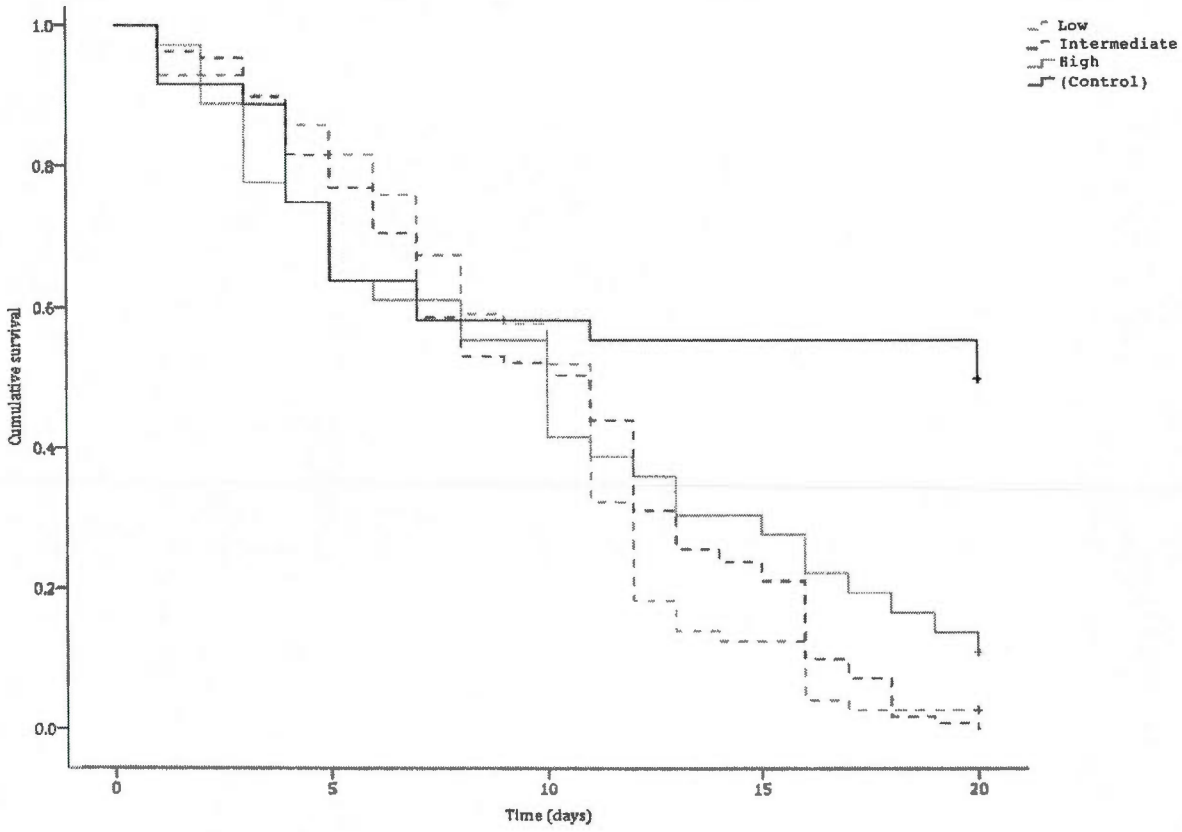



**Figure 3.2** — Kaplan-Meier survival curves of fourth instar performance trials across preference groups. *M. disstria* survival di not significantly differ across poplar preference groups ($X^2 = 2.978$, df = 2, p = 0.226).

**Table 3.5** — Average survival (± SE) of forest tent caterpillars beginning at the fourth instar stage when reared on a (a) control, highly, (b) intermediately or (c) lowly preferred hybrid poplar diet, over 20 days.

