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Compte rendu du 17e Atelier de recherche sur la tordeuse des bourgeons de l'épinette

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Proceedings of the 17th Eastern Spruce Budworm Research Work Conference

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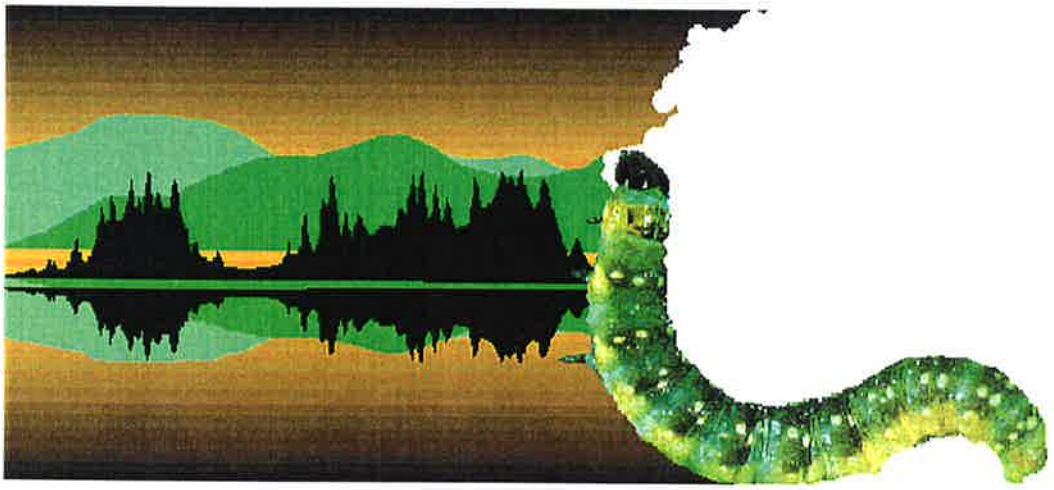

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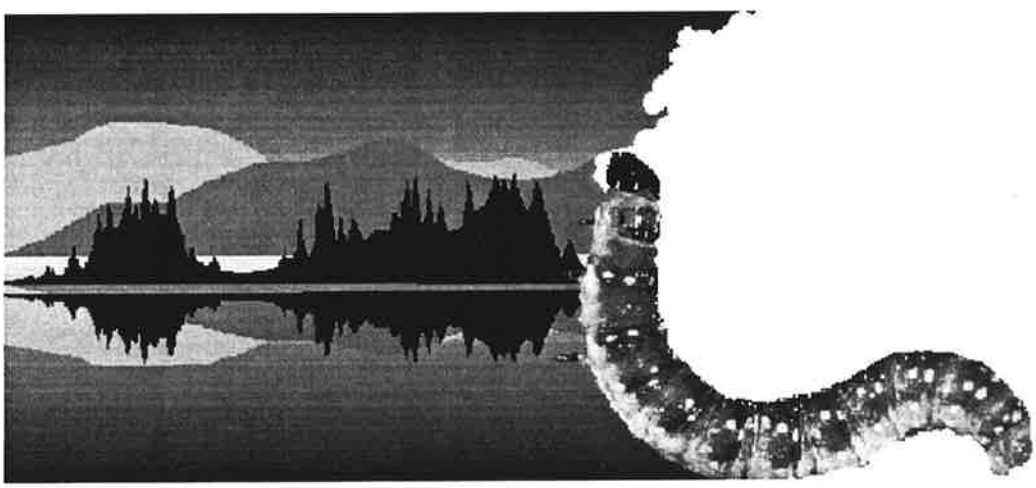

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AVANT-PROPOS

Le 17e Atelier de recherche sur la tordeuse des bourgeons de l'épinette a pris place au Hilton de Québec les 2 et 3 avril 1997. Y ont participé près d'une centaine de scientifiques du SCF et d'autres organisations canadiennes et américaines menant des travaux sur la tordeuse des bourgeons de l'épinette, ainsi que des représentants de l'industrie forestière et de fabricants d'antiparasitaires. Le principal objectif de la conférence était de fournir aux chercheurs et aux spécialistes de la lutte contre la tordeuse une tribune d'échange des informations les plus récentes sur l'écologie de l'insecte et la lutte menée contre la tordeuse. Cette conférence tombait à point nommé, car l'insecte fait de nouveaux ravages dans l'est de l'Ontario et l'ouest du Québec, en particulier le long de la vallée de l'Outaouais, ce qui laisse présager une nouvelle pullulation généralisée sur une grande partie du nord-est de l'Amérique du Nord dans un avenir rapproché.

Le programme du 17e Atelier a été élaboré par un comité formé d'Éric Bauce (Université Laval), de Michel Cusson et de Johanne Delisle (SCF-Centre de foresterie des Laurentides), et de Vince Nealis (SCF-Centre de foresterie du Pacifique); j'assurais la présidence de ce comité. Le programme prévoyait trois ateliers d'une demi-journée sur les thèmes liés à l'écologie des populations; lutte avec la bactérie *B.t. (Bacillus thuringiensis)* et des virus, l'analyse spatiale des épisodes de défoliation survenus par le passé et la mise au point de systèmes d'aide à la décision (SAD). Chaque atelier comportait les présentations de 7 ou 8 conférenciers invités (20 minutes chacun) suivies de discussions en groupes (30 minutes). L'après-midi du premier jour a été consacré en entier à la présentation d'affiches. Au cours de l'atelier, on a mis des salles à la disposition de divers groupes d'intérêts afin qu'ils puissent se réunir. Il y a eu deux rencontres de ce type : le groupe de travail sur l'arpenteuse de la pruche s'est réuni en après-midi le 3 avril, et les participants au Programme de la dynamique des populations faisant partie du Réseau sur les processus des écosystèmes forestiers, qui relève du SCF, s'est réuni le matin du 4. Le calendrier relativement peu chargé a laissé beaucoup de temps libre pour la discussion, en particulier l'après-midi du 2 avril. Parmi les sujets abordés, les plus importants sont ceux qui touchent la sécurité entourant l'inévitable recours à la bactérie *B.t.* comme principale arme de contre-attaque au cours de la prochaine épidémie. Une suggestion soumise

FOREWORD

The 17th Eastern Spruce Budworm Research Work Conference (ESBRWC) was held at the Hilton in Quebec City on April 2nd and 3rd, 1997. The meeting was attended by almost 100 officially registered scientists conducting research on spruce budworm in the CFS and other institutions in Canada and the United States, as well as representatives of the forest industry and pesticide manufacturers. Its main objective was to provide an opportunity for spruce budworm researchers and control specialists to exchange the most up-to-date information on the insect's ecology and management. It came at a very opportune time because of new outbreaks in eastern Ontario and western Quebec, particularly along the Ottawa River valley, which lets us foresee the rise of a new generalized outbreak over much of northeastern North America in the near future.

The program of the 17th ESBRWC was developed by a committee composed of Eric Bauce (Université Laval), Michel Cusson and Johanne Delisle (CFS-Laurentian Forestry Centre), and Vince Nealis (CFS-Pacific Forestry Centre), and chaired by myself. The program consisted of three half-day workshops on the topics of population ecology, management with *Bt* and viruses, spatial analysis of historical defoliation records and DSS development. Each workshop consisted of 7 to 8 guest speakers (20 minutes each) followed by 30-minute group discussions. The entire afternoon of the first day was devoted to the poster session. Rooms were made available during the workshop so special-interest groups could get together. Two such gatherings took place: the Hemlock Looper Working Group met in the evening of April 3rd, and participants in the Population Dynamics Program of the CFS Ecosystem Processes Network met in the morning of April 4th. The relatively relaxed schedule allowed a considerable amount of time for discussion, particularly in the afternoon of April 2nd. Among topics that were discussed, the most important were the ones concerning the safety issues surrounding the inevitable reliance on *Bt* as the main line of defense during the next outbreak. One suggestion that was given to researchers developing alternative methods such as viruses or growth regulators was not to raise false safety issues about *Bt* in their justification for the need to

aux chercheurs travaillant à la mise au point de solutions de rechange fondées notamment sur les virus ou les régulateurs de croissance a été de ne pas sonner l'alarme inutilement en ce qui concerne le *B.t.* pour justifier la nécessité de ces solutions de remplacement, à moins de présenter des preuves à l'appui. Pour l'instant, il existe peu d'indications, sinon aucune, étayant la probabilité ou même la possibilité que la tordeuse développe une résistance par rapport au *B.t.* compte tenu des protocoles d'utilisation, surtout du fait que l'application est localisée et que la pression de sélection est faible. De même, il existe beaucoup d'éléments prouvant la sécurité environnementale relative du *B.t.*, à la condition que les instructions apparaissant sur l'étiquette soient suivies à la lettre.

L'Atelier met également en lumière les progrès considérables réalisés au chapitre de la dynamique des populations et la nécessité de poursuivre les recherches sur les populations en phase endémique et au début des pullullations. Des travaux extrêmement intéressants sont en cours en vue de l'analyse et de l'interprétation de l'épidémiologie de la tordeuse, par l'analyse dendrochronologique et spatiale des mentions de défoliation. Les similitudes dans les profils observés et la diversité des démarches analytiques suivies laissent penser qu'il serait souhaitable d'intensifier la collaboration et l'échange d'information dans ce domaine en évolution rapide. Les résultats des recherches sur l'épidémiologie et la dynamique des populations ont une incidence directe sur l'amélioration des méthodes de prévisions et l'utilité des outils d'aide à la décision (SAD) en voie d'élaboration. La recherche sur l'interaction du *B.t.* avec la tordeuse des bourgeons de l'épinette nous rapproche d'une compréhension claire et détaillée des facteurs influant sur l'efficacité, à tel point que l'on peut maintenant simuler très précisément ces interactions et optimiser les approches d'application pour la protection du feuillage, la diminution des populations et même la préservation des ennemis naturels de la tordeuse. Les travaux sur les virus ont donné lieu à des percées très encourageantes, en particulier concernant les organismes génétiquement modifiés mais, de toute évidence, nous sommes encore loin de la phase opérationnelle d'utilisation de la plupart des virus dans les programmes de protection du feuillage. L'une des craintes formulées lors de la rencontre concernait la grande diversité des domaines faisant actuellement l'objet des travaux et la nécessité d'une évaluation critique afin de déterminer les avenues les plus prometteuses auxquelles on devrait accorder la priorité.

develop such alternatives, unless such risks can be substantiated. At this point, there is little if any evidence that the development of budworm resistance to *Bt* is either likely or even possible given the use patterns, mainly because of localized, low selection pressure. Likewise, there is a considerable amount of evidence as to the relative environmental safety of *Bt* provided that label instructions are followed.

The program also highlighted the considerable progress that is being made in the area of population dynamics, and the need to pursue work on endemic and early outbreak populations. There is some exciting work going on in the analysis and interpretation of budworm epidemiology, through dendrochronology and spatial analysis of defoliation records. The similarities in patterns that are being found, and the diversity of analytical approaches being followed suggest that there is room for a higher degree of collaboration and exchange of information in this rapidly growing area. The results from population dynamics and epidemiology research have a direct bearing on refinement of forecasting methods and the usefulness of DSS tools that are being developed. Research on the interaction of *Bt* with spruce budworm is leading to a clear and detailed understanding of the factors affecting efficacy, to such an extent that these interactions can now be very accurately simulated and therefore that application strategies can be optimized for foliage protection, population reduction, and even natural enemy conservation. Work on viruses has shown some very promising advances, particularly in the area of genetically engineered viruses, although it is clear that we are still far from the operational use of most viruses in foliage protection programs. One of the concerns voiced at the meeting was the great diversity of avenues currently being investigated, and the need for critical evaluation to determine which avenues show the most promise and should be given higher priority.

It was both a pleasure and an honor for me to help organize this meeting. It was, according to many participants, a success. I want to thank the workshop moderators (Éric Bauce, Michel Cusson and Vince Nealis) for their contribution, and Johanne Delisle for coordinating the poster session. Local arrangements and the myriad details of organizing

Le fait de contribuer à l'organisation de cet Atelier a été pour moi un plaisir et un honneur. Selon beaucoup de participants, la conférence a été couronnée de succès. J'aimerais remercier les modérateurs des ateliers (Éric Bauce, Michel Cusson et Vince Nealis) pour leur contribution, ainsi que Johanne Delisle pour avoir coordonné la présentation des affiches. Les dispositions sur place et les innombrables détails ont été pris en charge de façon très efficace par trois personnes dévouées et compétentes, Pierre Duval, Édith Jalbert et Jacques Larouche, tous du SCF - Centre de foresterie des Laurentides. J'aimerais saluer le très bon travail de tous les intervenants, notamment les conférenciers invités (Gilles Trudel, directeur de la SOPFIM, Naomi Cappucino, chercheur au University of Texas, et Barry Cooke, étudiant au doctorat au University of Alberta), tous les autres conférenciers, ainsi que les présentateurs d'affiches. C'est à vous tous que nous devons le succès de cet Atelier. En outre, le SCF a fourni une contribution financière importante à cette rencontre, puisqu'il en a assumé environ la moitié des coûts.