(a)

| *Experimental days alive* | *Mean number of larvae alive per experimental setup* | |
|---|---|---|
| | (Control) *P. tremuloides* | High preference group EM915508 |
| 0 | 3.00 ± 0.00 | 15.00 ± 0.00 |
| 1 | 2.75 ± 0.13 | 13.17 ± 1.01 |
| 2 | 2.75 ± 0.13 | 12.67 ± 1.23 |
| 3 | 2.67 ± 0.14 | 12.17 ± 1.51 |
| 4 | 2.33 ± 0.28 | 11.50 ± 1.41 |
| 5 | 1.92 ± 0.34 | 11.17 ± 1.64 |
| 6 | 1.92 ± 0.34 | 11.00 ± 1.77 |
| 7 | 1.75 ± 0.35 | 10.67 ± 1.73 |
| 8 | 1.75 ± 0.35 | 9.17 ± 1.70 |
| 9 | 1.75 ± 0.35 | 8.33 ± 1.67 |
| 10 | 1.75 ± 0.35 | 7.83 ± 1.74 |
| 11 | 1.67 ± 0.38 | 6.83 ± 1.78 |
| 12 | 1.67 ± 0.38 | 6.50 ± 1.88 |
| 13 | 1.67 ± 0.38 | 6.00 ± 1.73 |
| 14 | 1.67 ± 0.38 | 5.00 ± 1.41 |
| 15 | 1.67 ± 0.38 | 4.00 ± 1.61 |
| 16 | 1.67 ± 0.38 | 2.67 ± 1.26 |
| 17 | 1.67 ± 0.38 | 2.33 ± 1.05 |
| 18 | 1.67 ± 0.38 | 2.17 ± 0.95 |
| 19 | 1.67 ± 0.38 | 2.17 ± 0.95 |
| 20 | 1.50 ± 0.36 | 2.17 ± 0.95 |

(b)

| *Experimental days alive* | *Mean number of larvae alive per experimental setup* Intermediate preference group | | |
|---|---|---|---|
| | EM916401 | MB915319 | BM915005 |
| 0 | 3.00 ± 0.00 | 3.00 ± 0.00 | 3.00 ± 0.00 |
| 1 | 3.00 ± 0.00 | 2.67 ± 0.14 | 3.00 ± 0.00 |
| 2 | 2.92 ± 0.08 | 2.67 ± 0.14 | 3.00 ± 0.00 |
| 3 | 2.75 ± 0.13 | 2.67 ± 0.14 | 2.58 ± 0.23 |
| 4 | 2.67 ± 0.14 | 2.50 ± 0.19 | 2.33 ± 0.33 |
| 5 | 2.67 ± 0.14 | 2.33 ± 0.26 | 2.08 ± 0.34 |
| 6 | 2.58 ± 0.15 | 2.00 ± 0.21 | 1.92 ± 0.34 |
| 7 | 2.42 ± 0.15 | 1.58 ± 0.23 | 1.42 ± 0.31 |
| 8 | 2.33 ± 0.19 | 1.25 ± 0.22 | 1.33 ± 0.31 |
| 9 | 2.33 ± 0.19 | 1.17 ± 0.21 | 1.33 ± 0.31 |
| 10 | 2.33 ± 0.19 | 1.08 ± 0.19 | 1.25 ± 0.30 |
| 11 | 2.17 ± 0.21 | 0.75 ± 0.25 | 1.17 ± 0.32 |
| 12 | 1.50 ± 0.29 | 0.25 ± 0.13 | 1.17 ± 0.32 |
| 13 | 1.17 ± 0.24 | 0.17 ± 0.11 | 1.08 ± 0.34 |
| 14 | 1.17 ± 0.24 | 0.08 ± 0.08 | 1.00 ± 0.33 |
| 15 | 1.08 ± 0.19 | 0.08 ± 0.08 | 0.75 ± 0.25 |
| 16 | 0.50 ± 0.19 | 0.00 ± 0.00 | 0.50 ± 0.23 |
| 17 | 0.42 ± 0.19 | 0.00 ± 0.00 | 0.25 ± 0.13 |
| 18 | 0.08 ± 0.08 | 0.00 ± 0.00 | 0.08 ± 0.08 |
| 19 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.08 ± 0.08 |
| 20 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |

(c)

| *Experimental days alive* | *Mean number of larvae alive per experimental setup* Low preference group NM3729 | BM3374 |
|---|---|---|
| 0 | 3.00 ± 0.00 | 3.00 ± 0.00 |
| 1 | 2.92 ± 0.08 | 2.67 ± 0.14 |
| 2 | 2.92 ± 0.08 | 2.67 ± 0.14 |
| 3 | 2.75 ± 0.18 | 2.67 ± 0.14 |
| 4 | 2.58 ± 0.19 | 2.50 ± 0.19 |
| 5 | 2.50 ± 0.19 | 2.33 ± 0.26 |
| 6 | 2.50 ± 0.19 | 2.00 ± 0.21 |
| 7 | 2.42 ± 0.19 | 1.58 ± 0.23 |
| 8 | 2.25 ± 0.22 | 1.33 ± 0.26 |
| 9 | 2.25 ± 0.22 | 1.25 ± 0.25 |
| 10 | 2.08 ± 0.19 | 1.08 ± 0.23 |
| 11 | 1.25 ± 0.13 | 0.75 ± 0.28 |
| 12 | 0.83 ± 0.21 | 0.33 ± 0.14 |
| 13 | 0.67 ± 0.19 | 0.25 ± 0.13 |
| 14 | 0.67 ± 0.19 | 0.17 ± 0.11 |
| 15 | 0.67 ± 0.19 | 0.17 ± 0.11 |
| 16 | 0.17 ± 0.11 | 0.08 ± 0.08 |
| 17 | 0.08 ± 0.08 | 0.08 ± 0.08 |
| 18 | 0.08 ± 0.08 | 0.08 ± 0.08 |
| 19 | 0.08 ± 0.08 | 0.08 ± 0.08 |
| 20 | 0.08 ± 0.08 | 0.08 ± 0.08 |

**Table 3.6** — Forest tent caterpillar survival, beginning at fourth instar, until the end of performance experiments.

| *Preference group* | *Percent survival* |
|---|---|
| (Control) | 50.0% |
| High | 11.1% |
| Intermediate | 0.0% |
| Low | 2.8% |

**Table 3.7** — Caterpillar instar duration when fed control versus highly preferred foliage, and highly compared to intermediately preferred foliage.

| *Preference comparison* | *Fourth instar* | | |
|---|---|---|---|
| | *Z* | *N* | *p* |
| High vs. (Control) | -2,588 | 24 | 0.014* |
| High vs. Intermediate | -3.733 | 48 | < 0.001* |
| Intermediate vs. Low | -0.245 | 60 | 0.806 |

**Table 3.8** — Average molt duration (± SE) of forest tent caterpillars beginning at the fourth instar when reared on a control or preferentially differing hybrid poplar diet.

| *Preference group* | *Tree identification* | *Mean fourth instar duration (days)* |
|---|---|---|
| (Control) | *P. tremuloides* | 3.59 ± 0.69 |
| High | EM915508 | 4.00 ± 0.21 |
| Intermediate | EM916401 | 6.83 ± 0.72 |
| | MB915319 | 5.92 ± 0.84 |
| | BM915005 | 8.64 ± 1.59 |
| Low | NM3729 | 5.75 ± 0.90 |
| | BM3374 | 8.50 ± 1.16 |

### 3.5 Discussion

In the current study, less and intermediately preferred foliage were unacceptable for the survival of *M. disstria*, where instar durations were longer and mortality rates were higher than individuals kept on a higher preferred or aspen diet. Several foliar factors may influence the performance leaf-eating insects, such as tree parentage, nutrients and deterrent concentrations. Robison (1993) demonstrated that forest tent caterpillars developed slower and had poorer survival rates when fed hybrid poplars of *P. nigra* crossed with [X] *P. maximowiczii* or *P. simonii* X *P. berolinensis* parentage. Similarly, the current study found the *P. nigra* X *P. maximowiczii* along with *P. balsamifera* X *P. maximowiczii*, clones were non-suitable hosts for the forest tent caterpillar, where instar durations were lengthened and survivability was much poorer when compared to larvae that were fed highly preferred or control foliage.

Little information regarding physical or chemical foliar characteristics of the hybrid poplars in the current investigation were known; however, it may be suggested that foliage from different preference groups had differing foliar chemistry. For example, caterpillars fed highly preferred foliage showed slightly higher larval survivability and short instar durations, which could be due to a good protein-carbohydrate balance, sufficient leaf nitrogen levels and low deterrent concentrations (Feeny 1970, White 1974, Scriber and Feeny 1979, Karowe 1989a, Despland and Noseworthy 2006). For example, Despland and Noseworthy (2006) found that forest tent caterpillar performance was generally highest on slightly protein-biased or similar rationed protein-carbohydrate leaf levels, whereas larvae did not perform well when either nutrient was extremely biased. As well, Mattson (1980) suggested that lower levels of available nitrogen may result in herbivore malnutrition causing slower growth rates and longer generation times. White (1974, and references therein) examined outbreak instances of five species of Lepidopterans, of genera *Erannis* and *Choristoneura*, and found that lower leaf nitrogen levels stressed individuals, causing an increase in free amino acids within their bodies, which rendered them vulnerable to viral infections and higher mortality rates. Preferred foliage could also contain low concentrations of deterrents, such as tannic

acids; Karowe (1989a) found that *M. disstria*'s survival and relative growth rates were greatly reduced when larvae were fed an artificial diet of 0.5% tannic acid.