Si j'avais à organiser à nouveau cet Atelier, je serais peut-être tenté de réduire le nombre de présentations, d'allonger un peu leur durée et de leur donner une orientation plus générale; je réserverais aussi plus de temps pour les discussions à la fin des séances. J'ai l'impression que les participants ont apprécié cette forme de programme où ils ont eu une partie de la journée pour voir les affiches et discuter à bâtons rompus entre eux.

Nous avons passé le flambeau au ministère des Ressources naturelles et de l'Énergie du Nouveau-Brunswick pour qu'il puisse commencer les préparatifs du 18e Atelier qui se tiendra à Fredericton (N.-B.) en 1999. L'organisation du 17e Atelier a transféré à la nouvelle équipe une somme importante pour la préparation de la prochaine rencontre.

Une fois de plus, j'aimerais exprimer ma gratitude à tous ceux qui ont contribué à faire de cet événement un succès!

Jacques Régnière
SCF - Centre de foresterie des Laurentides

the workshop were very well looked after by three dedicated and very efficient people: Pierre Duval, Edith Jalbert and Jacques Larouche, all from CFS-Laurentian Forestry Centre. Everyone involved, including the guest speakers (Gilles Trudel, director of SOPFIM, Naomi Cappucino, researcher at the University of Texas, and Barry Cooke, PhD student at the University of Alberta), all other speakers, and those who presented posters, did a very good job and can collectively take credit for the event's success. CFS headquarters contributed financially to this meeting to a very large extent, assuming almost 50% of the cost.

Should I have to organize this work conference again, I might be tempted to reduce the number of presentations, make them somewhat longer and more general, and increase the amount of time reserved for discussion at the end of sessions. I also believe that allowing participants to have part of the day to view the posters and to talk informally is a very successful agenda format.

The torch has been passed on to the New Brunswick Department of Natural Resources and Energy so that it can start preparing the 18th ESBRWC in Fredericton NB, sometime in 1999. A considerable amount of "seed funding" is being transferred from the 17th to the 18th ESBRWC organization.

Once again, thanks to everyone who got involved to ensure that this event was a success!

Jacques Régnière
CFS - Laurentian Forestry Centre

TABLE OF CONTENTS

CONFERENCE SUMMARIES

Opening Address
by
Mr. Gilles A. Trudel
General Manager
Société de protection des forêts contre les insectes et maladies

Ladies and Gentlemen,

Before I begin, I would like to thank the organizing committee for the honour of leading off this 17th annual Research Work Conference. I would also like to take this opportunity to welcome our colleagues and partners, particularly those who are visiting here from outside Québec.

As you know, I am here representing the SOPFIM, the only recognized organization for the prevention of insect epidemics in Québec forests, particularly those caused by the spruce budworm. Like all of you who have come to this conference, we are deeply concerned by the stakes and issues involved in spruce budworm epidemics. That is why we have been eagerly anticipating today's meeting. It is events like these which show how researchers and forest users are genuinely determined to find the best solutions for combating the damage caused by the budworm. All share the same desire to develop high-quality, effective means with which to protect our forests. I am quite positive that this conference will provide a unique forum for discussion and dialogue allowing us to advance collectively.

Without question, the spruce budworm is the number one enemy of North American forests today. The last infestation affected almost the entire coniferous wood populations in Québec, causing timber losses of 235 million cubic meters, or the equivalent of the entire industry consumption in Québec over a ten-year period.

We are now facing a new epidemic, here as in the other provinces. It is an epidemic which must be taken extremely seriously. It threatens to be as devastating as the last. In addition, it is occurring in a context in which the demands made on protection measures are much higher than was the case 20 years ago.

When the last spruce budworm epidemic broke out, the production capacity of our forests surpassed harvesting requirements. Now, a new epidemic is about to develop at a time when fibre resources are increasingly scarce. In Québec, supply sources have been totally allocated, and yet they barely manage to meet industry demand. What is more, the current allocation scheme provides no room to maneuver in the case of losses which may result from an insect epidemic. Thus, if we are confronted with the same losses we experienced in the past, undoubtedly this will mean that mills will close and many jobs will be lost in a sector considered to be a mainstay of economic development for several regions in Québec.

In another development, international markets have become increasingly demanding in terms of the quality of forest products. The global economy has benefited the Québec forest industry, with more than half of the province's annual production now being exported. However, the competition has become increasingly fierce. In addition, new standards for environmental certification will no longer allow using dead or insect-damaged wood.

It's also worth mentioning that this new epidemic poses a threat not just in terms of industry interests. First and foremost, the forest is also a living environment, offering a multitude of resources and a broad range of uses, including recreation. This manner of considering all environmental concerns and the needs of all users amounts to a new way of picturing the forest. By adopting such a perspective, we become concerned not only with the health of trees, but also with the quality of the entire woodland environment.

These, then, are the new parameters confronting forest researchers and field operators alike. Whether we are dealing with research or day-to-day management, these are the realities which will guide intervention against insect epidemics from now into the near future. In a context such as this, I can hardly overemphasize the importance of a meeting like this Research Work Conference. By bringing together researchers and operators at the same table, I believe we have a unique opportunity to reconcile ongoing research efforts with current and future needs for protective action against the spruce budworm.

We are on the eve of a new epidemic. We are also in a period of budget restrictions and rationalization. Partnerships and close working relationships of the kind which are developed here will be all the more valuable as a result. There are two pitfalls we must avoid: one is to needlessly repeat the same intervention measures, the other is to concentrate research efforts on previously solved problems. The times no longer permit us to engage in "races to discover", or to carry out projects in isolation from one another. In the present time, we are confronted with identifying the most urgent needs and establishing our priorities. To do so, we will need to encourage the spread and exchange of information as much as possible.

In short, the challenge ahead for us in the next few days, as in the future, will be to find ways of strengthening our alliances and pooling our knowledge. That is how we can best channel research along paths which hold real promise in terms of grasping the dynamics of epidemics and gauging the scope of their impact. With this information in hand, we will be in a better position to develop the best measures and strategies for providing our forests with rapid, optimum protection.

As you can see, there is much to be gained from an event such as ours. It is my sincere hope that you will all take advantage of this opportunity as much as possible. Thank you.

SESSION I: POPULATION ECOLOGY WORKSHOP

(V. Nealis)

Endemic spruce budworm populations in New Brunswick

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For the past 10 years, spruce budworm populations in southern New Brunswick have been slowly declining to very low (endemic) levels. To examine the survivorship of budworm, and to determine and evaluate the significant mortality factors operating in these endemic populations, experimental implantation techniques were developed. Individual, lab-reared budworm were placed on trees at the rate of one individual per tree so as not to alter the effect of the low natural density. Every budworm was observed 2-3 times per week and, at each observation, all missing, preyed on, parasitized or dead specimens were recorded and were replaced with another individual of the appropriate instar/stage.

In 1992 and 1993, implanted budworm were exposed to all natural mortality factors (parasitoids, predators and diseases), whereas in 1994 and 1995, in addition to a fully exposed group, we enclosed some in cages and sleeves. The cages excluded large predators, but allowed small invertebrate predators, and parasitoids to enter; the sleeves excluded all natural enemies (except diseases). Because many larvae have a tendency to wander in search of a feeding site after initial implanting, in the latter two years, all implanted larvae were enclosed in a sleeve for one day following implantation to reduce the number of "missing" larvae.

In this presentation, we examine various methods to determine the survivorship of endemic budworm populations using the above implantation technique, and compare the impact of natural mortality factors in 1992 with those in 1995 when the budworm population reached its lowest density.

Endemic populations of the spruce budworm in Québec

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A study of the population dynamics of the spruce budworm in endemic populations has been ongoing in Québec since 1994. Fourteen study sites were chosen throughout the province. In sites of sufficient population densities, sampling of branches were done weekly and larvae that were collected were reared in the laboratory until death. In sites of low population densities, larvae from colonies reared in the laboratory were introduced in the field at the 3rd instar and were studied until they disappeared, died or reached adulthood. Half the larvae were put inside cages to measure the impact of avian predation. In 1994, 200 3rd instar larvae were initially introduced. Missing or dead larvae were replaced weekly. The number of insects proved to be insufficient and the number of cohorts (one per week) was too high for a good sampling of the mortality causes. In 1995, 600 larvae were introduced initially. Missing and dead larvae were replaced at the 5th instar and again at the pupal stage to insure adequate sampling of the mortality rate at the 6th instar and at the pupal stage. In 1996, the number of larvae in the initial introduction was reduced to 400 in an effort to reduce costs. Observations of the cohorts were made weekly. Dead or moribund larvae were collected and sent to the laboratory where the causes of mortality were identified for all larvae collected from the Branch Sampling Method and for all dead or moribund larvae found in the Cohort Survival Sampling. Survival rates in 1995 and 1996 were relatively high and constant from the 3rd to the 6th instar, but declined sharply starting with the 6th instar. In 1994, this 2-step pattern of survival was not noticed, possibly because of the weekly replacement of the larvae and the low number of insects introduced in the field compared with 1995 and 1996. In most sites, less than 1% of the insects survived and reached adulthood during the 3-year period. However, the western study sites showed survival rates between 2 and 6%.

Parasitism accounts for an average of 75-80% of larvae mortality that are brought back to the laboratory. Miscellaneous causes of mortality (crushed insects, bad molts, insects lost in the lab, etc.) account for 10-20% of mortality. Fungi and micro-organisms (viruses, protozoans, microsporidia) each account for about 1-4% of mortality.

On any given year, more than 40 different causes of mortality were identified. A multiple correspondance analysis (MCA) was conducted on a contingency table made of the mortality causes and the 14 study sites for each year in order to synthesize the data and identify relationships between natural enemies and sites. The analysis allowed us to develop a framework for interpreting the MCA results and we were able to identify 4 types of relationships: 1) young epidemic populations with low control potential of natural enemies, 2) older epidemic populations with high control potential of natural enemies, 3) young endemic populations with high control potential of natural enemies and 4) older endemic populations with low control potential of natural enemies. The location of our study sites within that interpretation framework and the variations from year to year will probably allow us to predict the occurrence of new spruce budworm epidemics.

Spruce budworm studies in western Canada

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The spruce budworm, *Choristoneura fumiferana*, is transcontinental in distribution and outbreaks in western Canada might persist for several decades. Differences in population behaviour between western and eastern populations thus require explanation. There are several aspects of the budworm's bionomics in the West that are quite different from conditions reported for populations in eastern North America. Phenological studies indicate that post-diapause development of the budworm requires fewer heat units (degree-days) than populations in Ontario. Rearing populations at several constant temperatures from locations along a latitudinal gradient of 15 degrees showed that there are no genetic differences among populations that would account for differences in phenological development. The observed differences might be due to budworm populations tracking host phenology. Balsam fir, *Abies balsamea*, becomes less important in forest stands as one proceeds west so that the major host for the insect in western Canada is white spruce, *Picea glauca*. Populations may persist for many years in white spruce stands because of the peculiar interaction between the insect and white spruce bud dynamics. The collapse of historic outbreaks have been associated with late spring frosts. As the intervals between such frosts is projected to increase under climate change projections, outbreaks are expected to last longer. Tree ring studies are underway to describe the association between long-term population behaviour and climate variables. Over the short-term, work with experimentally manipulating populations suggest that processes that control recruitment to the feeding stage may be critical in determining population trends.