Although neonates reared on hybrid foliage suffered high viral mortalities (personal observation), such performance experiments remain valid due the strong possibility that less favorable foliage contained higher tannic acid levels, enabling the polyhedrosis virus to replicate, which may have caused an increase in the mortality of larvae fed highly preferred foliage as the virus quickly became airborne in the laboratory (Karowe 1989a, Kukan and Myers 1997). Interestingly, fourth instar larvae seemed extremely hesitant to consume less preferred foliage at first (personal observation). Such was also found in previous behavioural experiments when fourth instar forest tent larvae were given less preferred foliage to consume: the behaviour of searching was initially much higher and overall nibbling without actual feeding occurred over an observed period of six hours (Chapter 2). Mature forest tent caterpillars have been shown to be less choosy regarding a given meal, as it is at these stages that larvae tend to explore and consume foliage from neighboring trees (Fitzgerald 1995, Meeker 1997). Therefore, less preferred hybrid leaves were presumably composed of high deterrent properties that caused older larvae to choose starvation over consumption (Robison 1993).

Importantly, a forest of less preferred hybrid poplars should not be solely cultured for the poplar industry in Quebec, as such could potentially eliminate or intoxicate *M. disstria* in the surrounding areas, resulting in a diet change of neighboring food webs, as larvae are an important source of food for various spiders, wasps and birds (Fitzgerald 1995). It is very important that chemical analyses be conducted to determine the foliar contents of the hybrid poplars in the current study, particularly on those that mature larvae avoided. As a compromise, Quebec poplar silviculture would benefit from planting intermediately preferred (BM915005, MB915319, EM916401) hybrid poplars, as forest tent caterpillar survival was not as high on such foliage as it was when fed their primary host, *P. tremuloides* (Meeker 1997). By doing so, insect numbers will be controlled and maintained without disturbing the

natural balance of the surrounding environments and in turn, reducing the potential for entomological outbreaks.

# CONCLUSION GÉNÉRALE

Le feuillage des peupliers hybrides a été préféré de façon différenciée par les larves de *M. disstria.* Ces différences ont été constantes de 2009 à 2010, et principalement entre la 3ième à la 7ième semaine du débourrement en 2010. Le groupe d'hybrides le moins préféré était composé principalement de clones avec un lien de parenté avec des peupliers baumiers ou japonais, ces clones provoquaient constamment des réponses dissuasives auprès des chenilles. Ces chenilles consommaient beaucoup moins et cherchaient rapidement à consommer un feuillage plus approprié. Il est apparent que ces hybrides ont des forces de dissuasion contre leurs prédateurs. Les groupes d'hybrides modérément et hautement préférés sont composés de parents liés avec les peupliers deltoides ou euraméricains, et avaient des réponses, en général, d'acceptation par les chenilles durant les expériences de consommation; ces chenilles ont beaucoup consommé le feuillage.

La performance de la livrée des forêts a aussi varié selon les groupes de préférence qui ont été créés en fonction des essais de consommation. La mortalité élevée et les stades plus allongés ont été observés quand les chenilles ont été nourries avec du feuillage provenant de croisements entre *P. balsamifera* et *P. maximowiczii.* La survie était plus élevée et la durée des stades larvaires était plus normale quand les chenilles ont été nourries de la diète préférée. Un tableau sommaire a été préparé pour suggérer des différences foliaires physiques et chimiques entre chaque groupe (Annexe 1). Les feuilles plus âgées (de 7 semaines) en 2010 ont minimisé la consommation des chenilles dans tous les groupes de préférence, dû à des changements physiques et chimiques.