Spruce budworm impact and parasitism rates in a diverse landscape: patterns, mechanisms and future directions

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The hypothesis that vegetational diversity may lessen the impact of forest insect pests by favoring natural enemies is appealing to those who seek ecologically sound solutions to pest problems. We investigated the effect of forest diversity on the impact of the spruce budworm *Choristoneura fumiferana* following the last outbreak, as well as the budworm's current abundance and parasitism rate, in the Abitibi region of northwestern Québec. Mortality of balsam fir caused by the budworm was greater in extensive conifer stands than either in "habitat islands" of fir surrounded by deciduous forest or on true islands in the middle of a lake. Adult spruce budworm abundance, assessed by pheromone traps, did not differ significantly between the three types of sites. Larval and pupal parasitism rates were examined by transferring cohorts of

laboratory-reared larvae and pupae to trees in the three site types and later collecting and rearing them. The tachinid *Actia interrupta*, as well as the ichneumonid pupal parasitoids *I. conquisitor*, *E. ontario* and *P. maculicornis*, caused higher mortality in the habitat islands than on true islands or in extensive stands. *Exochus nigripalpis tectulum*, an ichneumonid that attacks the larvae and emerges from the pupae, caused greater mortality in the extensive stands of conifers.

One mechanism that might explain why certain parasitoids are more important in diverse sites or landscapes is the availability of nectar for adults. The deciduous forest surrounding the habitat islands has an understory that is much richer in flowering herbs than that of the coniferous forest. We evaluated the influence of understory nectar on parasitism rates in an experiment in which we either removed understory flowering herbs or sprayed a sucrose solution on the understory vegetation in 50 m x 50 m quadrats. Cohorts of laboratory-reared larvae and pupae were then transferred to the field to evaluate parasitism in the quadrats. Parasitoids of young larvae (Apanteloids and *Elachertus cacoeciae*) caused greater mortality in the supplemental sucrose treatment than in the vegetation-removal treatment or the controls. Parasitoids of older larvae and of pupae did not respond to the treatments. Larger-scale treatments may be necessary to elicit a response by the larger parasitoids that attack older larvae and pupae.

Deciduous forest may also support lepidopterans that act as alternate hosts for budworm parasitoids. This will be the subject of future experiments in which we propose to manipulate the density of deciduous-feeding lepidopterans on small islands and gage the subsequent impact on the parasitism rate of the budworm.

Future research should also include a closer look at the question of spatial scale. Forest diversity changes over a continuum of spatial scales: conifers can be mixed with deciduous vegetation within stands, and coniferous patches of various sizes may be embedded in a matrix of deciduous vegetation. Each natural enemy species, as well as the budworm itself, will respond to patchiness at a particular scale. The development of sound management practices will require an understanding of the scale at which diversity most strongly favors the budworm's natural enemies.

Reproductive strategy and migration

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The impact of male larval diet on male and female reproductive success was investigated in the eruptive oligophagous species, *C. fumiferana*. In this study, males were fed on the same host species (balsam fir) but the quantity of foliage was controlled, in order to simulate endemic and epidemic phases in the population cycle. We showed that the different parameters used to assess male reproductive performance varied significantly between diet treatments. For instance, males fed on YF (young foliage) were significantly bigger, more successful in acquiring mates and produced larger spermatophores than those fed on OF (older foliage). Male larval nutrition also affected female reproductive success, as those mated with males fed on high quality foliage were less likely to resume calling (the emission of the sex pheromone) and produced significantly more viable progeny than conspecifics mated with males reared on low quality food. These findings were used to develop a model of the ecophysiological mechanisms governing reproduction and migration in *C. fumiferana*. We postulated that in epidemic conditions, females will have a low JH titer: this would slow down egg production, stimulate calling and increase female sensitivity to the high ambient pheromone levels that would be present in epidemic situations due to the high number of females that resumed calling following mating with low quality males. Under such conditions, females would have a high tendency to migrate. In contrast, in endemic conditions, females will have high levels of JH, resulting in normal ovarian maturation, with females rarely calling after the first mating and having low sensitivity to ambient pheromone. Under these conditions, migration will not occur. To test this model, we studied the role of juvenile hormone (JH) on the physiology of SBW reproduction, including ovarian maturation and pheromone synthesis. We showed that the corpora

allata (CA) of SBW virgin females become activated during the last two days of pupal development with the highest rate of increase in JH production coinciding with an increase in oocyte growth, implicating JH in ovarian development. We also demonstrated that following mating there was an increase in JH titer, suggesting that either males transfer JH directly to the female or a factor associated with mating stimulates the female's CA to produce JH. Whether male quality actually influences the level of JH produced remained to be determined.

Studies on the physiological regulation of pheromone synthesis in SBW showed that pheromone production in decapitated or mated females may be induced by injection of Hez-PBAN or a brain extract of SBW virgin females. However, contrary to our expectation there was no evidence that the decline in pheromone synthesis following mating was under either hormonal (JH) or humoral (blood or male accessory secretions) regulation. In contrast, transection of the ventral nerve cord prior to mating did not inhibit pheronome production in mated females, strongly suggesting that the release of PBAN from the suboesophageal ganglion is under neural control. Additional studies are underway to further investigate to what extent, if any, JH plays a role in the regulation of SBW migratory flight.

A spruce budworm outbreak in a boreal mixedwood stand

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The spruce budworm is a specialized folivore. When infestations occur in boreal forests comprised of a mixture of host and non-hosts species, the impact of the budworm is selective and the consequent change in the forest community complex. Outbreak densities of spruce budworm have persisted in a boreal mixedwood stand near Black Sturgeon Lake (BSL) in Northern Ontario for at least 14 years. Density of budworms has been highest on white spruce (wS) and lowest on black spruce (bS) and there has been little year-to-year variation throughout the time series. Density of budworms on balsam fir (bF) was identical to that on wS at the beginning of the outbreak but has declined in recent years so that now it is more like that of bS. Within-generation declines in budworm density are greatest between egg and early larval stages and again at the large-larval stage. There is evidence that although moths lay eggs and many budworms overwinter on bS, emerging larvae leave bS early in the season when buds are relatively retarded in development. Budworms may return to the bS later in the year when current-year foliage of bF and wS is depleted. In general, declines during the feeding stages were modest on all 3 host species at BSL.

These density patterns are reflected in the pattern of current-year defoliation measurements. Defoliation of wS and bF were comparable while that of bS was lower. Despite comparable levels of defoliation, more than 90% of the co-dominant bF have died in the stand while only 50% of the wS have died during this same period. Most of the bS have survived. Surviving trees of all 3 host species were the largest individuals in the stand and all exhibited prolific adventitious growth of buds following several years of defoliation.

The result of this differential mortality of host trees is conversion of a predominantly conifer stand with a substantial bF component to a hardwood stand with large, relict wS, a significant bS component, and regenerating bF. Gaps created by tree mortality support profuse development of species-rich shrub and herbaceous layers.

As spruce budworm populations continue to decline, the emphasis of the study is shifting to examine the chronosequence of the plant community and associated insects. The greater diversity of plants will support a greater diversity of insect folivores that may, in turn, support a greater diversity and higher mean population level of the generalist natural enemies that are associated with rapid decline of budworm populations and maintenance of endemic levels of the spruce budworm for several generations.

Towards a moderate-complexity model of spruce budworm population dynamics

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A simple descriptive model is being developed to (1) test current understanding of the spruce budworm's life system, and (2) serve as a tool to predict SBW dynamics that is responsive to management interventions but is of manageable complexity. The model was designed to help predict the outcome of the interactions between spruce budworm and its major natural enemies as a function of environmental conditions. In this model, natural enemies have been divided into three groups: generalist predators, the microsporidian *Nosema fumiferanae* (Régnière, J. 1984 Theor. Biol. 107: 287-301), and multivoltine parasitoids that require alternative hosts for completion of their life cycle. A logistic function was used as a description of SBW interactions with host plants. Generalist predators are represented by a type II functional response. Specialist predators and multivoltine predators are simulated concurrently by a type II functional response and a numerical response simulated by logistic function where the carrying capacity is the lesser of either SBW abundance or that of alternate hosts (or prey). A preliminary investigation of the behavior of this model was presented. Interesting parallels can be established between model outputs and actual budworm populations in terms of the changes in relative importance of the three groups of natural enemies over the course of an outbreak. Also, there is striking resemblance between model output and observations in terms of outbreak severity, duration and frequency, in response to changes in parameter values reflecting changes in environmental conditions (habitat harshness and species diversity). The model can simulate major features of SBW population dynamics: long and highly stochastic outbreak intervals and biogeographical variation in outbreak duration (severity) and frequency. The model can even simulate temporary drops in defoliation followed by a resurgence such as have been commonly observed. Further model development being planned is the consideration of negative host-plant damage feedbacks, and extension to metapopulations to investigate the role of migration in synchronizing populations with different inherent cycle frequencies.

SESSION II
MANAGEMENT METHODS/VIRUSES

Baculoviruses as management tools in the control of spruce budworm and other forest pest insects

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Insects, as a group, are known to be infected by about 20 virus families. Amongst these virus families, the Baculoviridae, Poxviridae, Polydnaviridae, Parvoviridae and Reoviridae cause most of the known viral diseases in the spruce budworm (*Choristoneura fumiferana*) and other lepidopteran forest pest insects. The two genera within the Baculoviridae, *Granulovirus* (GV) and *Nucleopolyhedrovirus* (NPV) have attracted the most interest as potential agents for use in the suppression of forest pest insect populations. What is attractive about the Baculoviridae is that they are restricted to arthropods, primarily to insects, as they tend to be host specific and many are known to cause epizootics within host populations. For example, population crashes due to NPV epidemics occur in many species of sawflies (Hymenoptera: Diprionidae). Here, NPV infection is density-dependent and these insects are particularly susceptible to the communication of the disease as most are communal and feed openly on the foliage. Attempts to use NPVs to suppress or eliminate sawfly populations have usually been met with success (1). Similarly, in forest Lepidoptera, successful use of NPVs in pest suppression has been in insects that feed openly on the foliage and where NPV epizootics occur in a density-dependent fashion. Examples where some degree of

population suppression has been achieved through the application of NPVs have been the Douglas-fir tussock moth (*Orgyia pseudotsugata*), the white-marked tussock moth (*O. leucostigma*) and the gypsy moth (*Lymantria dispar*). In successful cases, in both Lepidoptera and sawflies, aerial application rates of virus polyhedral inclusion bodies (PIBs) have ranged from around 10^9 to 10^{12} PIBs/ha (2). Applications of NPVs against lepidopteran larvae, like the spruce budworm, that feed in conifer buds have not been so successful (2).

Baculoviruses are transmitted through ingestion by a suitable host. In the case of the gypsy moth, NPV (LdMNPV) infection can occur when a larva chews its way out of an egg whose surface has been contaminated by the female at the time of oviposition or later through environmental contamination (3). LdMNPV can survive in the soil and leaf litter for years, on tree trunks for months and on foliage for days (4). Early gypsy moth instars may also pick up LdMNPV infections as they cross the forest floor as they do with *Entomophaga maimaiga* infections (5). In a given season, LdMNPV infection of gypsy moth larvae is bi-modal (6) where infection of the early instars is vital to infection of the later instars and the development of an epizootic. In the spruce budworm, the life cycle of the insect is such that the potential for infection of the early instars does not exist as it does in the gypsy moth. Contamination of the egg surface by budworm NPV (CfMNPV) is theoretically possible but, after chewing their way out of the egg, budworm L_1s disperse, seek overwintering sites, spin hibernacula and molt to L_2 without feeding. In late April - early May of the next year, L_2s disperse and mine into 1- or 2-year-old needles and then tunnel into the expanding buds where the L_3s through L_6s feed, individually, in their tunnels. Where larval densities are high, L_5s and L_6s may be forced to backfeed on older foliage. Thus, only the later instars may be accessible for viral ingestion and infection. Unfortunately, L_5s and L_6s require an order of magnitude more of CfMNPV PIBs than do L_3s and L_4s (7). Cunningham and Kaupp (2) asked whether low horizontal and vertical transmission of CfMNPV was due to low virus virulence or to the behavior and ecology of the budworm. CfMNPV when applied to western spruce budworm (*C. occidentalis*), which has a similar behavioral ecology to eastern spruce budworm but which is 2,000 times more susceptible to the virus, failed to initiate an epizootic (2). It would appear that budworm behavioral ecology is the problem and that an effective virus will have to be one that can kill later instars at very low dosages. The most likely avenue for obtaining such a virus is through genetic engineering. In this vein, two options appear open. The first is to insert a novel gene into the virus under a strong promoter resulting in a translation product that is not produced by the wild-type CfMNPV, such as an arthropod insect-selective toxin (8) or a hormone inhibitor (9). Alternatively, the strong viral promoter may be used to produce an excess of antisense transcripts complementary to the mRNA of a host gene, thereby blocking the translation of a protein essential for normal larval growth and development (10).

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Development of NPV-T3 for controlling the spruce budworm

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The nuclear polyhedrosis virus (named Tortrivirus-NPV-3T) was sprayed experimentally by ground application during the 1996 spruce budworm (SBW) season. The trees were moderately infested white spruce located in the Wakefield, QC area. The NPV-3T was applied by means of a calibrated Stihl mist blower at a flow rate of 51 L/ha and a dosage of $1.1x10^{11}$ PIBs/ha.

The results were as follows:

a. Control Trees

(1) Pre-Spray Population = 20.0 Larvae/45 cm branch
(2) Larval Mortality = 87.5%
(3) % defoliation = 32.0%

b. NPV-3T Treated Trees

(1) Pre-Spray Population = 11.7 Larvae/45 cm branch
(2) Larval Mortality = 95.7%
(3) % defoliation = 23.0%

c. Treatment efficiency = 80.0%

Microscopic analysis performed on dead larval showed that 55% of the larvae obtained from control and 100% of larvae obtained from the NPV-3T treated trees were infected with the virus. This could explain the high larval mortality and low defoliation observed on the control trees. No other cause of larval mortality was identified within our control trees. Further in the other experimental blocks outside of our area of operations (i.e. SOPFIM's Spray Blocks in the Wakefield/Low area), the presence of the NPV virus was not observed.

The above results confirm those which were obtained during the 1987 to 1990 NPV-3T spray trials.

Other research which we have conducted was to determine the optimum average amount of PIBs which could be obtained from one SBW larvae. Since the initiation of this project, we have been able to increase significantly the average amount of PIBs produced by one SBW larvae in comparison with the PIBs which were originally obtained. Future research concerning the development of NPV-3T will have the following objectives:

a. To confirm by aerial application in 1997 the potential of NPV-3T in controlling the SBW.
b. To develop and to refine methods for the industrial production of NPV-3T.

Cypoviral mixed infections and effects on pathogenicity of CPV on spruce budworm

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Insect viruses have long been considered for their potential role in the biological control of insect pests. They present many important advantages as insecticides. For one, the viral agents used for biological control occur naturally in the environment, and are simply amplified before being reapplied. Among the viruses being considered for use as a biopesticide is the cypovirus of the *Choristoneura fumiferana* (CfCPV). This virus is classified in the genus Cypovirus, and in the family Reoviridae. Its genome consists of 10 segments of double-stranded RNA. The virions are icosahedric (50-70 nM diameter) and one spike is found at each vertex. The polyhedrin bodies may occlude one to several virions. However, during bioassays with CfCPV suspensions, important variations in insecticide potencies were observed. This study presents some evidence of cypoviral mixed infections in spruce budworm larvae that may affect the pathogenicity of CfCPV viral suspensions.

As previously mentioned, the genomic pattern of CfCPV is characterized by the presence of 10 segments (Type A genomic pattern). However, after

in vivo passage in spruce budworm, variations in genomic pattern of CfCPV is observed which provided a multi-band pattern called Type B. These observations suggest that a mixed CfCPV infection may occur in spruce budworm larvae. In fact, mixed CPV infections have already been observed in *Malacasoma distria* (Hayashi and Krywienczyk 1972), *Heliothis armigera* (Rubenstein 1976, Belloncik et al. 1996) and *Artica caja* (Payne 1976).

Using RNA extracted from larvae infected with different concentrations of the CfCPV Type A genomic pattern, the threshold for the appearance of the Type B pattern has been estimated to be between 1.03×10^5 and 5.17×10^5. Genomic reversion of this pattern is observed between 2.34×10^7 and 4.68×10^6 when larvae are exposed to Type B decreasing infectious concentrations. Moreover, chronology analysis shows that the Type A genomic pattern always occurs before the Type B pattern when the insects are infected with Type A or Type B viral suspensions.

Using the CfCPV Type A genomic pattern at the initial step, multiple *in vivo* passages on spruce budworm larvae were performed. An increase in the intensity of the bands unique to the Type B genomic pattern was observed over those associated with the Type A pattern. Moreover, no homology was detected between segments associated with Type A and those unique to Type B. Finally, the appearance of the Type B genomic pattern seems to trigger an increase of the mortality and the debilitating effects associated with CfCPV infection. These observations and results strongly suggest that, in the case of spruce budworm, a mixed CPV infection is occurring.

Adversely interfering with molting: a novel pest management method

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The steroid hormone, ecdysone, initiates and coordinates molting and metamorphosis through a cascade of gene expression and repression events. Like other steroid hormones, ecdysone acts through intracellular receptors at the transcriptional level. The stable ecdysteroid analog RH-5992 controls insects by interfering with the process of molting. To understand the mode of action of this compound and to verify whether it is possible to interfere with molting and metamorphosis by either over or under expressing one or more of the key regulatory molecules, *Choristoneura* hormone receptor 3 (CHR3) from the spruce budworm, *Choristoneura fumiferana* was cloned and characterized. The mRNAs for CHR3 increase in abundance during the ecdysteroid peaks for embryonic, larval, pupal and adult molts but not during the intermolt periods. RH-5992 induces the expression of CHR3 mRNA in the midgut, fat body and epidermis of *C. fumiferana*. We have produced a recombinant *C. fumiferana* nuclear polyhedrovirus (CfMNPV) expressing the CHR3 gene under the polyhedrin promoter in the EGT locus. Infection of the spruce budworm larvae with this recombinant virus resulted in a precocious molt which was similar to the effects of the stable ecdysteroid analog, RH-5992. This research was supported by the Canadian Forest Service and the National Biotechnology Strategy fund.

A parasitoid's best friend: the polydnavirus of the wasp *Tranosema rostrale*

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Endoparasitoids must overcome various obstacles in order to complete their embryonic and larval development. Among the obstacles, the two most important are (i) the potential immune reaction of the host and (ii) an incompatible host developmental rate. An unimpeded immune reaction normally results in the formation of a cellular or melanotic capsule around the parasitoid egg or young larva, a process that leads to the death of the encapsulated insect. Similarly, initiation of host metamorphosis can be fatal to a parasitoid whose development must be completed before host pupation. Many species of endoparasitic wasps have evolved mechanisms to avoid being recognized as foreign by the immune system of their host or to actively depress the host's defense system. Polydnaviruses

(PVs) count among the agents that are used by some ichneumonid and braconid wasps to effect such an immune depression. These same agents can also alter the host's hormonal balance so as to modify its developmental rate to the benefit of the parasitoid.

PVs have a polydispersed genome comprising of different-sized double-stranded circular DNAs derived from linear copies integrated in the wasp's chromosomes. Viral replication and encapsidation take place in the nuclei of calyx cells that line the wasp's ovary between the ovarioles and lateral oviducts. The nucleocapsids acquire one or more envelopes before being released into the lumen of the ovary, where they form the particulate fraction of the "calyx fluid" (Cxf). During oviposition, Cxf is injected along with eggs into the host caterpillar, where the virus infects various tissues in which specific viral genes are expressed. There is growing evidence that polydnaviral gene products are the causal agents of symptoms such as alteration in the behaviour of capsule-forming hemocytes, reduction in the number of circulating hemocytes and inhibition of phenoloxidase (PO) activity in the hemolymph, all of which can contribute to a suppressed immune response. Other significant effects attributed to PVs include developmental retardation, hormonal disruption, growth reduction and altered trehalose levels. The polydnaviral genes responsible for these pathologies are receiving increasing attention, given their potential use in the development of recombinant baculoviruses with improved insecticidal activity. Elucidation of the mechanisms underlying PV-induced physiological disruptions and identification of the relevant genes are the prime objectives of our research on the PV of *Tranosema rostrale*, a spruce budworm (*Choristoneura fumiferana*; SBW) parasitoid.

T. rostrale's ovary is the site of replication of typical polydnaviruses (*T. rostrale* Virus or TrV) which become lodged between chorionic hair-like projections on the egg surface. In the SBW, this virus is believed to be responsible for the inhibition of melanization and a reduction in the number of hemocytes observed in parasitized larvae. In addition, last-instar SBWs parasitized by *T. rostrale* early in the stadium display arrested development and fail to initiate metamorphosis. Injection of the wasp's Cxf into healthy caterpillars induces a dose-dependent delay in pupation or permanent arrest of development which can be abolished by prior treatment of Cxf with UV and the DNA cross-linker psoralen. These results suggest that TrV is the factor responsible for the observed developmental disruptions.

In an effort to identify the physiological processes that are perturbed by TrV, we examined the effects of parasitism and injection of Cxf on host plasma juvenile hormone esterase (JHE) activity, JH titers and ecdysteroid titers in last-instar budworms. We observed a significantly depressed level of JHE activity in both parasitized and Cxf-injected larvae, relative to controls, and preliminary data on JH hemolymph titers indicate that this reduced level of JH degradation by JHE is reflected in higher JH titers. Maintenance of a high JH titer early in the last stadium of parasitized and Cxf-injected larvae is believed to be responsible for the very low titers of 20-hydroxyecdysone (20-HE), a hormone whose production during the ultimate instar is normally triggered by a drop in the JH titer. Maintenance of high JH titers may also require that elevated rates of JH production be sustained in infected larvae. Similarly, inhibition of 20-HE biosynthesis could be due to a loss of prothoracic gland (source of 20-HE) integrity. We are currently examining these hypotheses.

When compared to other PVs, TrV has a relatively small genome (only 8 DNA circles are seen on agarose gels), a feature that should prove advantageous in the identification of genes involved in host pathologies. In this respect, we are currently working on the identification of mRNAs that are observed only in virus-injected larvae.

SESSION III: MANAGEMENT METHODS / *Bt*, SILVICULTURE AND BIOLOGICAL CONTROL

Effects of food quality on *Bt* lethal and sublethal effects on spruce budworm

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Laboratory rearing of spruce budworm in conjunction with aerial spray of *Bt* indicated that food quality influenced both lethal and sublethal effects of *Bt*. In laboratory work, using Foray 48B treated disks that simulated three balsam fir tree foliage nutritive qualities (high, medium, low) and three levels of *Bt* concentration used in the field (low: 15 BIU, medium: 30 BIU, high: 60 BIU, we found that 15 to 70% of budworm larvae survived from *Bt* exposure. Both the feeding cessation and the *Bt* avoidance phenomenons allowed these larvae to survive. However, these phenomenons were strongly influenced by the quality of the food provided to the larvae. *Bt* efficacy was better at medium food quality than at high or low food quality. Increasing *Bt* concentration from medium to high enhanced *Bt* efficacy at medium food quality only. Moreover, at low food quality, *Bt* had less impact because much of the larval mortality resulted from low food quality. Food quality interacted with *Bt* concentrations on dose acquisition, feeding cessation, *Bt* avoidance, larval development and post-*Bt* exposure food ingestion. Because food quality decreases as spruce budworm outbreak progresses and is influenced by several stand and host tree characteristics such as tree age, flowering, stand thinning, site quality, soil drainage, host species etc., several strategies of *Bt* utilization could be developed based on stand parameters and past disturbances.

Aerial *Bt* spray trials (1x50 BIU, 2x50 BIU (5 d interval), 2x30 BIU (5 d interval), 2x30 BIU (10 d interval) (2.37l/ha)) were conducted in 1996 in the Ottawa region where a new budworm outbreak is expanding. Results from these field trials supported those obtained from laboratory rearings. Preliminary results from foliage chemical analyses suggested that host tree foliage was of good quality for spruce budworm. As suggested from the laboratory rearings with high quality food, *Bt* efficacy, in terms of larval mortality and foliage protection, was not improved by increasing the concentration from 30 BIU to 50 BIU. However, *Bt* efficacy was improved when a second spray (30 BIU or 50 BIU) was conducted 5 or 10 days after the first one. As found in the laboratory experiments, *Bt* had several sublethal effects on spruce budworm. In fact, larvae that survived *Bt* aerial spray treatments had longer development time, which could affect the impact of their natural enemies, lower pupal weight, and lower fecundity than untreated larvae. Moreover, *Bt* treated budworms, not only produced fewer eggs, but when treated with two sprays of *Bt*, their eggs were slightly smaller and their offspring contained slightly less glycogen than control budworms. Because glycogen is used by diapausing larvae to produced cryoprotectants, *Bt* might have some influence on the winter biology of the F1 generation. Ongoing experiments should allow us to test this hypothesis.