En conclusion, il est essentiel de documenter la chimie foliaire du feuillage des seize peupliers hybrides étudiés, pour mieux comprendre la préférence de la livrée des forêts. D'autres études à long terme sur les jeunes larves, les papillons adultes (l'oviposition) et dans le temps (sur plusieurs années) donneront plus de détails concernant les effets sur la performance de *M. disstria.* D'après les résultats et les analyses de cette étude, il est suggéré

que le ministère des ressources naturelles et de la faune et l'industrie forestière du Québec aménage les plantations de peupliers hybrides, en alternant modérément (E3333, I3225, I3230, E3585, E131, EM916401, MB915319, BM915005) et moins (NM3729, BM3374, MB915302, MB915313) préférables. Par contre, si une analyse chimique des feuilles moins préférées démontre une résistance toxique contre leurs prédateurs, il faudra faire attention afin que les toxines n'affectent pas les niveaux trophiques dans leurs environnements actuels et voisins.

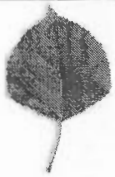
# ANNEXE A

## LES CARACTÉRISTIQUES PHYSIQUES ET CHIMIQUES POTENTIELLES DES FEUILLES DE PEUPLIERS HYBRIDES ÉTUDIÉS

Il est supposé que les préférences, les comportements et les performances de la livrée des forêts différaient en raison de produits chimiques et les caractéristiques physiques foliaires dissemblables dans les groupes de préférences différentes. Cette prédiction a été réalisée en analysant les résultats et la littérature trouvés dans les discussions des deuxième[1] et troisième[2] chapitres de ce mémoire.

| *Identification de l'hybride* | *Groupe de préférence* | *Robustesse*[1] | *Balance protéines:glucides*[1] | *Disponibilité de l'azote*[1,2] | *Les tannins*[1,2] | *Image des feuilles* |
|---|---|---|---|---|---|---|
| BM3374 | Moins préféré | Élevé | Très biaisé de protéines ou glucides | Basse | Modéré à élevé |  |
| BM915005 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |
| MB915302 | Moins préféré | Élevé | Très biaisé de protéines ou glucides | Basse | Modéré à élevé |  |

| | | | | | | |
|---|---|---|---|---|---|---|
| MB915313 | Moins préféré | Élevé | Très biaisé de protéines ou glucides | Basse | Modéré à élevé |  |
| MB915319 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |
| NM3729 | Moins préféré | Élevé | Très biaisé de protéines ou glucides | Basse | Modéré à élevé |  |
| E131 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |
| E3308 | Très préféré | Basse | Équilibré ou un peu biaisé de protéines | Modéré | Basse |  |
| E3333 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |

| | | | | | | |
|---|---|---|---|---|---|---|
| E35570 | Très préféré | Basse | Équilibré ou un peu biaisé de protéines | Modéré | Basse |  |
| E3585 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |
| E3656 | Très préféré | Basse | Équilibré ou un peu biaisé de protéines | Modéré | Basse |  |
| EM916401 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |
| EM915508 | Très préféré | Basse | Équilibré ou un peu biaisé de protéines | Modéré | Basse |  |
| I3225 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |

| | | | | | | |
|---|---|---|---|---|---|---|
| I3230 | Moyennement préféré | Modéré | Biaisé de protéines ou glucides | Basse à modéré | Modéré |  |

# ANNEX B

## POPLAR HYBRID CROSSES INVESTIGATED FOR THE PRESENT MEMOIR

The following Annex is intended to give the reader a general, hypothetical, description regarding the hybrid crosses studied and their potential entomological susceptibilities in the present memoir.

### 4.1 *Populus balsamifera* X *Populus maximowiczii*

Little investigation has been performed on the artificial hybrid cross between balsam and Japanese poplars; however each species has been previously crossed with other *Populus* spp. Both tree species are found under the same section of poplars, Tacamahaca; yet they are not native to similar environments (Dickmann and Stuart 1983). It is possible to use either poplar as maternal or paternal (pollen-donating) contributors when crossed (Dickmann and Stuart 1983). Characteristics that would be beneficial to observe in a successful crossing of the two species would include (a) the hardiness, ability to overwinter under extreme conditions and pest resistance that *P. balsamifera* tends to possess and (b) the very rapid growth rate that *P. maximowiczii* has (Dickmann and Stuart 1983, Dickmann 2002).