Although our conclusions need to be confirmed by additional experiments, our results indicated that the efficacy and the cost of aerial *Bt* spray programs could be optimized by using different strategies of *Bt* utilization (concentration of formulation, number of applications) based on the variables that influence the quality of the food ingested with *Bt* by budworm larvae. For example, because past defoliations affect foliage quality, different strategies could be used depending if aerial spray programs are conducted during the beginning, the midle, or the end of an outbreak. Additional experiments will be conducted as budworm outbreak progresses in the Ottawa region to test this hypothesis.

Spruce budworm feeding behaviour and *Bt* dose acquisition

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We examined the role of larval feeding behaviour in *Bt* dose acquisition. Spruce budworm larvae feed in discrete bouts which vary in length and frequency. For both fourth and fifth instars feeding on fresh balsam fir needles at room temperature, feeding bout duration ranged from 1 to 7 minutes with an average of 2.2 and 2.4 min, respectively. Intervals between feeding bouts ranged from 5 to 50 min for fourth instars and from 15 to 90 minutes for fifth instars. Fourth instars fed on average twice as frequently as fifth instars (mean interval length of 18 versus 36 min, respectively). In the case of fifth instars, interval length was positively correlated with duration of the preceding feeding bout. For every min increase in feeding bout duration there was a 12 min increase in interval length. Dissection of fifth instars at various stages during the feeding cycle demonstrated that feeding bout duration corresponded to midgut loading time. The food bolus remained in the midgut between feeding bouts. Termination of the feeding bout interval was always associated with opening of the pyloric valve and passage of the bolus into the hindgut. The volume of foliage consumed per feeding bout, or meal size, was estimated from the dimensions of the hole left after each feeding bout. The volume of foliage consumed per feeding bout varied from 0.015 to 0.255 mm^3 with a mean of 0.10 mm^3 per fifth instar. Variation in larval fresh weight accounted for some of this variation. Meal size increased with increasing feeding bout duration, but the relationship was too messy to conclude proportionality. In the presence of a *Bt* droplet (Dipel 12L, 120 µm) placed in the centre portion of the needle, the relationship between duration and intervals of feeding bouts prior to droplet ingestion was the same as for needles without *Bt*, suggesting that the presence of the droplet did not alter larval feeding behaviour (i.e., no avoidance). Of the 123 larvae, 108 ingested the droplet within 24 h, 72% of which died without further feeding within 48-72 h. The remaining 28% recovered and resumed feeding but not until at least 24 h after droplet ingestion. The pattern of droplet acquisition varied greatly among individual larvae, both in terms of time of ingestion and number of feeding bouts preceding ingestion, and influenced the effectiveness of the ingested dose (i.e., dose expression). About 50% of the larvae ingested the droplet within 2 h in one or two feeding bouts, 35% ingested the droplet between 2 and 8 h, and the remaining 15% between 8 and 24 h. Mortality of dosed larvae decreased from 85% in the first category to 53% in the last. On average, larvae that died had ingested the droplet in 1.5 feeding bouts as compared with 2.5 bouts for larvae that recovered and survived. Our data suggest that larval susceptibility is somehow related to level of feeding activity. This will be investigated in more detail in the near future.

A simulation model of *Bt* efficacy and parasitoid conservation

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Cooke and Régnière (1996) have developed a model of *Bt* (*Bacillus thuringiensis*) efficacy against spruce budworm which considers the intricate processes of foliage growth, budworm development and feeding, parasitoid development, and the acquisition and expression of lethal and sub-lethal doses of *Bt* by budworms. The model simulates, over the course of a season, the impact of a *Bt* spray on budworm development, densities, defoliation and parasitism. It has recently been modified to simulate double-applications of *Bt*. We tested the validity of the model by comparing predictions to data collected from two double-application trials conducted in western Quebec in 1996. The model accurately depicted the amount of retardation, population reduction, and foliage protection resulting from the sprays. In brief:

- Spray plot 10 was predicted to have 46% defoliation, and it experienced 60%.
- Spray plot 68 was predicted to have 19% defoliation, and it experienced 17%.
- Control plot 75 was predicted to have 71% defoliation, and it experienced 78%.

Had they not been sprayed at all, plots 10 and 68 were predicted to experience 97% and 46%

defoliation. From a management perspective, two key points can be made: (1) plot 10 needed protecting, while plot 68 may not have, and (2) spraying preserved foliage in both plots, but it was particularly beneficial in plot 10. We note in passing that the simulation approach allows direct comparisons between sprayed and unsprayed scenarios in the spray blocks. With simulation, one does not have to resort to tenuous comparisons between sprayed blocks and distant "control" blocks which often differ greatly in terms of budworm densities -as in the present study, where L2 densities per bud were 0.76, 0.29 and 0.36 in plots 10, 68 and 75.

The model shows promise as a decision-support tool. Future modelling will be directed towards (a) optimizing efficacy through the choice of spray deposit characteristics and spray-timing, (b) exploring the impacts of sub-lethal effects of *Bt* on budworm feeding and parasitism, (c) predicting defoliation on a variety of tree species in various conditions, (c) evaluating the effects of *Bt* on various parasitoid species, and (d) determining the impacts on longer-term budworm dynamics.

Cooke, B.J. & J. Régnière. 1996. An object-oriented, process-based stochastic simulation model of *Bacillus thuringiensis* efficacy against spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Int. J. Pest Manag. 42:291-306.

Interactions between large-scale *Trichogramma minutum* releases and spruce budworm as an example of integrated management

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A total of 480 million females of the egg parasitoid, *Trichogramma minutum* Riley, were aerially released on 30 ha of boreal forest infested by the spruce budworm, *Choristoneura fumiferana* (Clem.), in Ontario. Objectives for the release were 1) to scale up aerial application methods for *Trichogramma* and 2) assess the interactions between imposed mortality caused by egg parasitoids and subsequent mortality caused by naturally occurring budworm parasitoids.

Trichogramma minutum were released in parasitized eggs of the factitious host, the Mediterranean Flour Moth, *Ephestia kuehniella* Zell. Emergence of released *T. minutum* peaked at 80%, 5 days after the parasitoid releases. *T. minutum* were active in the release plots up to 15 days after the first parasitoid release based on parasitism of sentinel egg masses.

The mean rate of parasitism of budworm egg masses by *T. minutum* was 68% in 3 treatment plots versus less than 2% in the matching control plots. The reduction in budworm density in the treatment plots at the egg stage in August 1993 was maintained in the overwintering 2nd instar budworms (October 1993) and for the 6th instar budworms sampled in June 1994. An additional 51% of the foliage available in June 1994, was protected in the treatment plots compared to the control plots.

The rate of parasitism by the late-larval tachinid complex, consisting primarily of *Winthemia fumiferanae* Toth. and *Lypha setafacies* (West), increased in the treatment plots in 1994. An increase in parasitism by the late-larval parasitoid complex has been argued to be a required component for a potential budworm population collapse. The effectiveness of most biological control agents may be improved by linking the selection of the biocontrol agent to a vulnerable host stage based on the host's population dynamics, and using the biocontrol agent to complement naturally occurring mortality factors.

Silvicultural control of spruce budworm

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Laboratory rearing of spruce budworm in conjunction with field rearing, gravimetric analyses, transfer experiments, foliage chemical analyses, and

bioassays with individual and blends of chemicals indicated that the greater resistance of young balsam fir trees to spruce budworm compared with mature trees is related to variations in foliar secondary compounds. During the budworm's sixth instar, young trees produce a high quantity of monoterpenes which serve as a mechanism of resistance by reducing the feeding rate of budworm larvae.

Stand thinning was conducted in young (precommercial thinning) and mature (commercial thinning) balsam fir stands in order to manipulate host tree mechanisms of resistance to spruce budworm. Field insect rearing experiments and foliage chemical analyses were conducted in thinned and control plots between one and several years after stand thinning to test if these procedures have the same impact on the spruce budworm-balsam fir system when conducted during or prior to a budworm outbreak.

Both commercial and precommercial thinnings have positive short-term (one year after the treatment) effects on budworm larval performances and host tree defoliation, but for different reasons. Commercial thinning stimulates larval food ingestion, apparently by reducing the amount of foliar monoterpenes, while precommercial thinning increases larval survival, apparently by reducing the amount of foliar tannins. Based on these results, thinning should be avoided during a spruce budworm outbreak.

Two years after the commercial thinning and three years after the precommercial thinning, trees were less vulnerable to spruce budworm because there was an increase in foliage production that exceeded the increase in defoliation, hence a net gain in foliage. These results suggest that thinning could increase the resistance of balsam fir trees to spruce budworm if it is conducted several years prior to budworm outbreak, but the same silvicultural procedure could reduce the resistance to the insect if it is conducted during an outbreak. Several years of field and laboratory work will have to be conducted to determine how long the increase in host tree resistance to spruce budworm will last.

SESSION IV: SPATIAL ANALYSIS, HISTORICAL RECORDS AND DSS

Spatial analysis of spruce budworm pheronome trap

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Each year pheromone-baited traps are distributed throughout the range of the spruce budworm in North America by cooperating agencies and the number of male moths captured is determined. However, these point data cannot be used to analyze spatial patterns in a geographic information system (GIS). A series of software tools, that convert the point data into contour maps for GIS use, have been developed and incorporated into a user-friendly graphic user interface (GUI). Opening the database module from the GUI allows the user to add, edit or delete trap catch and related data. In the geostatistical module, for a subset of the data (i.e., by year and region), the spatial relationship between point data is described using a variogram model and data between points is interpolated using a technique known as kriging. IDRISI, an inexpensive, fully-functional, raster-based GIS is used to display, manipulate and analyze the kriged output data. The resulting maps have contour intervals showing estimated areas of equal moth densities or 'isomoths'. CorelDRAW!, the vector-based structured drawing program, is used to prepare high quality maps for reporting trap catch results.

As the first step in developing a logistic regression model for predicting spruce budworm defoliation, individual annual defoliation maps (1941-1994) provided by the Forest Insect and Disease Survey Unit were summed in the GIS to produce a frequency map showing proportion of years defoliated. This frequency of defoliation map was combined with individual defoliation maps and interpolated pheromone maps (1986-1994) to create

a logistic regression model. To predict defoliation for 1995, the logistic regression model was solved using the previous year's defoliation map (1994) and the previous year's pheromone catch (1994) as input variables. The resulting map depicts the probability of defoliation for Ontario in 1995. This probability map was compared with the observed defoliation map for 1995. For areas where estimated probabilities were available, there was good correlation between observed defoliation and probability values greater than 0.20.

Ontario historical data

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In Ontario, the current policy implies that forests should be managed in a way to mimic natural disturbances; however, this requires understanding the patterns of natural disturbances in time and space. Our long-term goal is to develop a spatio-temporal model of spruce budworm defoliation, one of the major natural disturbances in eastern Canada.

Historical data of spruce budworm defoliation have been mapped in Ontario since 1941 by FIDS (the Forest Insect and Disease Survey unit of the Canadian Forest Service) using aerial survey of defoliated areas. The resulting maps have been digitized and saved in a GIS (Geographical Information System) database. Different data sets related to various environmental variables such as climate, vegetation, and elevation have been added to the database. These data will be used to build a stochastic, spatially explicit, landscape-level model of defoliation by the spruce budworm.

Preliminary results about the spatio-temporal occurrence of defoliation in Ontario indicate three distinct areas of the province where spruce budworm defoliation has been common over years. These areas are located, from east to west: in central Ontario, around Lake Nipigon and around lac Seul. These three areas are separated by two zones of apparently little defoliation.

A preliminary analysis suggests that two spruce budworm outbreaks have been recorded during the period of time covered by the database. These two outbreaks appear to have started in central Ontario and moved progressively to the west of the province over time.

A spatial analysis of the ESBW historical data of Québec

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The ESBW DSS under development by the CFS in Fredericton, NB, estimates accumulated benefits accruing to a forest stand from a protection scenario applied until scheduled harvest. The DSS simulates and compares stand growth under budworm-protected and budworm-unprotected scenarios to estimate these benefits. A critical factor in the simulations and estimations is the forecasted budworm epidemic. The DSS currently applies the same 30-year budworm cycle pattern to all stands, regardless of their spatial location or eco-physiological condition. A spatial analysis of historical defoliation patterns may reveal spatial patterns in the defoliation and/or eco-physiological conditions associated with the defoliation patterns. The results from such an analysis could be used to provide improved, location-specific forecasts of budworm outbreaks to the DSS.

Our data are the 1965-1996 SBW defoliation records for Quebec. A grid of 222 columns and 84 rows divides the province into 9502 cells (58 km^2 area). Within each cell the defoliation category (none, light, moderate, heavy, low host mortality visible, high host mortality visible) has been recorded each year. Each cell has also been

categorized according to its eco-physiographic characteristics (Robitaille and Saucier 1996).