Two studies of crossed *P. maximowiczii* hybrids, pertaining to insect susceptibilities towards the poplar-and-willow borer (*Cryptorhynchus lapathi* L (Coleoptera: Curculionidae) and poplar aphids (*Chaitrophorus leucolmelas* Koch (Homoptera: Aphididae), have demonstrated that insects were less likely to establish high densities on them (Ramirez et al. 2004, Broberg et al. 2005, Hannon et al. 2008). Such observations may indicate that the Japanese poplar could have specific foliar properties that discourage insects to inhabit it, perhaps also detracting potential forest tent caterpillar plantation pests.

Similarly, documented actions of Aboriginal peoples have shown that burning *P. balsamifera* was a tried and true way of deterring forest insects from a habitation (Dickmann and Stuart 1983). It has been hypothesized that balsam poplars' unique fragrance and resinous buds may deter insects (Bryant and Kuropat 1980). Robison and Raffa's (1994) data has demonstrated that second instar forest tent larvae, under no-choice tests, consume considerably less foliage from hybrid poplars crossed with *P. balsamifera*; however such did not hold true for later instar larvae.

### 4.2 *Populus deltoides* X *Populus nigra*

An already common and natural hybrid found throughout many poplar plantations in North America, the hybrid cross of *P. deltoides* and *P. nigra* is collectively known as *Populus euramericana*, or the Euramerican poplar (Dickmann and Stuart 1983). In this hybrid poplar, the maternal parent must be an eastern cottonwood and paternity must be due to a black poplar (Dickmann and Stuart 1983). Both tree species are derived from the same section, Aigeiros; however, they do not share similar climatic or environmental origins. An ideal hybrid cross between these *Populus* spp. would involve both their rapid growth rates and the strong, well-desired wood that *P. deltoides* produces.

Although little is known concerning insect pests of the black poplar, investigations have demonstrated that these tree species are susceptible to a canker and a wet-wood bacterium (Dickmann and Stuart 1983). Also, the forest tent caterpillar has been found to host upon *P. deltoides*; therefore this hybrid could be more susceptible towards insect threats (Morris et al. 1975). The Euramerican poplar has demonstrated great variability when tested for pest, disease and climatic resistance, leaving researchers questioning their chemical characteristics (Dickmann and Stuart 1983). On the other hand, wood cuttings of *P. euramericana* have shown higher rooting abilities than the eastern cottonwood alone and a study testing hybrid resistance amongst crosses made with *P. nigra* demonstrated more resistance towards insects (Abrahamsorn et al. 1977, Dickmann and Stuart 1983).

### 4.3 *Populus trichocarpa* X *Populus deltoides*

The natural hybrid poplar cross between both black and eastern cottonwoods is also known as the Interamerican poplar, *P. interamericana*; both species may be either maternal or paternal parents in the cross (Dickmann and Stuart 1983). These *Populus* spp. come from the same continent and are relatively adapted to similar climatic and environmental conditions, although their poplar sections differ. Similar to Euramerican poplars, an ideal hybrid cross between these *Populus* spp. would involve both their rapid growth rates and the strong, well-desired wood that *P. deltoides* produces.

As black cottonwoods come from the same family as the balsam poplars, they also have fragrant buds and leaves that may deter insect pests (Dickmann and Stuart 1983). They have also, individually and when crossed, demonstrated great growth abilities and high canker and disease resistance, leading to high productive rates for plantations (Dickmann and Stuart 1983). As hybrids, black and eastern cottonwoods should be quite tolerant to insect pests, such as the forest tent caterpillar.

### 4.4 *Populus euramericana* X *Populus maximowiczii*

An artificial cross between Euramerican and Japanese poplars has been introduced into Quebec's plantations. Little concerning this hybrid is known; however it may be hypothesized that this cross will perform better than *P. euramericana* alone, as *P. maximowiczii* parentage seems to have increased resistance towards insect hosts in past findings (Ramirez et al. 2004, Broberg et al. 2005, Hannon et al. 2008).

### 4.5 *Populus nigra* X *Populus maximowiczii*

Sharing lineage with black cottonwoods that have demonstrated tolerance towards insect pests in the past, the *P. nigra* X *P. maximowiczii* hybrid should show substantial resistance towards insects, such as the forest tent caterpillar (Abrahamsorn et al. 1977,

Dickmann and Stuart 1983). This hybrid cross has not been readily studied; therefore literature pertaining to such a hybrid remains unavailable, particularly concerning its insect resistance.

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