We examined the data for very large scale trends in the first-year-of-defoliation in the episode. Such trends should be removed prior to any spatial analysis in order to satisfy requirements of stationarity (Isaaks and Srivastava 1989, Legendre 1993). A second-order polynomial was used to estimate the trend, and the defoliation pattern within each cell was rescaled from its original 1965 - 1996 time scale to a time scale relative to the predicted first-year-of-defoliation for the spatial coordinates of the cell.

We used disjoint clustering (SAS: PROC FASTCLUS) and an agglomerative clustering procedure (SAS: PROC CLUSTER) to group similar defoliation patterns while maintaining 80% of the total variability present in the patterns. The cells of each of the 32 clusters that emerged from the procedure were seen to have a high degree of spatial contiguity. Our analysis will next look at potential associations between clusters and the eco-physiographic characteristics of the member cells of the clusters.

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Using dendrochronology to investigate spatio-temporal dynamics of spruce budworm outbreaks

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Dendrochronology is the science of dating events and environmental variation that occurred in earlier periods by the comparative study of growth rings in trees and aged wood. The object of this presentation is to show the potential use of this technique in investigating spatio-temporal dynamics of spruce budworm outbreaks. Dendrochronology is subdivided into many subfields. Among the most important are dendroclimatology, which consists of reconstructing past climate using ring width or density, and dendroecology which encompasses all the subfields which use tree rings to study ecological problems and the environment. For example, the study of hydrology, dendrohydrology, geomorphic processes (dendrogeomorphology), fire, forest and stand dynamics and so on. Dendrochronology has been widely used to reconstruct past insects outbreaks by comparing the radial growth curves of host trees with nonhost trees. Important chronologies showing past eastern spruce budworm outbreaks have been developed by Robert Blais. The western spruce budworm has been extensively studied by Thomas Swetnam and his collaborators. Other insects that have been studied include the forest tent caterpillar, the larch sawfly, the Swaine jackpine sawfly, the larch bud moth in Europe, etc. The majority of these studies have used the reduction in ring width to study the timing, the duration and the severity of outbreaks. More information on outbreaks can be found by analyzing earlywood and latewood, and by using densitometry, stem analysis and age structures of populations in an area. Since earlywood is generally formed from trees reserves and latewood is formed as a result of the current years' growth conditions, defoliation is more likely to be registered first in the latewood. This will be reflected in the density profile of a sample. Stem analysis has shown that reduction of the latewood and of the ring width initially appears in the upper part of the tree, where the foliage is eaten first, and is registered 2 to 3 years later at the base of the tree. The study of ring width gives reliable results on the timing and duration of the outbreaks but is not really adequate in evaluating the intensity of an outbreak since we work only with surviving trees. It does not give us data on the relative importance of outbreaks nor on the amount of mortality in the population of an area. The analysis of age structures using stratified random sampling is more useful in this respect since we can evaluate the percentage of the remnant populations dating back to past outbreaks. The major limitation of dendrochronology is the age of the trees. Since we work with host trees, which are generally killed by

the budworm, especially balsam fir, we can have difficulties in finding old specimens. To overcome this problem, we use crossdating of well preserved dead trees (Picea sp. in particular) found in old wood buildings, in the bottom of lakes, in landslides, peat bogs, etc. Using these samples, we were able to reconstruct the chronology of spruce budworm outbreaks back to the middle of the 17th century. New samples from a lake are even older. Another limiting factor is the difficulty in separating insect effects from climatic effects especially when growth conditions are not favorable such as during dry summers. This problem has led to misclassification of some outbreaks, therefore it is of prime importance to properly characterize the impact of defoliation on ring infrastructure. To do that, we will study the formation of the ring in relation to the climatic environment and defoliation throughout the growing season by using electronic dendrometers, and we will compare the ring formation in trees of known defoliation history. Preliminary results indicate that we can register quite accurately the beginning of the defoliation using latewood reduction. Using all this information, we have put forward a study of the spatio-temporal dynamics of past outbreaks. A sample design including a plot every 50 km along 5 transects distributed in the principal ecological regions of the province of Quebec has been developed. The synthesis of all the known chronologies from Ontario and Quebec and the preliminary results of this study indicate that the smallest ring found during a severe outbreak is generally synchronous across the studied area. There are some differences however in the timing of outbreaks, especially the ones that are recognized as being less severe, for the different locations. Eventually, by refining this method to use the beginning of defoliation combined with a GIS, we think that dendrochronology can help us to better understand the dynamics of past outbreaks, which is a prerequisite to our understanding of present and future ones.

Sources of variation in western spruce budworm return intervals: perspectives for modelling long-term dynamics of tree populations

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Insect and disease managers and forest planners need to project forest conditions over multiple decades or centuries in order to evaluate the effects of succession, disturbance events, or various management alternatives. Long-term data records can be used to determine how frequently and severely biotic and abiotic disturbance agents perturb the system. Dendrochronologic reconstructions of disturbance events can be used in lieu of population data records in the study of insect outbreaks. These reconstructions can also be used to calibrate or test forest dynamics models. This presentation reported on comparisons of western spruce budworm (WSBW, *Choristoneura occidentalis* Freeman) dynamics models and long-term forest projections with tree-ring data.

The Forest Vegetation Simulator (Wykoff *et al.*) is used in western North America to project the development of forest stands for a variety of management options and pest agents, including WSBW. However, this model system lacks necessary information on budworm outbreak periodicity. During the development of a WSBW defoliation model (see poster abstract by Lynch *et al.*), algorithms describing outbreak return interval variation were developed from tree-ring data from the western United States (Swetnam and Lynch 1989, 1993; Swetnam *et al.* 1995). Return intervals, defined as the elapsed period between commencement of two succeeding outbreaks, were inferred from the tree-ring reconstructions, with initial years of reduced growth serving as proxy for the initiation of budworm outbreaks. Between-site variation occurs in outbreak return intervals, including interval length and outbreak onset, duration, and cessation. Similar variation occurs between watersheds and mountain sub-ranges and between trees, but this variation is not currently included in the model system. This information can be incorporated in similar model systems, formulated as either means and variance terms, or as probability distribution functions.

Another test of model results with the tree-ring reconstructions was performed using the Ludwig, Jones and Holling (LJH, 1978) model of budworm-forest dynamics. LJH parameterized the interaction between spruce budworm (*C. fumiferana* (Clemens)) populations and the forest as three linked differential equations governing the forest canopy, the budworms, and the forests' energy potential. This model produces a stable limit cycle with a regular period of about 40 years. Although superficially similar to budworm population dynamics, the regular periodic pattern produced by this model is very different from observed cycles, which vary greatly in interval length, outbreak duration and amplitude, and resurgent outbreaks. However, when the model is parameterized for western forest conditions and WSBW, and with drought added as an exogenous pulse to the forest canopy equation, the model more closely mimics observed cycles (Swetnam *et al.*, in preparation). This result indicates the LJH model may be a reasonable, although simplified, approximation of budworm-forest dynamics, and that the role of climatic variability in budworm outbreaks may operate primarily through influences on forest trees, rather than directly on insect populations.

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A decision support system for spruce budworm and forest management

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Composition and age structure of much of the spruce-fir forest in eastern Canada is related more to past spruce budworm (*Choristoneura fumiferana*) outbreaks than to harvesting or wildfires. These outbreaks are a natural component of forest succession, but must be taken into account in forest management planning, if plans are to be accurate. Managers need tools to predict outbreak occurrence and effects on forest development, to ensure that expected timber supply/stand types will be present at the expected time of harvest/other usage, and to utilize silviculture and management planning to reduce the severity of future outbreaks. We developed a budworm and forest management decision-support system under a 5-year multi-agency project supported by Canada's Green Plan. Our DSS design philosophy was to build individual tools targeted at specific forest management problems and to integrate these tools under an interactive graphical user interface and a GIS (currently implemented using Arc/Info). Two components of this DSS, a Protection Planning System and a dynamic Inventory Projection System are described.

The Protection Planning System (PROPS) provides a systematic methodology for designing forest protection (insecticide use) under the threat of spruce budworm. It is based on quantifying the marginal timber supply benefits of protecting stands. This methodology comprises three steps: 1) measuring the impacts of defoliation, 2) calculating the protection priority for each stand, and 3) evaluating protection strategies. A defoliation-based stand growth model (STAMAN) and a timber supply model (Woodstock or FORMAN+1) are used to forecast forest development with and without

defoliation. Protection priority (m^3/ha) is then calculated for each stand based on both direct (stand-level) and indirect (harvest queue disruption) marginal timber supply impacts associated with applying protection. This priority value is used as a mapping attribute to generate protection planning maps, and the user can digitize protection blocks into the DSS and quantify m^3/ha benefits. PROPS is being operationally implemented for all Crown forest in New Brunswick between 1996 and 1998, with funding for database set-up provided by NB DNRE and forest industry. Strategic planning analyses evaluating the consequences of budworm outbreak occurrence, protection policy, and of protection exceeding the target foliage retention level of 60% or of part of the landbase not being protected have been conducted.

The Inventory Projection System allows evaluation of effects of budworm outbreak and insecticide use scenarios on the forest inventory at user-specified times in the future. Stand dynamics are governed by volume yield curves and a set of rules which determine effects of two severities of budworm outbreak, protection, and successional changes. Display of current and projected stand attributes, attribute changes, different scenario results, and generation of thematic maps is under the user's control within a graphical user-interface. Common queries and map composites are prepackaged and selectable from a menu, and several forest performance indicators in the areas of landscape biodiversity, insecticide use, and timber supply perturbation are being developed. The idea here is to provide an efficient and effective way to visualize alternative future budworm outbreak and management scenarios.

POSTER SUMMARIES

Relationships between change in fire frequency and spruce budworm outbreak severity in the southeastern Canadian boreal forest

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We are presenting a simple empirical model that allows for an estimation of spruce budworm outbreak severity in relation to fire frequency and site characteristics. The occurrence of a recent spruce budworm outbreak at lake Duparquet (48°30'N, 79°20'W, elevation 300 m) in northwestern Quebec made it possible to reconstruct stand composition before the outbreak as well as mortality of balsam fir due to the outbreak. Balsam fir basal area increased with time since fire in all site types but at increasing rates: rock and shallow till < till & mesic clay < hydric clay. Severity (% loss of basal area due to the outbreak) increased with time since fire, but did not vary by site type. The increasing abundance of balsam fir with time since fire is mainly responsible for this increase in severity. Severity for a specific basal area is, however, lower for stands from the more recent fires suggesting a significant residual effect of time since fire. A landscape model that integrates severity of outbreak in stands of different ages is being developed. Both absolute and relative losses of basal area increased with the length of the fire cycles. According to this model, changes in the fire cycle seem to explain a large portion of the spatio-temporal variations observed in outbreak severity in the southeastern boreal forest of Canada.

Interactions between *Bt* and food quality on spruce budworm biological performance

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A recent increase of spruce budworm population levels in western Quebec forecasts the development of a new generalized outbreak. Therefore, important programs of aerial sprays of *Bt*, *Bacillus thuringiensis*, will have to be applied in order to protect wood resources in the next few years. *Bt* is a specific insecticide for Lepidoptera and thus induces low negative impacts on the environment. However, *Bt* treatments are not always effective, mostly because of *Bt*'s intrinsic biological characteristics. In order to be effective, *Bt* has to be ingested by the insect. Several insect species stop eating before ingesting a lethal dose, following which they resume eating when *Bt* is no longer effective.

We proposed to study *Bt* efficacy according to different parameters and factors. First, we hypothesized that *Bt* efficacy could be influenced by the chemical composition of the insect's food. Second, larval sex and timing of *Bt* application could affect *Bt* efficacy. In order to test these hypotheses under laboratory conditions, we reared larvae on artificial diets of different nutritive qualities and provided them with different concentrations of *Bt*. Preliminary results indicate a very high interaction between *Bt*, food quality, larval behaviour and performances. Male larvae seem to be more vulnerable to *Bt* than the female ones. Moreover, sixth-instar larvae are apparently more vulnerable than fourth-instar larvae. Third, we hypothesized that ingestion of a sublethal dose of *Bt* negatively affected 1) the reproductive performance of spruce budworm (fecundity and fertility) and 2) the overwintering survival of their offspring (survival rates, lipid and glycogen reserves). Different aerial sprays of *Bt* were applied during the summer of 1996, and in order to study the previously mentioned parameters, pupae were brought back to the laboratory. Two applications of *Bt* within 5 or 10 day intervals negatively affected pupal fresh weight, fecundity and egg mean weight compared to the control group and one application of *Bt*. Two applications of *Bt* also proved a better foliage protection.

The impact of stand thinning on the resistance of balsam fir trees to spruce budworm

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Spruce budworm growth development and food utilization were studied in young and old balsam fir stands using laboratory and field experiments. Laboratory bioassays were used to confirm the role of monoterpenes in the apparent resistance of young balsam fir trees to the insect. Stand thinnings were then carried out in young and mature stands to modify host tree resistance.

Changes in juvenile hormone esterase activity and ecdysteroid titer in larvae of the spruce budworm, *Choristoneura fumiferana*, parasitized by the *Tranosema rostrale*

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Last-instar *Choristoneura fumiferana* larvae parasitized by *Tranosema rostrale* early in the stadium display retarded development and failed to initiate metamorphosis. Similarly, injection of the wasp's calyx fluid (CF) into healthy caterpillars induces a dose-dependent delay in pupation, which can be abolished by prior treatment of CF with UV and the DNA cross-linker psoralen. These results suggest that the wasp's polydnavirus is the factor responsible for the observed developmental disruptions.

In an effort to identify the physiological processes that are perturbed by *T. rostrale* CF, we examined the effects of parasitism and injection of CF on host plasma juvenile hormone esterase (JHE) activity and ecdysteroid titers in last-instar budworms. Under our experimental conditions, control larvae displayed only one peak of JHE activity (~ 30 nmol JH III/min/ml), which occurred on day 4 of the last stadium. In saline-injected animals, a similar peak was observed, but on day 5. In larvae parasitized or injected with CF (0.5 female equivalent) on day 1, levels of JHE activity were depressed during the entire stadium, with a somewhat greater reduction induced by CF injection (~ 3 nmol JH III/min/ml on day 4) than parasitism ~ 8 nmol JH III/min/ml on day 4). Similarly, parasitism and injection of CF both completely prevented the rise in hemolymph ecdysteroid titer observed in control and saline-

injected larvae between day 3 and day 7 (rises from ~ 25 to 500-700 pg 20-hydroxyecdysone equivalents ml hemolymph). Synthetic "Growth Blocking Peptide" (purified from *Pseudaletia separate* parasitized by *Cotesia kariyai* 1995, J. Insect Physiol. 41: 1) injected in healthy *C. fumiferana* larvae had a very limited effect on JHE activity.

Hormonal regulation of reproduction in *Choristoneura fumiferana* and *C. rosaceana*

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Reproduction and migration play important roles in the population dynamics of the eastern spruce budworm (SBW), *Choristoneura fumiferana.* We examined the role of juvenile hormone (JH) in the reproductive activities of both this species and the oblique banded leafroller moth (OBL), *C. rosaceana,* which shares many life-history traits with *C. fumiferana* but which has not been observed to undertake migratory flights. In females of both species, corpora allata (CA) became activated near the end of the pupal stage. In SBW, a large increase in both JH I and JH II production was seen in the hour following emergence, with the upward trend continuing until the 12th hour of adult life. In 1-, 3-, and 5-day-old virgins, overall rates of JH biosynthesis remained high, but the proportion of JH I decreased while that of JH III increased. In OBL females, the trend was similar except that full activation of CA was not seen until day I and the proportion of JH I produced was generally much lower than in the SBW. In both species, the growth of basal oocytes paralleled the changes observed in JH production, suggesting a role for JH in ovarian growth. Decapitation of females at emergence reduced egg maturation in the next 48 hours as compared to controls, whereas a topical application of the JH analogue methoprene enhanced it, in both species. Vitellogenin (Vg) was detectable in the hemolymph 2-3 days before emergence, before activation of the CA, suggesting that JH is not essential for Vg synthesis in these two species. Indeed, decapitation of females on the 5th day of the pupal stage did not prevent accumulation of Vg in the hemolymph. Mating on day 0 caused a decrease in Vg titers and an increase in egg production, most obvious on day 5 and seemingly more pronounced in *C. fumiferana.* However, mating had no significant effect on *in vitro* JH biosynthesis 1, 3, and 5 days after mating. Surprisingly, mating caused a transient but significant increase in JH esterase activity on day 1, in both species. These results raise interesting questions about whether or not JH titers increase after mating in these two tortricids.

Male larval nutrition influences the reproductive success of both sexes of two *Choristoneura* species

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Work on the polyphagous species *Choristoneura rosaceana* (Delisle and Bouchard 1995, Oecologia 104: 508-517) demonstrated that while different larval host plants did not affect the proportion of virgin males of acquiring a mate, it had a significant impact on their ability to remate. Furthermore, the total fecundity and fertility of females mated with males reared on poor quality hosts (i.e. hazelnut) was significantly lower than those mated with males fed on high quality hosts (i.e. striped maple). A parallel study was undertaken to examine the effect of larval food quality in a related, eruptive oligophagous species, *C. fumiferana* (Delisle and Hardy 1997, Functional Ecology 4: in press). The reproductive success of both sexes was compared when males were reared on the same host species (balsam fir) but varying the foliage quality, to reflect endemic and epidemic phases in the population cycle. Females that mated with males reared on high quality foliage were more likely to remain refractory following first mating. Furthermore, the reproductive success of females mated with males reared on poor larval food were significantly lower than for conspecifics mated with males provided with high quality food during larval development. These results suggests that male quality significantly influences reproduction in both *Choristoneura* species.

Overwintering dormancy: an important phase in the life cycle of spruce budworm

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Although the spruce budworm spends 2/3 of its life cycle in overwintering, studies of this part of its life cycle have been few. Recent efforts have been made to fill this significant data gap. Our experimental results from physiological studies on diapause development, cold-hardiness, metabolic changes in cryoprotection agents and energy reserves as well as from ecological studies on overwintering survival indicate that overwintering dormancy is not a static phase and many potential factors can effect overwintering survival of the species. Our study points out that a better understanding of the life cycle of the insect cannot be fully reached without detailed knowledge on the winter biology of the spruce budworm.

Regeneration dynamics following budworm outbreaks

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Models of stand dynamics have been proposed for eastern fir forests in which the budworm causes a cycling of balsam fir stands. However, these forests are principally composed of balsam fir. In the boreal forest of western Quebec there is a greater number and greater abundance of other tree species. In these forests, openings created by the budworm are larger and the percentage of forest in canopy gaps increases with time since fire. Balsam fir regeneration density was found, however, to be negatively correlated to gap size. Its growth and changes in seedling architecture were found to be greatest in sudden openings and much slower in gradually created gaps such as caused by the budworm. In large gaps, the abundance of shrub species such as *Acer spicatum* may retard the recruitment of seedlings or reduce future stand density. At the tree level, budworm-created gaps maintain a small proportion of white spruce and birch while cedar increases in abundance. In the southern boreal forest spruce budworm outbreaks (in the absence of fire) will not lead to a continuous cycling of balsam fir forests.

The history of spruce budworm outbreaks

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The knowledge of the spruce budworm outbreaks is limited in time and space in boreal forests of Quebec. The information about the occurrence or absence of past outbreaks is important to compare the spatio-temporal history with the present. The analysis of tree-rings from living spruces and balsam firs rarely gives chronologies of more than 200 years. Dead trees (which can be found in old wood buildings or in lakes) can be used to get longer tree-ring series. Until now, the history of spruce budworm outbreaks has been reconstructed for the last three centuries by using a chronology from spruce sp. (living trees and historical material). This chronology shows two outbreaks in the 18th century, possibly three in the 19th century and three outbreaks in the 20th century. Longer chronologies are necessary to analyze the stability or changes in the spruce budworm outbreak frequency.

The reaction of host trees after spruce budworm outbreaks

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The impact of spruce budworm defoliation in the annual radial growth at the stembase or at breast height is well documented. Better understanding of a tree's response from the crown all the way down

to its roots is now available. However, the relation between the defoliation and the anatomical sign in the tree-rings in mature forest trees is still unknown. The radial growth of balsam fir has been analyzed along the stem from four permanent plots of the New Brunswick Department of Natural Resources and Energy in New Brunswick. The defoliation of each tree has been monitored for the last 13 years and the defoliation for each site has been registered for 26 years. The tree-ring patterns of balsam fir were analyzed along the stem to identify a time delay of reduction from the stem crown down to the stembase. The reduction at different stem heights was also compared to the defoliation data. The first defoliation registration in the tree samples was found in the upper crown region, with a reduction of the latewood. A reduction of the tree-ring width occurred in the same region one year later. With an additional one- or two-year delay, a reduction of the tree-ring width was registered at the stem base. The preliminary results show a reduction of the tree-rings occurring in the highest part of the crown the same year a severe defoliation occurred.

Bud-Lite: predicting defoliation by western spruce budworm

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This new model projects annual defoliation for western spruce budworm, *Choristoneura occidentallis* Freeman from key factors and processes, including weather, stand conditions, geographic location, natural enemies, and regional budworm population levels. Defoliation effects can be simulated when Bud-Lite is used in conjunction with the Damage Model in the Forest Vegetation Simulator - Budworm Model System (FVS-BMS). FVS-BMS projects insect population dynamics, defoliation, defoliation effects to forest stand growth and yield, and long-term vegetation dynamics. During development of the defoliation model, input and output options of FVS-BMS were greatly expanded, as was the range of available weather stations. The development of the initial, single-stand version of this model will be completed soon, and work on a multiple-stand version is planned.

Forest, species, and site effects on stand susceptibility to spruce budworm in New Brunswick

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The mosaic of forest stands across the landscape has been said to be an important factor which influences the impact of the spruce budworm. Forty spruce-fir stands located in north-central New Brunswick were measured for defoliation from 1989 to 1993 to determine tile effects of landscape (softwood, mixedwood), stand (balsam fir, spruce), and site (poor, good) conditions on stand susceptibility to spruce budworm. Landscape type was classified into one of two classes based on vegetation assessment within a 1 km radius of the sample stand: softwood (> 80% spruce/fir with minor components of other softwood species), or mixedwood (< 70% spruce/fir and > 30% hardwood). The spruce and balsam fir stand types consisted of $\geq$ 90% spruce fir with spruce $\geq$ 70% for the spruce stands and fir $\geq$ 70% for the fire stand. Site quality was based on moisture and nutrient regimes with moist/rich soils classified as good sites and wet/poor classified as poor sites. ANOVA was used to analyze the dependent variable defoliation for each year. Landscape did not significantly affect stand susceptibility; however, the interaction between landscape and stand type was found to be significant ($p < 0.0359$) for years 1989, 1990, and 1991, with an average of 14% more defoliation for fir stands in mixedwood than in softwood landscapes and 8% more defoliation for spruce stands in softwood than in mixedwood landscapes. Stand type was a significant ($p < 0.0095$) factor for all 5 years, with an average of 14% more defoliation in fir than in spruce stands. Site conditions were also significant ($p < 0.0466$) for all 5 years, with 10%

more defoliation on good than poor quality sites. Proximity to the nearest hardwood stand was also analyzed for effects on stand susceptibility. Patchy, light to moderate defoliation associated with declining budworm populations in New Brunswick may explain the landscape effects found in this study. Tree phenology and foliage nutrient quality could possibly account for the defoliation effects of stand and site type, respectively.

Accuracy of aerial sketch mapping estimates of spruce budworm defoliation in New Brunswick

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The accuracy of aerial sketch mapping estimates of spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation was evaluated from 1984-1993 in 222-325 sample plots in, spruce *(Picea sp)*- balsam fir *(Abies balsamea* (L.) Mill.) stands in New Brunswick. Operational aerial defoliation estimates were used, wherein all productive forest in known budworm infestation zones was surveyed each year from small aircraft with flight lines 2-5 km apart, and rated in classes of nil (0- 10%), light (11-30%), moderate (31-70%), and severe (71- 100%). Aerial defoliation estimates were compared with binocular estimates of current defoliation for an average of ten trees/plot (range 5-20). Overall, 56% of plots were correctly rated by aerial sketch-mapping in four classes (nil, light, moderate, and severe), with 37% of the plots underestimated and 7% overestimated. The predominant error (26% of plots) was rating defoliation as nil (0-10%) from the air when it was actually light (11-30%). This error was deemed not important in terms of predicting tree response, since data from the literature indicated that defoliation that represents less than 30% did not cause mortality, although, if continued, it would reduce growth. Using three defoliation classes (by combining nil-light, 0-30%), 82% of the plots were correctly classified by aerial sketch mapping. The probability of correct aerial classification of defoliation was significantly affected by defoliation class, weather conditions prior to and during observation flights, and the defoliation class x weather interaction. It was concluded that aerial sketch mapping of spruce budworm defoliation is a viable technique that can be used for both surveys and decision support systems that estimate forest response to budworm outbreaks and management activities (MacLean and MacKinnon. 1996. Can. J. For. Res. 26: 2099-2108).

Implementation of the spruce budworm D.S.S protection planning system for crown forest in New Brunswick

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One component of the Spruce Budworm Decision Support System is presented, which helps plan forest protection using the biological insecticide *Bt* against spruce budworm. The Protection Planning System (PROPS) calculates the marginal timber supply benefits of protecting individual stands, using a defoliation-based stand growth model and a timber supply model. Protection priority (m^3/ha) is calculated for each stand based on both direct (stand-level) and indirect (harvest queue disruption) marginal timber supply impacts associated with applying protection.

This priority value is used as a mapping attribute to generate protection planning maps in ARC/INFO and ArcView 2.1, and the user can digitize protection blocks into the DSS and quantify m^3/ha benefits. PROPS is being operationally implemented for all Crown Licenses in New Brunswick between 1996-98, with funding for database set-up provided by the New Brunswick Department of Natural Resources and Energy, the forest industry, and Forest Protection Ltd. The system will be demonstrated using strategic planning and sensitivity analyses conducted to assist in setting protection policy for two test land bases in northern New Brunswick. Analyses determined the effects on forest growing stock and sustainable harvest levels of insecticide use not

meeting foliage targets (defoliation exceeding the 40% maximum target by 10-50%) and that part (0, 20, 40, 60, 80 or 100%) of the landbase is not being protected. Timing and severity of future spruce budworm outbreaks can cause up to 100% uncertainty in spruce-fir timber supply, and sustaining planned harvest levels will require an aggressive protection program during the next outbreak, expected about the year 2000. Sustainability of harvests about 15-20 years into the future is particularly sensitive to budworm effects.

Effects of stand and site characteristics on susceptibility and vulnerability of balsam fir and spruce to spruce budworm in New Brunswick

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The relation of spruce budworm *(Choristoneura fumiferana* (Clem.)) defoliation, and host tree growth and mortality, to soil drainage, tree species, location (budworm outbreak status) and productivity class were examined in 356 spruce (*Picea* sp) balsam fir *(Abies balsamea* (L.) Mill.) permanent sample plots in New Brunswick. Tree species, location and drainage class were significantly related to susceptibility to spruce budworm, which was quantified using defoliation levels from 1985-88. On average, balsam fir sustained 6-9% more current and calculated cumulative defoliation than white spruce (*Picea glauca* (Moench) Voss) and 15-19% more than red (*Picea rubens* Sarg.) or black *(Picea mariana* (Mill.) B.S.P.) spruce. Soil drainage and location (active budworm outbreak versus more lightly defoliated areas) were each significantly related to two out of three defoliation variables and also showed significant interaction effects. Moderate to well-drained sites sustained 7-17% more current and 5-7% more cumulative defoliation than imperfectly or poorly drained sites. When pooled for species, rich sites sustained significantly higher current and calculated cumulative defoliation than poor or medium sites, and rich sites had higher visual cumulative defoliation than poor sites. Soil drainage showed significant main and defoliation x drainage interaction effects on both mortality and net basal area change. When pooled for stand type, imperfectly drained stands under moderate defoliation sustained significantly higher mortality and lower net basal area change than moderate to well-drained ones. Within stand types, drainage effects were significant only for white spruce under light defoliation and spruce-fir under moderate defoliation, with no significant differences occurring for balsam fir, red spruce, black spruce, or fir-spruce stand types. Neither stand types no productivity class showed strong effects on vulnerability; the lack of stand type effects was probably because defoliation did not exceed moderate levels during the study period.

Molecular analysis of the overwintering diapause in the spruce budworm

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The spruce budworm, *Choristoneura fumiferana,* exhibits an obligatory overwintering diapause in the second instar larva. The role of proteins and carbohydrates associated with this overwintering diapause was investigated. The *C. fumiferana* larva produces large quantities of two hexameric proteins (sub-unit size 72 and 74 kDa) that are diapause related. These proteins accumulate in the first instar larval hemolymph beginning at four days after emergence and reach maximum levels by seven days. High levels of these proteins are maintained throughout diapause. The mRNAs (2.4 kb) coding for these proteins were present in large quantities during all seven days of the first instar but they decreased to undetectable levels as soon as the larvae molted to the second instar and entered diapause. The mRNAs reappear in the middle of the last larval instar for 2-3 days before they disappear once again.

We have used a differential display of mRNAs technique to identify genes whose mRNAs either increase or decrease during overwintering diapause.

Two of these genes are identified as an insect chaperonin and defensin. Chaperonins have been shown to be involved in the proper folding of proteins. Defensins, on the other hand, are proteins that have antibacterial activity and are induced in response to bacteria and/or stress. This research was supported by the Canadian Forest Service, and the Science and Technology Opportunities Fund.

Cloning and expression of ecdysone receptor and ecdysone-inducible transcription factors from the spruce budworm, *Choristoneura fumiferana*

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We cloned three members of the steroid hormone receptor superfamily: *Choristoneura* ecdysone receptor (CfEcR), *Choristoneura* hormone receptor 2 (CHR2) and *Choristoneura* hormone receptor 3 (CHR3) from the spruce budworm, *Choristoneura fumiferana.* The mRNAs for these three receptors increase in abundance during the ecdysteroid peaks for embryonic, larval, pupal and adult molts but not during the intermolt periods. 20-hydroxyecdysone (20E) induces the expression of CfEcR, CHR2 and CHR3 mRNA in CF-203 cells. The molting hormone analog, RH-5992, also induces the expression of CfEcR, CHR2 and CHR3 mRNA in the midgut, fat body and epidermis of *C. fumiferana.* The induction pattern for each of these receptors is similar in both *in vitro,* in response to 2OE, and *in vivo,* in response to RH-5992. However, the time course of ecdysone-induction for each of these receptors is different. CfEcR was induced within an hour of exposure to 20E or RH-5992, and reached maximum levels after 3 hours, after which it decreased to normal levels after 6 hours. CHR2 mRNA was induced within an hour after exposure to 20E or RH-5992, and reached maximum levels after 3 hours followed by a decrease after continuous exposure for 6 hours. CHR3 mRNA started increasing after 3 hours and rose to a maximum level in 6 hours. After continuous exposure to 20E or RH-5992 for 12 hours, the mRNA levels started declining. Another difference observed among these three receptors is that CfEcR binds to the hsp27 ecdysone response element, but CHR2 and CHR3 bind to the AGGTCA core sequence as monomers. This research was supported by the Canadian Forest Service, and the National Biotechnology Strategy Fund.

Plaque purification of T3 isolate of a nucleopolyhedrovirus

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The occlusion bodies (OB) of T3 nucleopolyhedrovirus (NPV) obtained from Dr. J. Valero (Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre) were fed to *Choristoneura fumiferana* larvae, the infected larvae were bled, and the diluted infected hemolymph was used for plaque purification. Seven plaques have been isolated by plaquing three times in CF-70 cells, and the DNA isolated from OB and budded virus has been tested by the Restriction Enzyme (REN) analysis using Hind III, and has been found to be similar to *Cf*MNPV Inf–. Four plaques have been isolated by plaquing three times in CF-203 cells. Two of these plaques produced OB in these cells. The DNA isolated from OB from these two plaques was tested by the REN analysis using Hind III, and was found to be similar to *Cf*MNPV Inf+. The virus from the other two plaques isolated from CF-203 cells lysed these cells when we tried to amplify it. The virus from one of these plaques produced classical apoptosis accompanied by blebbing and nuclear fragmentation similar to that reported by Palli *et al.* (J. Insect Physiol. 42: 1061-1069, 1996), and the virus from the other produced apoptosis-like cell death similar to the one produced by *Ac*MNPV (Palli *et al.*, Virology 222: 201-213, 1996) and by CfMNPV Inf- (Palli *et al.*, unpublished data). Further characterization of these two plaques is underway. Six plaques have been isolated by plaquing three times in CF-124T cells. The virus from these plaques will be amplified in CF-124T cells and then analyzed by REN to check the identity of the progeny virus. Once the characterization of virus from all the plaques has been completed, we will test them for infectivity to the spruce budworm

larvae. This research was supported by the Canadian Forest Service and Bio-Sag Inc.

Defoliation and growth of balsam fir in mixed stands

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Changing stand composition by increasing the hardwood content has been suggested as a long-term method for reducing the susceptibility and vulnerability of balsam fir *(Abies balsamea* (L.) Mill.) to spruce budworm *(Choristoneura fumiferana* (Clem.)). Central to this issue is the impact of hardwood on balsam fir defoliation caused by spruce budworm and the impact of defoliation on balsam fir volume growth. Twenty-five mixed balsam fir-hardwood stands were selected in northern New Brunswick, with five stands in each 20% hardwood classes (0-20, 21-40% etc.). Defoliation each year from 1989 to 1993 was significantly ($p < 0.0001$) related to hardwood content, with r^2 ranging from 0.57 to 0.81 (as hardwood content increased, defoliation of balsam fir decreased). From 1989 to 1992, the years of moderate-severe defoliation, balsam fir stands with < 40% hardwoods sustained 58-71% defoliation average, compared to 12- 15% defoliation in stands with > 80% hardwood. A generalized model combining hardwood content and the estimated defoliation in pure softwood stands in a given year explained 77% of the variation in defoliation over stands and years [Su et al. 1996. Can J. For. Res. 26: 1620-1628].

The effects and mechanism of defoliation by spruce budworm on volume growth were also examined using one hundred dominant or codominant balsam fir trees that were harvested and analyzed for defoliation, tree dimensions, sapwood area, and volume increment. Average 1989-93 growth of a tree with mean defoliation in 26-50, 51-75, and 76-100% classes was 39,48, and 64% less in comparison with those with 0-25% defoliation. A curvilinear regression model based on cumulative defoliation explained 64% of the variation in specific volume increment among 100 trees. Since the reduction of volume growth of balsam fir was not linearly related to defoliation, the relationship between volume growth and sapwood area was checked to examine the mechanism involved in the response of balsam fir to defoliation. Regression analyses showed that the relationship between volume growth and sapwood area was altered by defoliation. With low to moderate defoliation, the effect was only on the intercepts of the regressions. With higher defoliation, both the intercepts and slopes of the regression lines were altered. This suggests that defoliation might affect the relationship between leaf area and sapwood area, or the sapwood area adjustment, or photosynthate allocation pattern.

This study indicated that mixed balsam fir-hardwood stand management, with hardwood content > 40%, could substantially reduce defoliation during spruce budworm outbreaks. Further research could be done to reveal the mechanism involved in the lower defoliation in mixed stands, to examine the effect of defoliation on the relationship between leaf area and sapwood area, and to learn whether the photosynthate allocation patterns changes under severe defoliation.

Sapwood deterioration of insect damaged balsam fir

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The purpose of this research was to identify the major wood inhabiting fungi, their decay capability, their interactions and the factors influencing sapwood deterioration rates after kill by spruce budworm. Trees that were seriously damaged or had been killed in the previous 5 years were sectioned at 1 m intervals and sampled radially from the inner bark to heartwood for wood inhabiting fungi. Decay capability of the major fungi was determined by wood chemistry tests and their associations by Chi square association analysis. *Amylostereum chailletii,* which causes red brown

stain and incipient decay, and *Hirschioporus abietinus,* which causes advanced white pitted sap rot, were the two major decayers isolated. *Hohenbuhelia pinacearum and Panellus mitis,* two moderate decayers, were also isolated. *Kirschteinielia thujina,* a dematiaceous imperfect was the most frequently isolated nondecay fungus. Association analyses and decay tests showed that decayers function independently of each other and competitively inhibit colonization of a stem region by another decayer. Sapwood deterioration rates can be predicted based upon knowing which decay fungus has become established. Secondary insects are the major factor influencing the establishment of *A. chailletii and H. abietinus.* Siricid woodwasps inoculate *A. chailletii* during oviposition into the sapwood of stressed and recently killed trees while activity of the balsam fir bark beetle, *Pityokteines sparsus,* facilitates the establishment of *H. abietinus.* Trees attacked by woodwasps and infected with *A. chailletii* deteriorate slower than those infected with *H. abietus.*

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